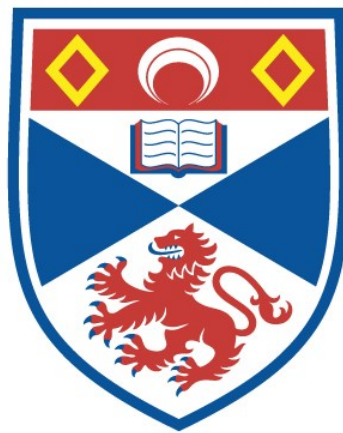


THE IMPACT OF MULTIPLE STRESSORS ON COASTAL
BIODIVERSITY AND ASSOCIATED ECOSYSTEM
SERVICES

Stephen Christopher Lewis Watson

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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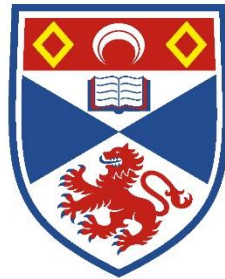
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**The Impact of Multiple Stressors on Coastal Biodiversity and
Associated Ecosystem Services.**

Stephen Christopher Lewis Watson



University of
St Andrews

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St. Andrews

April 2017

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Abstract

Marine and coastal ecosystems are subject to diverse and increasingly intensive anthropogenic activities, making understanding cumulative effects critically important. However, accurately accounting for the cumulative effects of human impacts can be difficult, with the possibility of multiple stressors interacting and having greater impacts than expected, compounding direct and indirect effects on individuals, populations, communities and ecosystems. Assessment of multiple stressors therefore requires extensive scientific research that directly tests how single or multiple ecological components are affected by stressors, both singly and when combined, and as a consequence, cumulative effects assessments are now increasingly included in environmental assessments. Currently, there is a need to assess these at larger spatial scales, with additional research also urgently needed on the responses of ecological components, processes and functions to single and cumulative stressors. As cumulative environmental impacts could be better addressed by regional stressor effects assessments that combine methods for predicting multiple pressures on ecosystem recovery alongside degradation, this study used several separate approaches that can be used in parallel to give support for local management measures. I tested four completely different methods – a range of multi-metric indices, a food web model (Ecopath), a predictive model (Ecosim) and a Bayesian Belief Network model. Each approach was tested and compared in two shallow water estuarine systems, in Scotland and England, initially concerning the impact of nutrient enrichment and subsequent recovery and was followed by an investigation of how the addition of multiple stressors (nutrient levels, temperature and river-flow rates) would impact the future state of each system. The response to stressors was highly context dependent, varying between and within geographic locations. Overall, each of the four different approaches complemented each other and gave strong support for the need to make big reductions in the pressures and to consider trade-offs between impacting pressures. The models and tools also indicate that in order to reach an improved overall environmental state of each ecosystem, a focus on nutrient reductions are likely to be the most effective of the controls on stressors explored and that cumulative effects of the management of nutrient inputs and increased water temperatures and river-flow are likely to exist.

Keywords

Climate change, marine systems, multiple stressors, biodiversity, ecosystem services, ecosystem health, resilience, nutrient stress, Ecopath, ecological indices, macro-invertebrates, demersal fish, waterbirds.

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Chapter 1: General introduction

Chapter Summary

The position of coastal ecosystems at the land-sea interface makes them very appealing environments to study, as they are subject to pressures from both terrestrial and marine sources and they are the most accessible of marine systems (Cramb, 2015). Estuarine systems in particular prove useful study systems in his regard, acting as a nexus between the environment and anthropogenic activity, they are categorised as having a large number of habitats which deliver invaluable goods and services (Barbier *et al.*, 2011) but at the same time are also subject to more human-induced pressures than other systems (McLusky & Elliott, 2004). This makes them excellent test-beds for studying the conflicts between the environment, ecology, conservation, and human use. Such study systems, however, require a broad understanding of the ecosystem of an estuary and how it functions as a whole. Thus, while recent single and multiple stressor studies have typically been conducted in laboratory or field settings, the observational and modelling approaches used in this thesis aim to investigate the impact of stressors at larger spatial scales (i.e. community and ecosystem levels). Sites were selected in Scotland and England to represent different geographic regions within the temperate zone. As future threats to estuaries are unlikely to occur in isolation, the rationale of this thesis, was to assess the impact of multiple climate stressors on various biodiversity proxies and the potential implications of human mediated changes on ecosystem structure, functioning (linked to the provisioning of ecosystem services and benefits) and resilience. By comparing two very different temperate estuarine systems, this study will serve as a foundation for future comparative studies between estuaries in northern hemisphere locations.

1.1 The impact of multiple stressors on coastal systems

In an era of advancing globalisation and environmental degradation, one of the greatest challenges for scientists, governments, stakeholders and practitioners around the world is to understand and predict how anthropogenic change will impact upon natural ecosystems and the social and economic services they provide (Schröter *et al.*, 2005; Pedrono *et al.*, 2016). Human impacts propagate across terrestrial and aquatic environments and throughout the atmosphere because of the inherent connection between these components and the biosphere (Hoegh-Guldberg & Bruno 2010; Doney 2012). A direct consequence of this connectivity is that human impacts can accumulate their effects in time or space, challenging the ability of organisms to live. This is particularly true for coastal marine ecosystems, which are the terminus of many terrestrial wastes and are simultaneously exposed to a number of stressors which may act at on local, regional and global scales (Drinkwater *et al.*, 2010) with

large scale disturbances potentially being an amalgamation of numerous local stressors (e.g. the impact of increased river-flow and salinity stress on marine organisms).

In ecological research, the term 'stressor' has frequently been used synonymously with "disturbance", "pollution", "pollutants" or "pressures" on the assumption that the effects of a stressor (or the equivalent descriptor) imply "stress" and must therefore be exclusively detrimental (Folt *et al.*, 1999). However, there is also contention that what is stressful (detrimental) to one species may be non-detrimental or even beneficial to another species (Piggott *et al.*, 2015). Therefore, for the duration of this thesis a stressor can be considered to be "*either an abiotic or biotic factor that results from human activity and exceeds its range of normal variation and affects individual physiology, population performance, community balance or ecosystem functioning, either positively or negatively*" (e.g., Barrett & Odum 1976; Auerbach 1981; Breitburg *et al.*, 1999; Cottingham., 1999; Vinebrooke *et al.*, 2004; Crain *et al.*, 2008; Townsend *et al.*, 2008). This makes the distinction between terms such as "pollution" or "pollutants" which requires a substance to cause a damaging biological or ecological response (Freedman., 1995).

Anthropogenic climate change for instance, is now considered to be an important suite of exogenic abiotic stressors (Elliot., 2011) which act to alter ecosystems over broad spatial and temporal scales (Arnell *et al.*, 2013). This is mainly due to increasing levels of CO₂ and other heat-trapping greenhouse gases (CH₄, NO₂, O₃ and chlorofluorocarbons) in the atmosphere (Stocker *et al.*, 2013; Karl *et al.*, 2015). The impacts of this human driven change include: global warming, sea level rise, eutrophication, increased stratification, changes in ocean chemistry, altered patterns in precipitation, circulation and fresh water inputs; with all of these impacts expected to be increasingly important in the future (Rajaratnam *et al.*, 2015).

The associated effects of CO₂ are not the only threats to marine systems with additional endogenic regional pressures (Elliot., 2011) such as increasing pollution; habitat destruction; over-exploitation of fish stocks; disease and invasive species, acting concomitantly with human induced climate change (Bulling *et al.*, 2010). Therefore, none of the aforementioned drivers act in isolation but instead have compound effects. While one factor on its own may not have serious consequences for an organism or community, the additive, synergistic or cumulative action of several factor stressors has the potential to lead to more significant damage than simply the sum of the individual threats (Crain *et al.*, 2008; Darling *et al.*, 2013). For example, marine and freshwater organisms under one form of stress (e.g. rising mean sea temperatures) may be less able to cope with the physiological demands of adapting to increasing frequencies of freshwater disturbance that might occur with changing

precipitation patterns and their resilience may be further weakened by exposure to industrial contaminants.

Predicting the ultimate effect a stressor or series of stresses will have is therefore difficult as anthropogenic and natural stressors do not produce uniform or consistent impacts at different levels of biological organisation, with both individuals and entire ecosystems responding nonlinearly to gradients of stressor severity (Vinebrooke *et al.*, 2008; Smith *et al.*, 2009). Depending upon the context within which stressors interact, they may have non-interactive or cumulative effects (Halpern *et al.*, 2009). Efforts to understand the cumulative ecological impacts of anthropogenic activities are often undertaken using an 'additive model' (e.g. Folt *et al.*, 1999; Piggott *et al.*, 2015). Under this framework, stressor effects can be categorised in three ways, either as additive (= to the individual effects); synergistic (> the sum of their individual effects) or antagonistic (< the sum of their individual effects). Despite considerable recent interest in mechanistic underpinnings of these different types of effects, there is still a mixed consensus on which effects are most prevalent in 'real' world marine systems (Darling & Côté *et al.*, 2008) This is largely due to the difficulty of establishing causality and the lack of factorial studies that have been conducted in this area at the community and ecosystem level (Van den Brink *et al.*, 2016).

Evidence of non-additive effects (i.e. synergistic or antagonistic) is common in nature (Crain *et al.*, 2008), particularly in coastal marine systems such as estuaries which are continuously exposed to a range of natural and anthropogenic stressors (Hewitt *et al.*, 2015; Ellis *et al.*, 2015). Hence, given the high likelihood of cumulative effects in these systems, scientists and policy makers are increasingly looking to implement strategies that consider the net effects of multiple human pressures (Breitburg & Riedel., 2005; Rosenberg & Macleod., 2005; European Union., 2008; Halpern *et al.*, 2008 a&b; National Ocean Council., 2013; Austin & White., 2016), especially those that generate unexpected non-additive impacts or 'ecological surprises', defined as unexpected findings about the natural environment (Lindenmayer *et al.*, 2010).

1.2 Implications of changing biodiversity on marine ecosystem functioning

Identifying key components of marine ecosystems from a biophysical perspective and describing the status of these ecosystems is a challenging, yet important, topic to address before we can fully understand the effects of environmental variability and anthropogenic drivers of change on coastal systems (Shackeroff *et al.*, 2009). Over the last few decades there has been considerable research into the understanding how escalating trends in human impacts are affecting structural aspects of ecosystems, their associated properties and how they function (Caliman *et al.*, 2007).

In the first instance, the structure of an ecosystem refers to its inherent physical and chemical properties alongside the identity and abundance of its biological constituents (or biodiversity). The term 'biodiversity' in particular is an important one, as it is a word used by many people to mean different things. Since being coined in 1988 (Wilson & Peters, 1988), it has become a common term used with public, scientific and political lexicons, all the while acting as a 'flagship' for promoting the cause of conservation efforts (Borja et al., 2016). In its broadest terms, it can be accounted for at a variety of organisational levels (e.g. genetic (between species), species (species richness) and ecological (community/ecosystem)) and is perhaps best encapsulated by the United Nations Environment Programme (UNEP) definition of biological diversity (United Nations., 1992);

“Biological diversity means the variability among living organisms from all sources including, inter-alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems.”

Biodiversity is also a key component of ecological structure. A keystone species for example, is a species that has a disproportionately large effect on its environment relative to its abundance (Bond., 1994; Paine., 1995). Such species are described as playing a critical role in maintaining the structure of an ecological community, affecting many other organisms in an ecosystem and helping to determine the types and numbers of various other species in the community (Strong *et al.*, 2015).

Although species abundance and richness is the most conspicuous aspect of biodiversity, recent efforts have focused more on the identity of species present and their functional roles within ecological systems (Bremner *et al.*, 2006). This interest in the relationship between biodiversity and ecosystem functioning (BEF) first rose to prominence in 1992, (Walker., 1992) and since has passed through many phases, in which the field has expanded considerably in volume, scope, rigor and complexity (see Naeem., 2009; Gamfeldt *et al.*, 2015 for a full review). In most approaches to the BEF debate, a hierarchy of ecosystem activity is recognised that eventually leads to the provisioning of a number of ecosystem properties (e.g. resilience), services and benefits (see forthcoming section 1.3). Recent meta-analysis of work from a wide range of ecosystems now suggest that the influence of biodiversity on ecosystem functioning is generally positive and saturating (Cardinale *et al.*, 2011; Hooper *et al.*, 2012; Cusson *et al.*, 2015), but varies considerably based on context and the identity of the species present. This variation is of particular interest for decision makers with responsibility for specific systems, who require tangible evidence for how the effects of future biodiversity loss in a given context, is likely to impact specific ecosystems or localities that have not yet been studied in their own right.

While the link between BEF is now widely accepted, users still have strong conflicting opinions about the use of terminology within such frameworks. For instance, ecosystem processes and ecosystem function are often used synonymously and can be defined in many different ways (Paterson *et al.*, 2012). Broadly, ecosystem processes can be described as the processing of energy and materials in ecosystems by physical, chemical or biological action. Many of these processes occur at very small scales but cumulatively combine to produce a transfer of energy or material often recognised as ecosystem functioning (Hooper *et al.*, 2005). Ecosystem functions, therefore, are considered as a subset of ecological processes (e.g. the processes drive the functions) and incorporate pools and fluxes (rates) of materials and energy (e.g. carbon and organic matter pools, nutrient cycling, primary productivity), which culminate in the flow of ecosystem services and benefits (de Groot., 1992).

While it is important to make clear distinctions about how changes in biodiversity are likely to be impacting marine ecosystems, there is also an increasing emphasis in how these changes are relevant for society. Making the leap towards linking BEF relationships with ecosystem services and human well-being is challenging for several reasons outlined by Raffaelli (2006):

- I. Multiple processes may give rise to one service.
- II. There may be weak relationships between biodiversity and a service if there are a number of direct and indirect processes involved.
- III. Processes may be differently affected depending on the biodiversity loss scenario.

Given these issues, an ecosystem service-led approach, that first identifies the service of interest (e.g. carbon sequestration and storage) and then explores the processes required for its delivery, followed by focusing on how a change in biodiversity has effected these processes, is now considered to be recommendable (Kremer., 2005). In this way, changes in BEF can be assessed with much less ambiguously and greater persuasively to policy makers. Moreover, as the observable deterioration in many marine ecosystems increases and the challenges presented in the form of environmental variability, climate change and other human induced change, efforts to understand ecosystem services and their link to human health and well-being are increasing.

1.3 Ecosystem services and benefits from marine systems

For over a millennia, humans have recognised that marine ecosystems provide a wide array of benefits vital for fundamental human health and wellbeing (Mooney & Ehrlich., 1997; Gómez-Baggethun *et al.*, 2010). However, it was not until relatively recently in the late 1960's and early 1970's, that the terms 'environmental services' and subsequently 'ecosystem services' were explicitly recognised as positive benefits society, gained from the functional properties of ecosystems (King., 1966; Helliwell., 1969; Ehrlich and Ehrlich., 1970; Dee *et al.*, 1973; Ehrlich *et al.*, 1977; Bormann & Likens., 1979). Interest in

ecosystem services (hereafter ES) arose from the need to better understand the link between ecosystems and human welfare. It has since led to extensive research that has aimed to identify how ecosystems provide services (Daily, 1997), how the loss of biodiversity will affect these services (Worm *et al.*, 2006) and whether technological developments can substitute for them (Farber *et al.*, 2002). It has acted as a catalyst for ecological research and also for research into the value of ES to humans and how these values can be used in weighting the impacts of human activities on ecosystems.

Despite this extensive theoretical development, and the recent exponential increase in publications pertaining to 'ecosystem services' (Fisher *et al.*, 2009), there is still a large amount of confusion surrounding the terminology, definitions and typologies (classifications) used in ES assessment frameworks. For instance, three papers have been published recently redefining and re-describing marine ES (Liquete *et al.*, 2013; Böhnke-Henrichs *et al.*, 2013; Hattam *et al.*, 2015).

For the purposes of defining ES for this thesis, ES are considered to be the specific results of ecosystem processes and are the components of nature that are used, directly or indirectly, to benefit human well-being and create economic wealth (e.g. Fisher *et al.*, 2009). These services are ecological in nature and may be made up of tangible goods (e.g. food and raw materials) or intangible services (e.g. regulation of our climate and remediation of waste), that would continue to exist irrespective of the presence of humans. It is important to make the distinction that these services are not provided *for* humans, rather they have the potential to derive value from these services as a by-product of naturally occurring ecosystem processes and hence are exploitable, but are not exploited at this stage. The ecosystems that provide these services are also sometimes referred to as "natural capital," using the general definition of capital as a stock that yields a flow of services overtime (Costanza & Daly., 1992).

In terms of classification, ES are commonly divided into three major categories (e.g. Beaumont *et al.*, 2007, Fisher *et al.*, 2009; Saunders *et al.*, 2010; Atkins *et al.*, 2011; Mace *et al.*, 2011): provisioning, regulating and cultural. A fourth category of supporting services was initially suggested by the Millennium Ecosystem Assessment (MA., 2003; 2005), but has since been re-defined in many classifications as ecosystem processes (e.g. The Common International Classification of Ecosystem Services (CICES), European Environment Agency (EEA) 2013). Similarly, a fourth category of habitat services was proposed by the Economics of Ecosystems and Biodiversity classification (TEEB, de Groot *et al.*, 2010), although these services are classified elsewhere as regulating services or ecosystem processes (CICES., 2013). Another confliction is the classification of cultural uses of the environment which have are often been considered alongside regulating and provisioning services. As all cultural uses of the environment must by definition require some level of human input (e.g. be prepared to

spend money to maintain and/or exploit), there is discontent wither these services should instead be considered as ecosystem benefits (Chan *et al.*, 2012).

Clearer descriptions of all these categories will help understanding of the concept of ES. In the interim, a brief description of each ecosystem service categorys is given below:

- **Provisioning services** are considered to be the products obtained from ecosystems including food, fibres, fuels, genetic resources and medicines.
- **Regulating services** refer to the contribution of ecosystems to the regulation of Ecosystem Processes, such as the regulation of climate, waste, water and disease.
- **Cultural services (benefits)** generate the non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation opportunities and aesthetic experience.

For the purpose of economic valuation, it is also important to distinguish between ES and the benefits they generate (Boyd and Baanzhaf, 2007), as it is the ecosystem benefits (thereafter EB) that can be measured in terms of economic value. EB (like services) are a human construct and result when an ES is exploited, directly or indirectly by humans. Intervention may include the investment of time, finance, or technology. EB may also be defined as “goods” but as these benefits are both tangible (fish) and non-tangible (cultural), the term benefits is considered to be more suitable. A general “rule of thumb” is, if its immediate value to human wellbeing is not apparent, then it is not considered an EB. In previous classifications, benefits have been confused with services and both have been valued, resulting in “double-counting” (Fisher *et al.*, 2009). Thus, there is an increasing emphasis on measuring ES outcomes from an ecological perspective, while accounting for EB from economic, social and health perspectives.

Marine ES and the EB they provide also occur over a range of scales both spatial and temporal. As such, some beneficiaries may accrue benefits very locally to the ecosystem services that provided them (e.g. recreational benefits). In other instances, marine EB may be realised inland, physically removed from the ecosystem processes and ES which initially support and provide them (e.g. clean bathing water). This may be a significant contributory factor in the previous mismanagement of marine systems as the beneficiaries are separated from the origin of the benefit (Turner & Schaafsma., 2015).

1.3.1 Ecosystem services: A conceptual framework

In this thesis a conceptual framework is used (Figure 1.1) that clearly separates marine ES from the EB that accrue from them. The framework also separates the ES (and EB) from the underpinning abiotic conditions, biodiversity and ecosystem processes/functions that provide them. Describing the interlinkages in this way allows marine ecosystems, biodiversity and the processes and functions resulting from them, to be described in ecological terms whilst the EB and their values can be described in the context of human wellbeing.

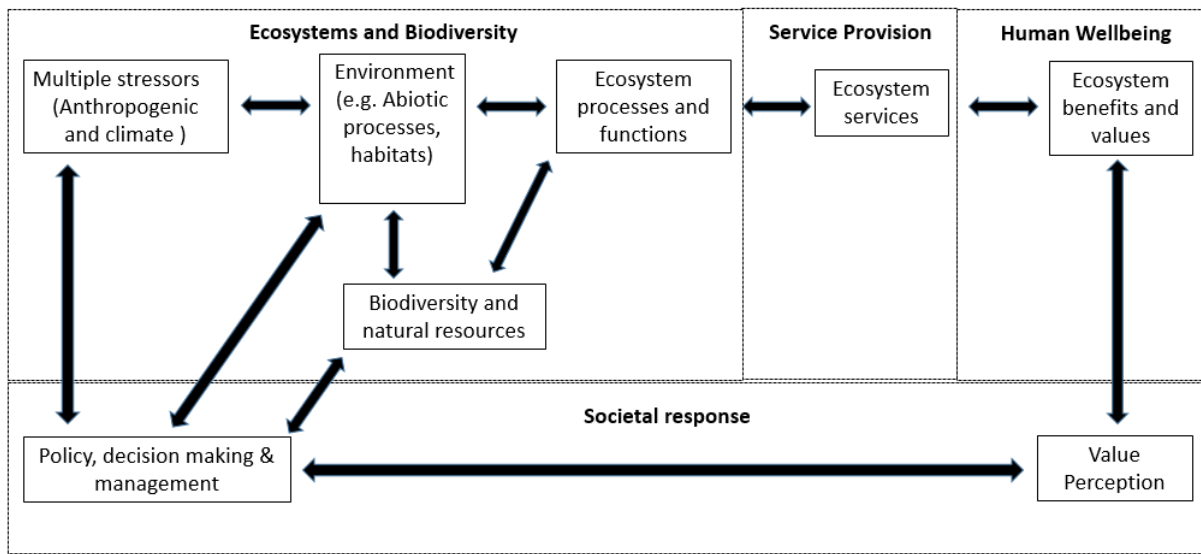


Figure 1.1 Schematic representation of the Ecosystem Service conceptual framework used in this study. The diagram shows equal strength of all interactions, but in reality the interaction strength between elements will vary considerably under different circumstances. Any change in one element can affect the others either directly or indirectly.

Linking these concepts, ES can be described from both an ecological and human wellbeing perspective but are always measured in ecological terms. Unlike other conceptual frameworks, I highlight that all functional groupings (i.e. impacts, processes, services and benefits etc.) are joined by double-headed arrows, which highlights their interdependency. Detailing the linkages in this way clarifies the dependence of all the benefits on all aspects of ecosystem services and processes and thus the breadth of potential impacts if these services and processes are altered. For example, anthropogenic climate change pressures can act either separately or synergistically on the marine environment potentially altering the biodiversity-ecosystem processes/functioning and ecosystem service-ecosystem benefit continuum.

At the opposite end of the continuum, societal response to how we chose to value and manage the environment and the EB derived from it, is likely to have a significant feedback effect on the capacity of ecosystems to provide ES and EB. For example, the marine environment provides for the service of waste remediation (Watson *et al.*, 2016) which has direct implications for the waste management of

water companies and other businesses who may derive benefits from such a regulation service at the local level. At the same time, that same use may have implications for the user community with interests in recreation and tourism at the local and regional level and in the conservation of marine biodiversity to combat climate change at the local through to the global level, depending on the particular site characteristics. Therefore as EB's are exploited and extracted, there are likely to be feedbacks on ecosystem processes and biodiversity.

Another nuance in defining ES assessment frameworks is incorporation of abiotic components of ecosystems, which up until recently have been largely excluded or ignored from such assessments (Haines-Young & Potschin., 2009). However it is now recognised that to successfully manage marine ecosystems, it is essential to include all uses and benefits. As such, it is recommended that abiotic processes and resources (e.g. wave and tidal flows can produce electricity and remediate waste products or geological structures that can act as tourist attractions) are included when applying ES classifications in a policy or decision making scenario (e.g. CICES, EEA 2013). These abiotic processes and resources are therefore included in my framework and should be considered alongside biotic ecosystem process that contribute to ESs and subsequently EBs.

1.3.2 Ecosystem services: Typology

Combined with the aforementioned framework, the ES typology (Table 1.1), that will be henceforth be used in this volume, was developed in the European VECTORS project by Hattam *et al.* (2015) and with respect to the ES of 'waste remediation' in the UK Ocean Acidification (UKOA) research programme by Watson *et al.* (2016). The typology builds upon previous frameworks developed by the MA (2003; 2005), Beaumont *et al.* (2008), Fisher *et al.* (2009), TEEB. (2010), Atkins *et al.* (2011), Mace *et al.* (2011) and Böhnke-Henrichs *et al.* (2013)

Table 1.2 Marine ecosystem service typology. Developed by the EU FP7 project VERCTORS by Hattam *et al.*, (2015)

Ecosystem service	Description	Examples
PROVISIONING SERVICES		
1 Food provisioning: a) Wild capture sea food b) Farmed sea food	All available marine flora and fauna extracted from unmanaged marine environments for consumption by humans Food from aquaculture for consumption by humans	Fish, shellfish, seaweed
2 Biotic raw materials (non-food): a) Genetic resources b) Medicinal resources c) Ornamental resources d) Other biotic raw materials	The provision/extraction of genetic material from marine flora and fauna for use in non-medicinal contexts Any material that is extracted from or used in the marine environment for its ability to provide medicinal benefits Any material that is extracted for use in decoration, fashion, handicrafts, souvenirs etc. Extraction of all other renewable biotic resources	Genetic enhancement of biofuel-producing microalgae Marine-derived pharmaceuticals Shells, aquarium fish, pearls, coral Extraction of marine products for cosmetics, the chemical industry, biofuels, fish for fish feed
REGULATING SERVICES		
3 Air purification	Influence of a marine ecosystem on concentration of pollutants from the atmosphere	The removal from the air of pollutants such as dust and particular matter, sulphur dioxide, carbon dioxide etc.
4 Climate regulation	The contribution of a marine ecosystem to the maintenance of a favourable climate through impacts on the hydrological cycle, temperature regulation, and the contribution to climate-influencing substances in the atmosphere	the production, consumption and use by marine organisms of gases such as carbon dioxide, water vapour , nitrous oxides, methane and dimethyl sulphide
5 Disturbance prevention or moderation	The contribution of marine ecosystem structures and functions to the dampening of the intensity of environmental disturbances such as storm floods, tsunamis, and hurricanes	The reduction in the intensity of and/or damage caused by high energy waves by salt marshes, sea grass beds, reefs and mangroves; absorption of excess flood water by salt marshes
6 Regulation of water flows	The contribution of marine ecosystems to the maintenance of localized coastal current structures	The effect of reefs and macroalgae on localised current intensity
7 Remediation of waste	The removal of contaminant and organic nutrient inputs to marine environments from humans	The breakdown of chemical contaminants and organic nutrients by marine microorganisms; filtering of coastal water by shellfish; burial of waste materials by burrowing seabed animals

8 Coastal erosion prevention	The contribution of marine ecosystems to coastal erosion prevention	The maintenance of saltmarshes by coastal vegetation and mudflat ecosystems; reduction in scouring potential that results from nearshore macroalgae forests and seagrass beds
9 Biological control	The contribution of marine ecosystems to the maintenance of population dynamics, resilience through food web dynamics, disease and pest control	The support of reef ecosystems by herbivorous fish that keep algae populations in check; the role that top predators play in limiting the population sizes of opportunistic species like jellyfish; the biological control of bacterial and viral diseases that impact humans directly or via the seafood they eat
CULTURAL SERVICES		
10 Leisure, recreation and tourism	The provision of opportunities for tourism, recreation and leisure that depend on a particular state of marine ecosystems	Bird/whale watching, beachcombing, sailing, recreational fishing, SCUBA diving etc.
11 Aesthetic experience	The contribution that a marine ecosystem makes to the existence of a surface or subsurface landscape that generates a noticeable emotional response within the individual observer. This includes informal spiritual individual experiences but excludes that covered by service	The particular visual facets of a 'seascape' (like 'blue' water), a 'reef-scape' (with abundant colourful marine life), a 'beach-scape' (with open sand), but also geological features, etc. that emotionally resonate with individual observers
12 Inspiration for culture, art and design	The contribution that a marine ecosystem makes to the existence of environmental features that inspire elements of culture, art, and/or design.	The use of marine landscape or species in pictures, films, painting, architecture and design (like waves or jewellery)
13 Cultural heritage	The contribution of marine ecosystems to the maintenance of cultural heritage, and providing a 'sense of place'	Appreciation of coastal/marine ecosystems as a source of cultural identity and heritage (e.g. UNESCO World Heritage sites).
14 Cultural diversity	The contribution of marine ecosystems to social and cultural values and adaptations that pertain to living at coasts and exploiting marine resources	Social and cultural structures and relations of fishing/coastal/island communities
15 Spiritual experience	The contribution that a marine ecosystem makes to formal and informal collective religious experiences.	e.g. Several Greek and Roman gods were connected to the sea; fish as a Christian symbol; whales and salmon play an important part in indigenous communities.
16 Information for cognitive development	The contribution that a marine ecosystem makes to education, research and individual and collective cognitive development	Scientific research (natural and social science) and applied scientific research (e.g. use of marine genetic materials/biological information, blue biotechnology and bionics/biomimetics); local ecological knowledge of marine communities (e.g. for exploiting resources); environmental education of children and adults through field excursions.

As is evident from the typology, marine ecosystems proved a constellation of different ES. Many of the services listed may be derived by similar habitat types (e.g. seagrass, coral reefs etc.) regardless of their environmental setting (e.g. coastal, pelagic or deep sea), due to the similar functional characteristics of the organisms that live in these environments (Palumbi, *et al.*, 2008). However, the amount of the service and hence the benefits derived can vary according to the habitat/location. Delivery of many of these services is also strongly interlinked and synergistic, with the abiotic or biological activity that occurs in a single location often responsible for multiple ES (Austen *et al.*, 2011). This means that impacts on particular elements of biodiversity (and hence ecosystem processes) can affect several ES simultaneously. These effects can also manifest themselves over different spatial scales, with any impact on biodiversity and functioning in one area having knock-on effects to adjacent habitats or ecosystems. Similarly these effects can arise at different points in time with some global scale processes responding to the impact of changes slowly (e.g. carbon sequestration), while more local processes may respond quickly (nutrient cycling). Therefore, to better understand and manage the complex, interlinked nature of ES, it is particularly important to improve our current knowledge of the extent and context to which key impacts are occurring at different spatial and temporal scales.

1.4 Concepts of ecosystem health, resilience and sustainability

Some ecological states are more desirable than others as they enable the delivery of ESs that people value. Given the dynamic nature of coastal systems and their increasing degraded status as a result of anthropogenic stresses, it is imperative to implement management strategies that preserve the integrity and resilience of desirable states. In this regard, the metaphor of ecosystem “health” has aided ecologists in conceptualizing ecosystem functioning as well as explaining the condition of systems to the general public and suggesting regulatory goals to governments (Costanza, 2012). While advocates of the health allegory argue for its simplicity as a communication tool, the approach also has been strongly scrutinised when personal or sectoral values are introduced (Lancaster *et al.*, 2000; Lacky, 2001) to what are claimed to be objective assessments. Despite such arguments, the concept of ecosystem health has now been applied to the level of landscapes and ecosystems (Rapport *et al.*, 1981; 1998a,b; 1989) and is proving to be a normative and useful concept in environmental management (Borja *et al.*, 2010; 2012), with many recent EU directives equating this condition with “good ecological” or “environmental status”, e.g. the European Marine Strategy Framework Directive (MSFD), 2008/56/EU and Water Framework Directive (WFD), 2000/60/EC.

Embodied within the concept of ecosystem health is the ideal that ‘the use of the environment and its resources must also be sustainable, which implies the ability of the system to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience) (Mageau *et al.*,

1995; Costanza, 2002). This definition is applicable to all complex systems from cells to ecosystems to economic systems and allows for the fact that systems may be growing and developing as a result of both natural and cultural influences (Costanza & Mageau., 1999). With regard to marine ecological functioning, marine monitoring should explicitly or implicitly encompass health at all levels of biological organization (Elliott, 2011). In addition, as emphasised throughout all major pieces of marine governance, there is a duty to assess and ensure the health of the whole ecosystem (Borja *et al.*, 2016).

Hereof, the 'resilience' of an ecosystem has become one of the most sought after criteria for assessing ecosystem health (Rombouts *et al.*, 2013; Nimmo *et al.*, 2015). An ecosystem is generally considered "resilient" if it retains the ability to return to its original state after a stressor and exhibits low temporal variability, whilst concurrently maintaining its structure, functioning and identity (Holling., 1973; Carpenter *et al.*, 2001; Folke *et al.*, 2004) across an interacting set of hierarchically structured scales (see "panarchy" (Gunderson & Holling 2002)). However, resilience is a multifaceted concept with numerous definitions in ecological (Brand., 2009) and social sciences (Biggs *et al.*, 2012) and has been the subject of considerable debate, both with regards to the semantics of its terminology (Pimm.,1984; Odum., 1989; Grimm & Wissel., 1997) and more recently in its theoretical application as a concept (Hughes *et al.*, 2005; Folke., 2006; Ives & Carpenter., 2007; Oliver *et al.*, 2015). Within ecology, the study of resilience has been largely focused on the stability of ecosystem structure and function and the rate (elasticity) and/or duration (return time) with which they recover (recovery or 'engineering resilience' e.g. Holling *et al.*, 1996) following the impact of stressors. More recently work on this area has broadened in concept, referred to as 'ecological resilience', accepting that ecosystems function in multiple stable states and, although thresholds (tipping points) may be crossed pushing systems towards a new configurations (regime shifts), systems have a degree of 'adaptive capacity' to resist changes, potentially through internal reorganisation (Suding & Hobbs., 2009). Resilience in this context is often referred to as 'resistance', defined by Odum (1989) as 'the ability of an ecosystem to withstand disturbance without undergoing a phase shift or losing structure or function'. Recent definitions of resilience generally incorporate both the concepts of resistance and recovery as complementary aspects of resilience (Hodgson *et al.*, 2015). All of these concepts can be considered key ecosystem properties, and are important for maintaining desirable ecosystem states (Gunderson *et al.*, 2010; Walker & Salt, 2012).

Therefore, If notions of ecosystem health and its constituents (e.g. sustainability and resilience) are to be used in implementing ecological science and policy, then coherent, clear, quantifiable definitions should be used (Ulanowicz., 1997). Based on the discussion above I henceforth use the definition of ecosystem health from Tett *et al.*, (2013) as: "*the condition of a system that is self-maintaining, vigorous, resilient to externally imposed pressures, and able to sustain services to humans. It contains*

healthy organisms and populations, and adequate functional diversity and functional response diversity. All expected trophic levels are present and well interconnected, and there is good spatial connectivity amongst subsystems". As stipulated by the authors, "any assessment of ecosystem health in relation to this definition must be made on appropriate spatial and temporal scales, and must take into account the local ecohydrodynamic conditions and the degree of openness of the system's boundaries".

1.5 Developing appropriate indicators for ecosystem service assessments under changing environmental conditions.

To set reasonable management objectives for ecosystems to continue to provide ESs and persist sustainably into the future, key ecosystem properties (e.g. biodiversity, structure, functioning and resilience) need to be assessed. In practice this can be done at a variety of spatial scales (Elliott., 2011), with assessments usually dependent on measuring ecological, social, economic or institutional characteristics that reflect the provisioning of ES; most often through the use of indicators (Holt *et al.*, 2012). In the context of ESs, indicators can be defined as 'proxies for complex phenomena and can be used to reflect the provision of a service and how it is changing over time' (Hattam *et al.*, 2015). Essentially indicators need to encapsulate the values of the EBs derived from ESs (e.g. economic valuation) , information about the functional aspects that provided them (e.g. linkages between BEF and ES provisioning) and how resilient socio-ecological systems are to change (e.g. resilience measure may be related to biodiversity). In doing so, indicators can be useful for supporting management activities (Niemeijer & de Groot., 2008) as well as contributing to studies aiming to model and value changes in ES provision (Queirós *et al.*, 2014).

In brief, while there are a number of classification systems for indicators involved in measuring ecosystem health and by extension the provisioning of ESs (e.g. Jackson *et al.*, 1990; Cairns *et al.*, 1993; Jørgensen *et al.*, 2011), practical guidelines for selecting indicators relevant to ecosystem condition in the marine environment are still lacking (van Oudenhoven *et al.*, 2012; Hattam *et al.*, 2015). For the discourse of this thesis, four general methods for employing a holistic approach to ESs and health assessment methods in marine and coastal environments are discussed:

I. Multi-metric indices

One approach to assessing how a system responds to stressors is by considering the aggregate properties of species and processes within a defined area (Duffy, 2008). In recent times, the structural and functional aspects (or traits) of species with assemblages have become increasingly examined as potential indicators (Crowe & Russell 2009; Petchey *et al.*, 2009), which can be used to relate ecosystem functions to ecosystem structure and overall ecosystem health (e.g. the European Marine

Strategy Framework Directive MSFD, 2008/56/EU, Water Framework Directive, 2000/60/EC, and Habitats Directive, 1992/43/EEC). However given the multifaceted nature of BEF and stability and their different implications of change for different ES, a suite of indicators is needed. They should correspond to the aspects of biodiversity involved, the ES of interest and may even need to be tailored to particular stakeholder groups (Müller & Burkhard., 2012). Ideally, they should be spatially explicit but also relevant at different scales (Feld *et al.*, 2009).

II. Thermodynamic and network analysis.

An alternative method to considering the organisms within ecosystems as an aggregate property, is to consider the emergent properties of the whole ecological system rather than of any of its components. Exergy, a thermodynamic concept, has been applied to ecology since the 1970s and is defined as the amount of work a system can perform when it is brought to thermodynamic equilibrium with its environment (Jørgensen & Mejer 1977, 1979). Congruently, network analysis can extract comprehensive information on the flow and cycling of matter from mass-balanced flowcharts, including trophic structure and transfer efficiencies, and the organisation of the food web (Field *et al.*, 1989, Gaedke 1995). Taken together, these methodologies have a long legacy in assessing ecosystem health and in holistically analysing complex interactions within ecosystems (Odum, 1953; 1969; 1996; Ulanowicz, 1986; 1997; 2012). Practical application of these concepts in marine ESs assessments however are lacking, with a few exceptions (e.g. Raffaelli, 2011).

III. Predictive model approach

Once ecosystem indicators are selected, modelling alternate futures and the likely trade-offs between management scenarios is an increasingly important stage for understanding any impacts on ES provisioning or changes to the resilience of the system (Levin *et al.*, 2009). The goal of these risk analyses is to qualitatively or quantitatively determine the probability that an ecosystem indicator will reach or remain in an undesirable state.

IV. Decision support tools

While the use of cause–effect modelling is extremely useful in establishing possible stressor effects, impacts and interactions, i.e. synergistic, antagonistic or additive (Jackson *et al.*, 2016), one difficulty with the use of ecological models might be translating these results to stakeholders in an effective manner, to accurately communicate both the power and the limitations of the tools (Fulton, 2010). As such, transforming conceptual cause–effect models into a quantitative platform using approaches that innately incorporate the dual probabilistic and deterministic nature of ecological structures, using graphical descriptions of risk and example narratives are becoming increasingly used in adaptive management practices and ecological risk assessments (Ascough *et al.*, 2008; Uusitalo *et al.*, 2015) .

1.6 Aims of thesis

In estuarine ecosystems major threats to biodiversity are numerous, with multiple anthropogenic stressors being well documented as a significant threat (Crain *et al.*, 2008; Dolbeth *et al.*, 2011; Ellis *et al.*, 2015). Thus, the aim of this project is to assess the impact of multiple climate stressors on biodiversity and estuarine ES's delivery, and in turn how these impacts affect the provision of ecosystem benefits and human well-being. The overarching approach will be to define and quantify the following relationships:

Climate stressors → Ecosystem Processes → Ecosystem Services → Ecosystem Benefits

As it is only by understanding these intermediary links that it is possible to project how changes in multiple climate stressors will impact the provision of ecosystem benefits, and therefore human wellbeing. Understanding these linkages also improves our capacity to manage the environment to minimise the negative impacts of climate stressors. It is recognised that the system is not linear, and there will feedback loops between the components, but for simplicity it is considered in this form. The focus of this research was on the provision of two regulatory ESs: carbon sequestration/storage and waste remediation although other ESs are considered.

While there are many types of estuarine ecosystems (Elliott & McLusky, 2002; McLusky & Elliott, 2007), the purpose of this thesis is to focus on benthic intertidal sedimentary habitats. Due to the incredibly varied conditions present within estuaries, these habitats they are inhabited by a wide range of organisms (e.g. macrophytes, invertebrates, fish, birds), often with high inherent ecological tolerances of environmental variability. However, despite this high resilience to variability, euryoecious estuarine organisms exhibit relatively low species diversity when compared to all the freshwater and marine species adjacent to the estuary (Elliott & Whitfield., 2011). Thus the loss or reduction of only a few species from the system can have a major impact on entire food chains (e.g. removal of keystone or foundation species) often with serious implications for overall system health, resilience and functioning.

The effect of single and multiple stressors on macrofaunal assemblages (and their associated food webs) were examined across two UK biogeographic provinces, with the objective of this work to test and visualise outcomes of various modelling tools and indicators that could be used for advising planning and management of multiple actions and pressures on the marine environment. Overall this study used four different approaches to estimate and visualise how the status of two estuarine systems (Tamar and Eden estuaries) can change after additions or reductions of anthropogenic stressors. Nutrient loading in the form of nitrogen and phosphorous were identified as a prominent

pressure for both estuary systems and was studied using two different assessment approaches, namely multi-metric indices and food web modelling. These approaches were subsequently built upon using deterministic and stochastic modelling techniques to investigate the more topical question of how the impact of multiple stressors such as temperature and increases in river-flow may interact with nutrient loading under alternative management scenarios. In doing so it is hoped useful predictions can be made of future ecosystem condition based on observations of present state and pressures. A more detailed description of the objectives of each chapter of this study is presented as follows:

Chapter 2: Background to the Tamar and Eden Estuaries & General Methods (Data collection)

In the first step, ecosystem specific data were identified by a structured systematic review, intensive data-mining and field work. Scoping involved identification of critical ecosystem management drivers and specific stressors on the ecosystems. Information was then placed into a broad systems context and compiled to create a meta-database of physiochemical and ecological information for each system, which would form the basis of analysis in Chapters 3-6.

Chapter 3: Review and evaluation of estuarine biotic indices to assess benthic structure and functioning under the influence of differing nutrient regimes in two UK estuaries. (Multi-metric approach)

In chapter 3 the performance of several benthic biodiversity indices were analysed under the periods of increasing and decreasing nutrient conditions. Structural indices such as abundance, biomass, taxonomic diversity, Shannon–Wiener, Margalef, Pielous evenness, Simpson’s index and various ecological quality status metrics (M-AMBI, IQI) were used to represent the ecological structure of the study sites. Recognising that every species has its own function in an ecosystem and the loss of one species will not necessarily change the ecosystem function, the measurement of ecosystem function in this chapter was based on a more novel approach using functional traits analysis. Two techniques were employed: Biological Traits Analysis (BTA) and community Bioturbation Potential (Bpc), to investigate functional relationships between two regulatory ESs: carbon sequestration/ storage, and waste remediation.

Chapter 4: A mass-balance approach to biodiversity–ecosystem service relationships in two estuarine ecosystems under the influence of nutrient reductions. (Thermodynamic analysis)

Following chapter 3, the functional role of macro-benthic invertebrates and their associated food webs were used to explore the relationship between food web structure and ecosystem functioning at higher (and lower) trophic levels. Indicators for estuarine stability, functioning, resilience and ESs provisioning were assessed using a mass-balanced modelling approach with the Ecopath (EwE) software package.

Chapter 5: Modelling the effects of multiple stressors on estuarine benthic food webs (Predictive model approach)

To understand how community and ecosystem level indicators might respond in the future under the effects of multiple stressors, a time dynamic simulation module in the form of Ecosim; was then used to quantify how indicators of ecosystem structure, functioning and resilience might respond to future stress. Stressors of varying intensity were forced on different ecosystem components and the shift in variables from their pre-disturbance state were compared.

Chapter 6: Holistic modelling approaches for defining sustainable and resilient boundaries in marine systems under the impacts of multiple climate stressors. (Decision support tools)

The penultimate chapter in this thesis uses the deterministic ecosystem modelling output developed in Chapters 4 & 5 to feed into a stochastic decision-support tool (Bayesian Belief Network) that can be used to evaluate the potential of different management strategies to influence the status of natural and human system indicators. Trade-offs have to be made and this approach illuminates what the trade-offs are as well as how to operate along those trade-offs. The link between ecosystem resilience, sustainability and the provisioning of ESs and human wellbeing is also investigated and discussed.

Chapter 7: General Discussion.

Finally, a summary of the empirical findings from chapters 3-6 is given. Following this, the implications of each chapter are discussed within the broader contexts of their relevance to multiple stressor and biodiversity--ES research, with considerations for how these findings might aid local and wider management efforts and promote future research.

Chapter 2: Background to the Tamar and Eden estuaries & general methods

Chapter Summary

Study sites were selected in Scotland and England to represent different geographic regions within the temperate zone. These areas allow a comparative study of the nature and resilience of estuarine benthic systems. In England the Tamar estuary, near the city of Plymouth in Devon, was selected. In Scotland the Eden estuary, near the town of Guardbridge and St Andrews, Fife, was selected (Figure 2.1).



Figure 2.1: Map of the UK, showing the location of the two case study areas: The Tamar and Eden estuaries.

Sites were also chosen for their physically different attributes (i.e. scale, geomorphology) and were considered based on known disturbance regimes within the systems, ease of access (within the time frame of the thesis) and availability of data. The many different habitats within the Tamar estuary for instance, have been studied intensively for more than a century by researchers of the Marine Biological Association (MBA), University of Plymouth (UoP) and Plymouth Marine Laboratories (PML),

who have conducted numerous hydrographic, chemical and biological surveys in the Western English Channel, including Plymouth Sound and Tamar estuary (see Southward & Roberts, 1987 for historical perspective). As a result, the Tamar estuary and its surrounding waters is one of the best documented estuarine complexes in the UK and is ideally suited to conducting seascape-scale or systems-based research. In comparison with the Tamar, the Eden estuary is one of the smallest estuaries in the UK. Despite this, the small size of the estuary (11 km-long) means that its physical conditions and natural characteristics are less challenging to investigate than for larger systems. Historically the intertidal mud and sand flats of the estuary have been sampled intensively by researchers from the University of St. Andrews, with many studies undertaken from of the Gatty Marine Laboratory (Bennett & McLeod, 1998) providing a robust baseline from which to draw comparisons. The limited application of management interventions and good ecological status of the system, also make it easier to disentangle the complex relationships associated with the investigation of multiple stressor interactions, than in the case of the heavily utilised and impacted Tamar estuary.

The purpose of this chapter was to review existing sources of data relating to the physicochemical characteristics, biological status, hydrodynamics and management initiatives in the Tamar and Eden systems that could be used for analysis in Chapters 3, 4, 5 and 6. The chapter begins by describing the background details of the study sites and then details the literature review and field study methods used in collection of data from the Tamar and Eden estuaries.

2.1 Tamar case study area

The Tamar estuary is a medium sized (31 km-long) estuary situated on the border between Cornwall and Devon (Figure 2.1) on the south-west coast of England (50°21' N, 004°10' W). The estuary itself comprises a complex of marine inlets (rias) stretching from Gunnislake weir (upper tidal limit) to Plymouth Sound (lower tidal limit) (Money *et al.*, 2011). Together, the Tamar Estuaries Complex (encompassing the River Lynher and St John's Lake in addition to the Tamar–Tavy, and hereafter referred to as the Tamar estuary) and Plymouth Sound, are designated as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (92/43/EEC) and a Special Protected Area (SPA) under the European Commission Directive on the Conservation of Wild Birds (79/409/EEC); supporting a large number of nationally important wildfowl and wader species such as the avocet (*Recurvirostra avosetta*) and little egret (*Egretta garzetta*). Collectively these two designated areas are referred to as a European Marine Site (EMS). Under UK legislation, much of the area is also notified as a Site of Special Scientific Interest (SSSI) with subdivisions of the estuary designated as a Marine Conservation Zone (MCZ) to protect important estuarine habitats and species,

including intertidal biogenic reefs, blue mussel beds and smelt. The designated MCZ is made up of two areas, covering an area of approximately 15 km² including the upper Tamar and Tavy estuaries.

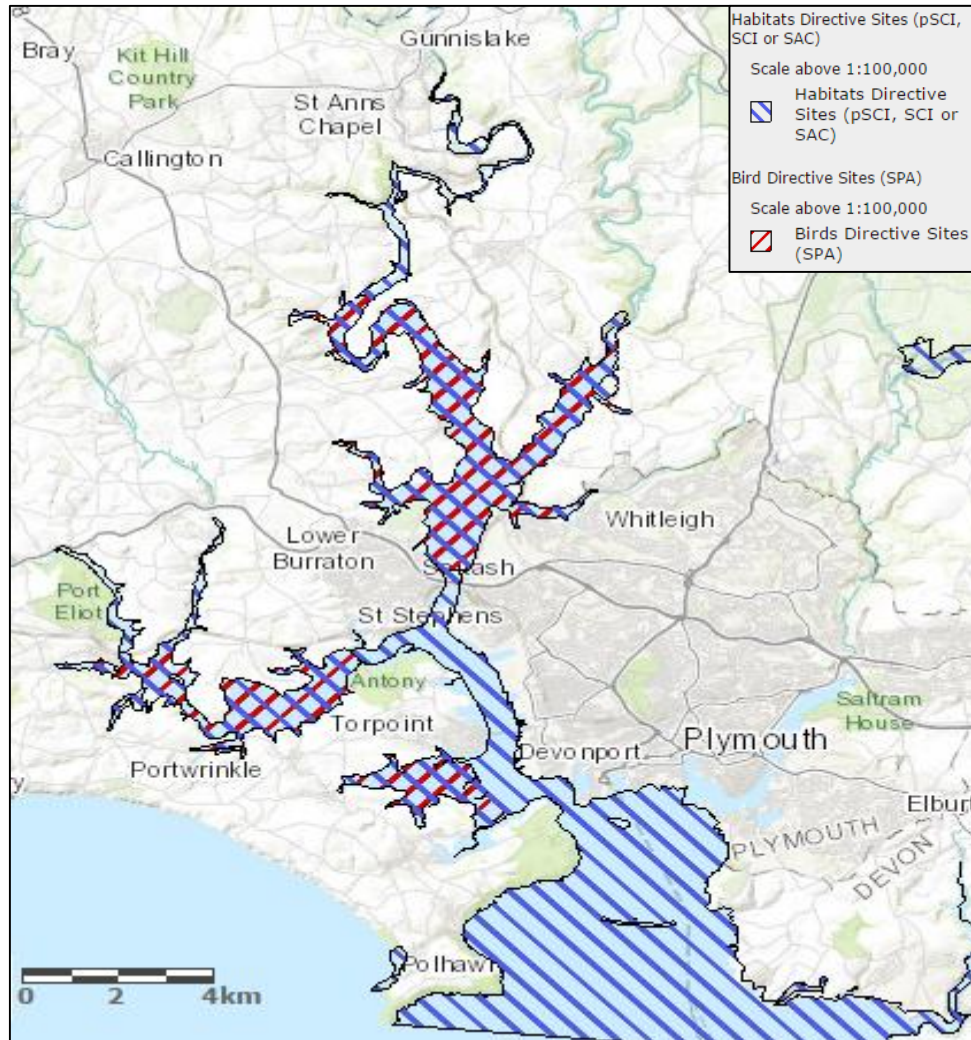


Figure 2.2: Map of the Tamar Estuary and Plymouth Sound European Marine Site. © Copyright European Environment Agency (EEA)

Overall the catchment area of the estuary is estimated to be approximately 1700km² (Evans *et al.*, 1993), with a 195 km² section of the Tamar river valley (Shaw & Moor., 2011) classified as an area of Outstanding Natural Beauty (AONB) by the Natural England. Topography of the estuary is highly variable with the upper and middle estuary catchment very much influenced by agriculture and old mines, whilst the lower estuary is subjected to substantial urban/industrial development, with The Port of Plymouth playing host to the largest naval base in Western Europe. The largest populations influencing the estuary are the city of Plymouth and towns of Saltash, Torpoint and Tavistock; totalling over 341,000 people, of which over 250,000 of these are in the Plymouth area (Tamar Catchment Flood Management Plan., 2012).

2.1.1 Physicochemical environment

Sediment and suspended particulate matter movements in the hydrodynamically energetic estuary are governed by a mixture of tidal and freshwater flow variations (Hartley & Spooner., 1938; George 1975; Uncles *et al.*, 1983; 1984; 1985; 1992; 1993; 1994; 1996; 2000; 2010). Tides in the estuary are semidiurnal with mean neap and spring tidal ranges of 2.2 and 4.7m respectively (Uncles & Stephens., 2001) while the net transport of particulate material is complicated by the presence of a high turbidity maximum (HTM), which is consistently associated with the lower salinity reaches of the estuary (Uncles & Stephens., 1993; Grabemann *et al.*, 1997; Dyer *et al.*, 2002; Tattersall *et al.*, 2003). During spring tides, the occurrence of strong tidal pumping of sea water from the lower reaches of the estuary to the central and upper reaches may extend the turbidity maximum within 5km of the weir at Gunnislake (Bale *et al.*, 1985; Uncles and Stephens, 1989; 2010; Uncles & Lewis., 2001). Average flushing times of the estuary can vary between 7-12 days (Uncles *et al.*, 1985), while water depth of the main channel differs between 2 and 8 m below mean spring high-water in the inner estuary and between 8 and 40 m in the outer estuary (Monbet *et al.*, 2009).

Chemical characteristics of the estuary have been described in detail by Milne, 1938; Armstrong & Butler., 1962; Butler & Tibbitts., 1972; Morris., 1978; Morris *et al.*, 1978; 1981; 1982 a; 1982 b; 1982 c; Langston., 1983; Loring *et al.*, 1983; Bale *et al.*, 1985; Knox *et al.*, 1986; Ryding & Rast., 1989; Miller., 1999; Millward., 1995; and Tappin *et al.*, 2013, reporting average dissolved concentrations of oxygen 2-10 mg L⁻¹; organic carbon 6 mg L⁻¹; suspended particulate matter (SPM) <5-1000 mg L⁻¹; a horizontal salinity range of 5-30psu and a pH range of 6.8-8.5 across the estuary.

2.1.2 Biology

From as early as 1899, extensive faunal studies have been conducted in the Tamar Estuary and Plymouth Sound culminating in a series of published papers and compilations on various ecological aspects of the estuary (Duncker, 1900; Ford, 1928; Percival, 1929; Hartley & Spooner, 1938; Cooper & Milne, 1938, 1939; Hartle.,1940; Milne, 1940; Spooner & Moore, 1940; Smith, 1956; Mommaerts, 1969, 1970) including three editions of the *Plymouth Marine Fauna*; first published by the Marine Biological Association of the UK in 1904, revised in 1931 and most recently in 1957. Although these investigations were conducted independently and with different immediate aims, they proved to have considerable bearing on one another and provide one of the earliest examples of a large scale ecosystem approach to collecting information and describing the balance of life in the estuary as a whole.

Since these early studies, this wealth of biological knowledge has been added to independently by various researchers and organisations, through numerous field or laboratory studies: (e.g. Nuttall &

Purves, 1973; Warwick & Gee, 1984; Gee *et al.*, 1985; Warwick *et al.*, 1991; Moffat & Jones, 1993; Davey & Watson, 1995; Moffat, 1996; Watson *et al.*, 1995; Kendall & Widdicombe, 1999; Cowie *et al.*, 2000; Bignell *et al.*, 2011) and a number of ecological surveys (Moore *et al.*, 1999; Langston *et al.*, 2003; Bale *et al.*, 2004; Widdows *et al.*, 2007; Curtis, 2010; Ware & Meadows, 2012).

Among the more conspicuous features of the whole estuarine area originally described by Hartley & Spooner (1938) and later by Uncles *et al.*, (2003) are the mud-flats. Described to be of considerable extent they cover hundreds of acres, extending up to the high tide mark in the lower portions of the estuary and all the way along the borders of the river channel to the river mouth in the upper reaches of the estuary. The fauna they harbour are regarded as one of the main elements of biomass in the estuary as a whole. Detailed investigations of the fauna inhabiting the flats by Spooner & Moore (1940) suggested that the mud was characterised by burrowing (or surface-living) estuarine fauna that included the worms *Hediste diversicolor*, *Nephtys hombergi* and *Ampharete grubei*; the molluscs *Cerastoderma edule*, *Scrobicularia plana*, and *Peringia ulvae*; and the crustaceans *Cyathura carinata* and *Corophium volutator*, all of which are considered an important food source for many of the bottom-feeding fish and various waterbirds known to inhabit the estuary.

Many of the mudflats (particularly in the lower reaches of the Tamar Estuarine system) sustain considerable swathes of the green algae (*Enteromorpha*) and the dwarf eel grass (*Zostera noltii*), providing a nationally important feeding and over wintering site for many wildfowl and wading bird species such as the wigeon (*Anas Penelope*), mute swan (*Cygnus olor*), shelduck (*Tadorna tadorna*), teal (*Anas crecca*), dunlin (*Calidris alpine*), oystercatcher (*Haematopus ostralegus*), curlew (*Numenius arquata*), redshank (*Tringa tetanus*) and, most recently a growing population of the avocet (*Recurvirostra avosetta*).

Adjacent to the tidal mudflats, saltmarsh and vascular plant habitats are not extensive across the SAC (<5%) due to historic land drainage practices (Hogan *et al.*, 2000) and the fringes of the estuary consist predominantly of common cord-grass (*Spartina anglica*), but they also support common salt marsh-grass (*Puccinellia maritime*) with sea plantain (*Plantago maritime*), sea milkwort (*Glaux maritime*) and saltmarsh rush (*Juncus gerardi*) (Curtis, 2010).

A detailed account of the fish populations in the Tamar is published by Hartley (1939) who undertook approximately one hundred hauls of fish between 1935 and 1937 and consequently, was able to give valuable insights into diet, growth and general ecology of commonly occurring and rarer species (Table 2.1). While the list of occurring species is fairly comprehensive, there are numerous omissions of occasional visitors to the estuary from the adjoining English Channel. For instance, Allis shad (*Alosa alosa*), an anadromous fish formerly known to spawn in several British river systems, has recently

been confirmed to spawn only in the Tamar Estuary. Sampling of the demersal fish assemblages in the English Channel off Plymouth Sound have been on-going for more than a century by the MBA starting in 1911 (McHugh *et al.*, 2011). Of the many species recorded entering the estuary, only the flounder (*Platichthys flesus*) is known to occur in the upper brackish reaches of the estuary (Russell., 1973; Dando., 2011). In the approaches to the Sound, some larger marine animals such as bottle-nosed dolphins, porpoises and basking sharks have also occasionally been sighted although they rarely venture into the estuarine site itself.

Table 2.1 Fish species in the Tamar Estuary with original nomenclature recorded by Hartley (1939).

Major Species	Occasional Species
<i>Pleuronectes flesus</i> –flounder	<i>Raia clavata</i> – thornback ray
<i>Pleuronectes limanda</i> –dab	<i>Raia maculata</i> – spotted ray
<i>Pleuronectes platessa</i> – plaice	<i>Clupea alosa</i> - allis shad
<i>Rhombus laevis</i> - brill	<i>Centronotus gunnellus</i> – butterfish
<i>Solea vulgaris</i> – sole	<i>Trachinus vipera</i> – lesser weaver
<i>Solea lascaris</i> – sand sole	<i>Arnoglossus laterna</i> – scald fish
<i>Clupea harengus</i> – herring	<i>Trigla gurnardus</i> – grey gurnard
<i>Clupea sprattus</i> – sprat	<i>Trigla hirundo</i> –tub fish
<i>Clupea pilchardus</i> – pilchard	<i>Trigla cuculus</i> – red gurnard
<i>Salmo trutta</i> – sea trout	<i>Cottus bubalis</i> - long-spined sea scorpion
<i>Salmo salar</i> –salmon	<i>Labrus bergylta</i> – bergylt
<i>Anguilla vulgaris</i> – eel	<i>Crenilabrus melops</i> – gilt-head
<i>Sygnathusacus</i> – pipe fish	<i>Ctenolabrus rupestris</i> – goldsinney
<i>Atherina presbyter</i> –sand smelt	<i>Zeus faber</i> – john dory
<i>Mugil chelo</i> and <i>M. auratus</i> –grey mullets	<i>Mullus surmulletus</i> –red mullet
<i>gadidae</i> –cod, pout, whiting, pollack	<i>Spinachia vulgaris</i> –sea stickleback
<i>Callionymus lyra</i> – dragonet	
<i>Gobiidae</i> –gobies	
<i>Agonus cataphractus</i> –the pogge	
<i>Caranx trachurus</i> –horse mackerel	
<i>Morone labrax</i> - bass	
<i>Scomber scombrus</i> -mackerel	

2.1.3 Anthropogenic stressors

For centuries the Tamar estuary and its surrounding valleys have provided an economical power source and important transport route for the main occupations of farming, fishing, mining and the military. As a result, there have been multiple anthropogenic impacts on the river system over the years – including sewage, organic pollutants, heavy metals and radionuclides (Dallas & Jha., 2015).

The area of Devonport has been an important naval shipping site since the 13th century (Hiscock & Moore, 1986) with its ship and boat-building yards, naval base and military port covering 4km of the lower estuary’s shoreline and has constituted a significant source of anthropogenic pollution to the

estuary in the form of sewage, heavy metals, and more recently radionuclides. This is due to authorisation which allows the discharge of radioactivity into the SAC and surrounding area, in relation to its submarine refit programme (Rawlins *et al.*, 2003).

Although there is no evidence of significant, current damage from oil pollution as result of shipping activities, there is a continual threat to all inshore marine habitats; with background polycyclic aromatic hydrocarbons [PAHs] being particularly pronounced in the SAC (Law *et al.*, 1997; Lindsay and Bell.,1997; Woodhead *et al.*, 1999) due to the intensity of shipping traffic in Plymouth Sound and the adjacent English Channel. While commercial traffic in the upper estuary ceased within the last fifty years and the area of estuary above the Tamar Bridge is currently used mainly for recreational activities, numerous quays on the estuary are testament to the volume of historic commercial traffic.

Legacy contamination of heavy metals and other organic contaminants are known to occur at varying concentrations in sediments across the SAC (Shaw & Moore., 2011). This is largely a result of historic mining for the metalliferous deposits of tin, copper lead, silver, iron, arsenic, zinc, tungsten and manganese which have been a feature of the Tamar valleys until the end of the 20th century (Dines, 1956; Langston *et al.*, 2003).

Ephemeral effects of macroalgal blooms and other eutrophic conditions have been a common feature of the Tamar's history, with nutrient levels within the site capable of supporting persistent algal blooms in the summer; particularly during long periods of low river flows within the upper estuary. Occasional reports have also been made of widespread hypoxic conditions and associated fish deaths as a result of the blooms (Darbyshire, 1996; Harris, 1988, 1992).The causes of these events are most likely linked to excessive nutrient enrichment from agricultural run-off due to land use changes in the upper catchment (Knox *et al.*, 1986), while continuous and intermittent sewage discharges could constitute a localised chronic source of contamination and nutrient-associated water quality problems in the lower estuary (Morris *et al.*, 1981; 1986; Readman *et al.*, 1986a). Over the last decade it has been estimated that loadings from anthropogenic sources may have decreased, primarily as a consequence of improved treatment of discharges, although the absolute significance of this reduction is still not clear (Curtis, 2010).

The present fisheries of the Tamar are characterised by a mixture of commercial, recreational and environmental, with Hartley (1940) describing a historic account of a small winter seine-net fishery in operation on the estuary. Although little is now caught commercially within the marine site itself, recreational angling has also grown significantly in popularity over the last decade within the catchment, delivering social and economic benefits. However, the possible impacts on the wider estuary are currently poorly understood and unquantified. Towed fishing gear is also prohibited on

the estuary due to expensive navel equipment, which means many of the reefs are in good condition. There is some evidence of biological disturbance *via* bait digging or the selective extraction of commercial species such as peeler crabs on a small section of the SAC at Tamerton Creek highlighted by previous studies (Godden., 1995; Fowler., 1999). The extent of such impacts is likely to be minor however due to the activities being concentrated in one relatively small area.

Despite the occurrence of these multiple stressors, based on recent ecological surveys by Widdows *et al.* (2007) and by Curtis (2010) there is currently none or little evidence of adverse anthropogenic impact within the Tamar estuary or Plymouth Sound in terms of:

- Sediment dredging (based on a survey of 65% of the inter-tidal area of the estuary).
- Increased turbidity or siltation of the estuary bed or intertidal communities.
- Abrasion of the estuarine habitats.
- Increased synthetic and/or non-synthetic toxic contamination.

2.1.4 Climate stressors

An understanding of climate change and how it might impact on the marine site is emerging as an important requirement for local managers and stakeholders across the catchment (TECF, 2012). Flooding, for instance, as a result of high tides coinciding with high rainfall has been a recorded feature of this catchment that dates back to the early 19th century, with the greatest concentration of properties at risk of flooding in the Plymouth area. The most recent Tamar Catchment Flood Management plan (2010-2015) suggests that over the next century, under increased river flows (20%) and sea level rise (900mm), floods will be more frequent with increased flood depths in key areas of the catchment unless greater mitigation strategies are put into place.

Historically there has been negligible reported effects of large-scale hydrodynamic changes to the estuary, including effects of habitat erosion of the intertidal areas of mud and saltmarsh (Bale *et al.*, 2007; Widdows *et al.*, 2007). However, climate change in the form of increased storminess, rainfall and sea-level rise could have the potential to impact on the erosion of important habitats and potentially alter the tidal flow regime in the estuary. Under such circumstances the already problematic occurrences of eutrophication and hypoxia in the estuary could become more frequent particularly when combined with projected increased summer temperatures (Stocker *et al.*, 2013), leading to the promotion of algal blooms and increased stratification of the water column.

Increasing sea temperatures in the adjacent English Channel have already resulted in the progressive spread of southern marine species northwards into the catchment, with a number of marine invasive species now being recorded within the site including the Pacific oyster (*Crassostrea gigas*), wakame (*Undaria pinnatifida*) and the wire weed (*Sargassum muticum*); all of which are increasing in

population density in the estuary. Sightings of sunfish (*Mola mola*), leatherback turtle (*Dermochelys coriacea*) and the barrel jellyfish (*Rhizostoma pulmo*) have also been increasingly spotted in the Plymouth Sound area.

2.1.5 Management initiatives within the catchment

The Tamar Estuaries and Plymouth Sound have a long history of management. Historically, due to its strategic military importance, much of the management initiatives of the site have fallen under the jurisdiction of the Ministry of Defence (MoD) to allow timely conduct of naval activities and shipping movements. However, in 1992 the MoD considered reducing their jurisdiction and geographical area of responsibility, which through a consultation process led to a revitalisation of the management and advisory group structures of the marine site and the production of the first 1997 Tamar Estuary Management Plan. Since then, the Tamar Estuaries Consultative Forum (TECF) which encompasses all statutory and bylaw-making bodies, has been working collaboratively with a number of stakeholders to manage the waters of Plymouth Sound and the Tamar Estuaries by developing a single scheme of management to respond to and deliver, the requirements of the Habitats Directive.

The most significant framework of interest to this study is the recent Tamar Catchment Plan (2012-2018) which has adopted a stakeholder-led 'ecosystem services' approach to catchment planning. This has involved the host organisation Westcountry Rivers Trust (WRT); working with over 55 different stakeholders to identify areas within the catchment which play, or have the potential to play, a particularly important role in the delivery of clean water and a range of other benefits (services) to society. Major initiatives linked to the project include the Clean Sweep (1998), Upstream Thinking (2008-2015) and Catchment Sensitive Farming (2008-ongoing) projects, all with the joint objective of implementing environmental improvements aimed at improving water quality in compliance with Water Framework Directive (WFD) measures and the Nitrates Directive. Many other precursor projects such as the Tamar 2000 project have also been specifically proclaimed as a UK example of the successful implementation of the ecosystems approach further amplifying the Tamar's appropriateness for this ecosystem service case study. Whilst there is growing awareness of the need for an integrated approach to marine management within the Tamar area, there is still much to do to assess the estuary as a whole and to put many of the proposed management tools into practice.

2.2 Eden case study area

The Eden Estuary is a small (11km-long) shallow bar built or ‘pocket’ estuary, located between the village of Guardbridge and the town of St. Andrews (Figure 2.8) on the East coast of Scotland (56°22' N, 2°50' W). The main source of fresh water into the catchment comes from the River Eden (draining 260km² out of 320km²), which approximately dissects the catchment from west to east. The main channel of the estuary is flanked by relatively wide intertidal areas (8km²) that plays host to large populations of overwintering waterfowl and wading bird species. Surrounding the Eden, the hinterland is highly developed, comprising Leuchers military station, St. Andrews Links (the largest public golf complex in Europe), Eden.Mill (Scotland’s first brewery-distillery, formally Guardbridge Paper Mill) and large swathes of highly productive agricultural land, that make up 76% of the land use within the catchment (Macgregor & Warren 2005). The main towns bordering the estuary are the towns of Leuchars, Guardbridge and St. Andrews with inhabitants totalling over 20,500 people, of which over 17,000 of these are in the St. Andrews area (Census, 2011).

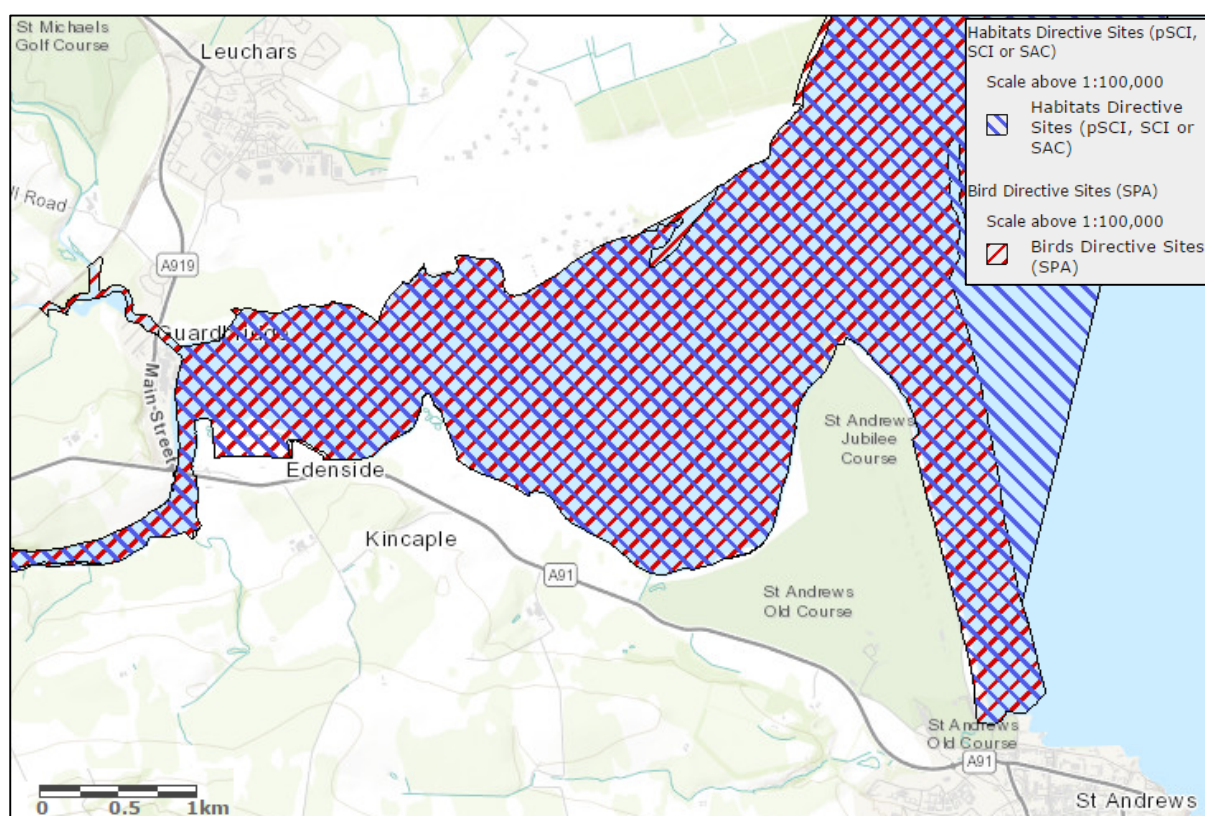


Figure 2.3: Map of the Eden Estuary European Marine Site. © Copyright European Environment Agency (EEA).

Collectively the Eden estuary along with the Firth of Tay Estuary is designated as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (92/43/EEC) and a Special Protection Area (SPA) under the European Commission Directive on the Conservation of Wild Birds (79/409/EEC). The Eden estuary itself is also classified as a Local Nature Reserve (LNR), Site of Special Scientific Interest (SSSI) and RAMSAR site (Wetlands of International Importance).

2.2.1 Physicochemical environment

Sedimentary and hydrological processes indicate that the Firth of Tay, Tay Estuary and Eden Estuary can be regarded as a single unit due to influence of local wave-induced long-shore currents that are a dominant feature of St. Andrews Bay (Bates *et al.*, 2004). In particular, tidal currents rather than wave action, dominate the hydrodynamics of the Eden estuary due to a sand bar across the mouth of the estuary (Jarvis & Riley, 1987). Freshwater input also has a relatively low influence compared to tidal flood water (SEPA, 1999), with average flow in the River Eden being 4 m³/s; although daily mean flows of 40 m³/s have been measured in winter (Al-Bayati & McManus, 1984). Residence time of fresh water in the estuary is estimated to be approximately 6 days at average river flow. Wave heights have been recorded up to 0.4-1.0 metres (Posford & Duvivier, 2000) with equinoctial tidal ranges of 3.5m, 5m and 6m respectively (Duck & Wewetzer., 2001). During flood tides fine sediments are brought in and are deposited on the tidal flats during the still period of the high tide.

The sediments of the estuary are spatially complex and heterogeneous, consisting of regions dominated by 63-250µm grain size (Eastwood, 1976). At the mouth of the estuary, 90% of the sediments are quartz material: whilst further up the estuary, muds and silty sand are found that exhibit a cohesive behaviour (Taylor & Paterson, 1998).

Inter-annual variations in chemical determinants such as nitrogen and phosphorous compounds have been shown to be dominated by fluctuations in river flow, with nitrogen levels within the catchment known to be particularly high (SEPA, 2006). Salinities across the estuary are noted to be fairly uniform ranging between 20 and 30ppt in both sand and mudflat environments at high tide (Johnston *et al.*, 1979). Waters flowing through the estuary are well oxygenated with dissolved oxygen measured on routine quality surveys consistently in the range of 80-90% saturated (OSPAR, 2006).

2.2.2 Biology

The Eden estuary is a biologically varied estuary of local and European importance, particularly in terms of its waterbird populations. Nationally important species include the shelduck (*Tadorna tadorna*), oystercatcher (*Haematopus ostralegus*), grey plover (*Pluvialis squatarola*), black-tailed (*Limosa limosa*) and bar-tailed (*Limosa lapponica*) godwits and redshank (*Tringa tetanus*), which occur in nationally significant numbers, using the estuary for feeding and roosting. Other species of regional

importance include wigeon (*Anas Penelope*), teal (*Anas crecca*), dunlin (*Calidris alpine*) and curlew (*Numenius arquata*).

Primary production on the estuarine mudflats is represented by diatoms and cyanobacteria (mainly *Oscillatoria* sp), which form visible biofilms, alongside large complexes of algal mats *Enteromorpha* and *Ulva* sp. Fringing the mudflats the salt marshes of the Eden are relatively small (0.11km²) varying from stable, flourishing communities to discontinuous patchy remnants, many of which are undergoing active erosion (Maynard, 2015). Not all of the Eden's saltmarsh is deteriorating however, with some patches being stable if not actively developing, with a long term 'saltmarsh regeneration' project currently underway (Maynard, 2003; Maynard *et al.*, 2011) by members of the Sediment Ecology Research Group (SERG) at the University of St. Andrews. More than 50% of the estuaries saltmarsh is composed of *Puccinellia maritima* communities fronted by the annual pioneer species *Salicornia europaea*.

Fish populations within the estuary are largely diadromous transitional species (table 2.2) such as the common sturgeon (*Acipenser sturio*), European eel (*Anguilla Anguilla*) and flounder (*Platichthys flesus*) which use freshwater upper reaches of the river Eden as spawning ground. Atlantic salmon (*Salmo salar*) and the brown/sea trout (*Salmo trutta*) are also abundant, with the latter being periodically added to the river in noteworthy numbers (>700 individuals) to sustain local angling associations (personal communication).

Toward the mouth of the estuary, the outer sediment flats of the support infaunal communities characteristic of exposed, low organic content sandy beaches such as *Arenicola marina*. In the more sheltered areas of the inner estuary, dominant populations vary from marine polychaete worms, *Hediste diversicolor* to the amphipod *Corophium volutator* and the gastropod *Peringia ulvae*. In the inner most brackish part of the estuary, the substratum consists of glutinous soft mud and sandy mud, home to once commercial cockle *Cerastoderma edule* and mussel beds *Mytilus edulis*. In addition to the macrofauna, the Eden supports a nationally important breeding colony of common seals (*Phoca vitulina*) (2% UK population) that are known to range freely throughout the site and are closely monitored by the Seal Mammal Research Unit (SMRU) at St. Andrews.

Table 2.2 Fish species recorded in the Eden Estuary. Based on records from the National Biodiversity Network Centre.

Major Species	Minor Species
<i>Acipenser sturio</i> [Common Sturgeon]	<i>Alosa alosa</i> [Allis Shad]
<i>Anguilla anguilla</i> [European Eel]	<i>Lepomis gibbosus</i> [Pumpkinseed]
<i>Barbatula barbatula</i> [Stone Loach]	<i>Salvelinus fontinalis</i> [Brook Charr]
<i>Gasterosteus aculeatus</i> [Three-spined Stickleback]	
<i>Osmerus eperlanus</i> [Smelt]	
<i>Phoxinus phoxinus</i> [Minnow]	
<i>Platichthys flesus</i> [Flounder]	
<i>Rutilus rutilus</i> [Roach]	
<i>Salmo salar</i> [Atlantic Salmon]	
<i>Salmo trutta</i> [Brown/Sea Trout]	
<i>Tinca tinca</i> [Tench]	

2.2.3 Anthropogenic stressors

Anthropogenic pressure in the form of increased nutrients and eutrophication from arable and livestock production is one of the most significant pressures influencing the SAC with high levels of nitrogen compounds entering the estuary *via* the river Eden (Clelland, 1997). Historically this has led to a number of ecological problems such as the closure of mussel beds as unfit for human consumption and widespread fish mortalities (Defew & Paterson, 2008). As a consequence the catchment was designated as a nitrate vulnerable zone in 2003 (SEERAD, 2003). Future nutrient inputs are expected to decline thanks to increased legislation resulting from the Nitrates Directive (NVZ) and Sensitive Area (UWWTD) designations, including an upgrade of the Guardbridge sewage treatment works in 2008 and the closure of the Guardbridge paper mill and adjacent pig farm with their associated effluent.

While it is not known if the Eden sediments contain large concentrations of persistent contaminants or other wastes such as microplastics, there is some evidence of increased metal content near former landfill sites and isolated outbreaks of pesticide discharge into the estuary have been reported in the past (The Glasgow Herald - Jun 16, 1970; The Courier 20 April 2011).

The fisheries of the estuary are exclusively for recreational purposes (although there has been preliminary investigations into whether St. Andrews Bay at the mouth of the Eden could support an inshore shellfish fishery (Defew *et al.*, 2011)) with the River Eden hosting over 20 miles of prime salmon and trout fishing ground. Bait digging or harvesting of commercial invertebrate species is prohibited on the estuary under the 2008 Byelaws. However the reserve allows a small amount of

mussel collection for personal use with 4 permits being issued annually. Other forms of recreational disturbance such as water sports and horse riding are prohibited within the estuary local nature reserve but occur on West Sands. Wildfowling does occur but there are two sanctuary areas where no shooting is permitted.

2.2.4 Climate stressors

Increases in storm frequency, precipitation and sea level rise associated with climate change, could have profound effects on the Eden estuary, with the Scottish Environment Protection Agency's (SEPA) flood map showing approximately 60-70% of the Links Trust golf course could be underwater in the event of a 1 in 200 years storm surge. This is complemented by recent evidence by Chocholek (2013) showing a long term correlation of monthly rainfall averages and an increasing freshwater input into the Eden since the 1960's (Figure 2.13).

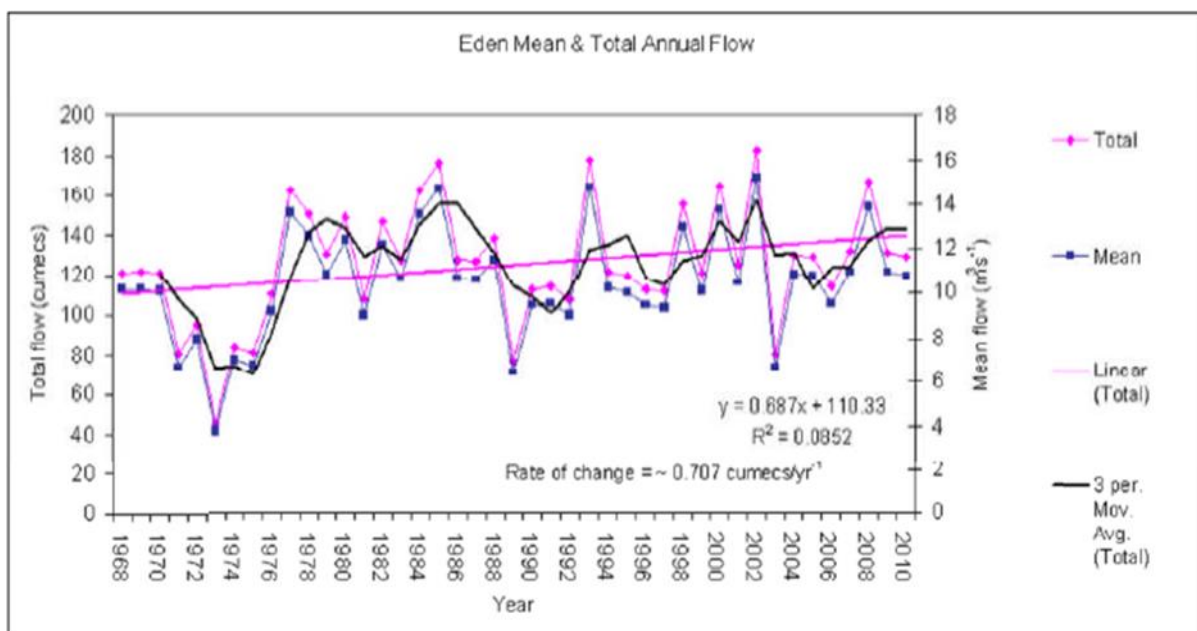


Figure 2.4 River Eden mean flow (m^3s^{-1}) and total annual flow in cumecs (Chocholek., 2013).

With regards to sea level rise there is some evidence that isostatic uplift of the sea and land levels around the Eden Estuary may counteract or exceed current sea level rises (Duck *et al.*, 1995), particularly at the mouth of the estuary. However any increases in flow variations within the system is still likely to lead to changes in sediment salinity, coastal erosion and patterns of sedimentation. Likewise due to the degraded state of many of the Eden's salt marshes it is doubted whether they will be adequate to withstand any future increase in tidal energy from accelerated hydrodynamic regimes (Crawford, 2008) with serious consequences for the future cost of coastal protection.

2.2.5 Management initiatives within the catchment

Since 1978 when the estuary was declared a Local Nature Reserve (LNR), the site has been managed by staff, volunteers and a dedicated countryside ranger from the Fife Coast and Countryside Trust in accordance with the Eden Estuary Management Plan. Under the LNR wildfowling is controlled by a permit system, with monitoring of the bird species is undertaken by the ranger and volunteers. In addition the Eden Wildfowling Association has also set up voluntary sanctuary zones at Guardbridge and the East Shore which are observed by the majority of wildfowlingers.

The long term goal for this site is to maintain the Eden Estuary as a feeding, roosting and breeding site for wildfowl, waders and terns, and to maintain its diverse estuarine and coastal vegetation types. Although still in its development phase, there is a current drive to develop an Integrated Coastal Zone Management Plan (ICZM) for the Eden in conjunction with key partners and local stakeholders.

2.3 Metadata base & data collection methods

For both case study areas, a formally structured literature review was conducted to collate all available physicochemical and biological data for the Tamar and Eden estuaries, with the aim of investigating relationships between abundance of biota and potential environmental stressors. While biotic data collection ranged from: macrophytes, macroalgae, microphytobenthos, demersal fish, epibenthic crustaceans, macro-benthic invertebrates and waterbirds only the macro-fauna collection methods are outlined below as they formed the basis of all four data chapters. The methods of collection for the other biotic data sets are outlined in their respective chapters. Similarly the physicochemical data outlined below is primarily used in chapter 3, but estimates of river-flow are also used in chapter 5 and hence the general methodology for collection is outlined here.

The format of the review followed that of a 'systematic review', following guidelines recommended by the Centre for Evidence-Based Conservation (see Pullin & Stewart, 2006) with the details of the protocols followed outlined below.

2.3.1 Search strategy and screening procedure

The literature search was composed of three distinct phases:

1. Searching online databases and catalogues.
2. Searching organizations and professional networks.
3. Searching the web literature.

The primary search strategy was based around a scoping search of online databases to find publications suitable for use in analysis. Searches were conducted using the information resources

available to the St. Andrews University Library and National Marine Biological Library (NMBL) *via* the following data bases:

- Google Scholar.
- Web of Science (ISI).
- Science Direct and Scopus.
- NMBL Catalogue.
- St Andrews University Library Catalogue (SAULCAT).

The search terms used were based around a general search of the study areas: “Tamar” or “Eden” (lengthened to include variations) combined with other terms relating to climate variability, ecosystem structure and environmental management using the Boolean operator ‘AND’ or ‘OR’ within a set of outer brackets. In broad terms these searches covered:

- Climate variability.
- Physio-chemical processes.
- Biological surveys and monitoring.
- Remote sensing.
- Ecotoxicology and risk assessments.
- Environmental management.
- Socio-economics.

Once the search procedure was complete, publications were compiled in a general bibliography managed using the Endnote[®] bibliographic reference management software. The publications were then assessed through a two stage screening process to identify relevant studies using a set of predefined inclusion criteria. In the first instance the title and abstract of each source was examined to determine relevance. This approach was conservative to retain data if there was reasonable grounds it could be appropriate. Remaining articles were then viewed in full and potentially useful data extracted (see procedures below) for use in analysis or categorised for use as supporting information using keywords suggested by the authors themselves. With regards to the biological data collection, it was elected to include only studies examining community level assessments of species abundance, richness, evenness, biomass, diversity, production and/or respiration as it was felt these were the most important community or ecosystem-level indicators of structure and functioning in marine systems as suggested by Lyons *et al.*, (2012;2014).

To access the widest possible range of information, supplementary data were also gathered from the so called ‘grey literature’ by searching or requesting information from organisations, professional networks and the web *via* standard search engines to target any information that would not be

obtained from a conventional database search. In most cases documents or in some cases entire data sets were available freely through an organisations web page often with the caveat of it being used in academic research. In other cases items referenced in a directory were requested in a digital format or if this was not possible hand searched involving visits to institutions to extract all relevant material.

The main examples of sources consulted are outlined as follows:

- Environmental databases.
- Environmental survey and monitoring reports.
- Doctoral theses and conference proceedings.
- Professional networks e.g. Plymouth Marine Sciences Partnership (PMSP) comprising Marine Biological Association (MBA), University of Plymouth (UoP) and Plymouth Marine Laboratories (PML).
- Current research projects including: Coastal Biodiversity & Ecosystem Service Sustainability (CBESS), UK Ocean Acidification (UKOA), VECTORS of Change in European Marine Ecosystems and their Environmental and Socio-Economic Impacts (VECTORS) and the Marine Ecosystems Research Programme (MERP).
- The Marine Biological Association Archive Collection.
- Devon and Cornwall County archives.
- Plymouth City Council archives.
- Calstock Parish Archives.
- Plymouth Marine Science Electronic Archive (PlyMSEA) research output from the following three organisations based in Plymouth: The Marine Biological Association (MBA), Plymouth Marine Laboratory (PML) and the Sir Alister Hardy Foundation for Ocean Science (SAHFOS).
- Unpublished reports.
- News articles.
- Press releases.

2.3.2 Data extraction and collation

After the initial literature screening process, data extracted from articles were recorded in excel spreadsheets to allow synthesis and analysis. Where possible absolute values, means, standard errors, standard deviations and sample size information were taken directly from the text or tables of the articles. In the few cases this was not possible data extraction software such as DataThief© (Tummers, 2006) was used to extract information from figures. Physico-chemical data were also collected where possible from the same study or from the available literature to compare with the biological datasets.

2.4 Description of the Tamar data sets used

Over the 80 year period (1936-2015) for which the Tamar was investigated, it was possible to locate sufficient inter-comparable data, which could be used as a basis to draw conclusions about long term changes in the Tamar estuary. Full details of the collection and treatment of the selected data is given in the two following sections, along with details of the physiochemical data collected from the same reference periods.

In general, data was selected from five time periods (Table 2.3), that were considered to have enough information for an detailed estuarine comparison in the Tamar case study under the effects of various environmental drivers.

Table 2.3 Time periods investigated for the Tamar in this thesis.

Temporal reference	Reason for inclusion	Summary of system status
1937	Historic reference period	Estuary is generally perceived to be in “moderate” ecological condition as evidenced by Hartly (1936) who noted that there was “ <i>no pollution of the rivers by commercial effluents</i> ”. However little monitoring data is available from this period there is evidence of crude sewage widely entering the estuary.
1990	Period of pronounced eutrophication	Low river flows combined with high nutrients lead to excessive production of organic matter in the form of algal blooms, coinciding with hypoxic symptoms and fish deaths in the upper estuary.
1991	Recovery year following eutrophic symptoms.	River flows and nutrient levels return to ‘normal’ levels, although nutrients remain high across catchment.
1992	A pre-management period with the Introduction of nutrient mitigation measures across catchment.	Various management efforts put in place to clean up nutrient related issues across the estuary.
2005	A post-management period following the implementation of various mitigation measures.	Twelve years following the implementation of mitigation measures, there is still questions as to the environmental state of the system.

Based on evidence from the literature, it was clear that there have been major changes to the main rivers that drain the agricultural and inhabited areas of hinterland and therefore the estuary itself during the time frame under investigation. In common with many British estuaries, from the 1970s to the late 1980s, the Tamar experienced significant nitrogen and phosphorous enrichment due to excessive agricultural run-off due to land use changes in the upper catchment (Knox *et al.*, 1986), while sewage discharges constituted localised chronic contamination and nutrient-associated water quality problems in the lower estuary (Morris *et al.*, 1981; 1986, Readman *et al.*, 1986a). As a result during these periods the system was considered eutrophic, with respect to nitrogen under criteria proposed by Dodds *et al.*, (1997) (>1.5 mg/L) and the EU guideline of 9 ($\mu\text{g/L}$) for the protection of coarse freshwater fish, but not considered polluted in terms of nitrogen according to criteria under the Nitrates Directive (>5.65 mg/L) for official designation as a eutrophic system.

This culminated during the period of 1990 when low river flows, high water residence times and high nutrient concentrations in the form of phosphorous compounds, interrupted upstream communication with the upper portion of the system, resulting in large blooms of benthic microalgae and increased biomass of macroalgae across the estuary. The resultant conditions included widespread salmonid fish deaths caused by localized areas of low oxygen conditions (Darbyshire., 1996; Harris., 1988, 1992), in addition to relatively low pHs and high suspended solids (trapped in the upper estuary following spring tides), leading to reported changes in biodiversity and functioning of the system. During this period annual reactive phosphorous concentrations exceeded 100 ($\mu\text{g/L}$) and the Tamar was officially classed as eutrophic using interim standards set by the Environment Agency (EA, 1998).

Following a recovery period the following year (1991), in 1992 various management efforts such as the “New South West – Clean Sweep and Beyond project” and the “Plymouth Urban Diffuse Pollution Project” were put in place to clean up nutrient related issues across the estuary. As a result much of the eutrophic symptoms associated with the pre 1990’s had subsided by the early 2000’s. For example average reactable phosphorus concentrations were shown to decrease from 1976 to 1990 levels of 84($\mu\text{g/L}$) to 59.2 ($\mu\text{g/L}$) for the period of 1991 to 1999 and to an even lower 49.5($\mu\text{g/L}$) across the years 2000 to 2005 (Mankasingh., 2005); coincident with measures introduced on other estuaries by the Urban Wastewater Directive (UWWd) for improved treatment of wastewater.

2.4.1. Tamar physicochemical data collection

Due to there being a lack of physicochemical data collected at the same time (or to the same parameters) as the biological data sets used in this study, interpolation of suitable data from the available literature and environmental databases was necessary. Initially, to compare general trends

across the estuary as a whole, environmental-type was obtained from a Microsoft Access database provided by the Environment Agency, with a summary of the chosen variables shown in table (2.4). Annual average concentrations of selected determinants included temperature (°C), pH, dissolved oxygen (mg l^{-1}), salinity (psu), biochemical oxygen demand (mg l^{-1}), ammonium (mg l^{-1}), nitrite (mg l^{-1}), nitrate (mg l^{-1}), filterable reactive phosphorus ($\mu\text{g l}^{-1}$) and chlorophyll *a* (mg l^{-1}); all determined *in situ* at the tidal gauging station at Gunnislake. Due to the historic nature of the time period, there was little to no information available to compare environmental variables across the whole estuary during the 1937 period.

Table 2.4: Summary of annual average concentrations of selected environmental variables for the Tamar estuary (1990-2005).

Variable	Year	Source
Temperature(°C)	1990-1992; 2005	Environment Agency
pH	1990-1992; 2005	Environment Agency
Surface salinity (psu)	1990-1992; 2005	Environment Agency
Dissolved oxygen (mg l^{-1})	1990-1992; 2005	Environment Agency
Biochemical oxygen demand (mg l^{-1})	1990-1992; 2005	Environment Agency
Ammonium (mg l^{-1})	1990-1992; 2005	Environment Agency
Nitrite (mg l^{-1})	1990-1992; 2005	Environment Agency
Nitrate (mg l^{-1})	1990-1992; 2005	Environment Agency
Filterable reactive phosphorous ($\mu\text{g l}^{-1}$)	1990-1992; 2005	Environment Agency
Chlorophyll <i>a</i> (mg l^{-1})	1990-1992; 2005	Environment Agency
River flow (m^3/s)	1990-1992; 2005	The National River Flow Archive (NRFA)
North Atlantic Oscillation index	1990-1992; 2005	Hurrell, (1995)* updated <i>via</i> the associated website

In addition to the other physiochemical variables, summer (annual and monthly) river flow data for the Tamar, was obtained from the National Rivers Archives website (www.nerc-wallingford.ac.uk/ih/nrfa/index.htm) for the 1955 to 2015 period, also measured at Gunnislake (Figure 2.14). These estimates account for 73% of the fresh water input into the estuary with remaining 23% entering *via* the Rivers Lynher and Tavy. The most recent (1864-2015) copy of the North Atlantic Oscillation (NAO) winter index (December–March) illustrated in Figure 2.15 was also extracted from

Hurrell (1995, updated on Hurrell's website) to compare inter-annual surface sea-level pressure across estuary

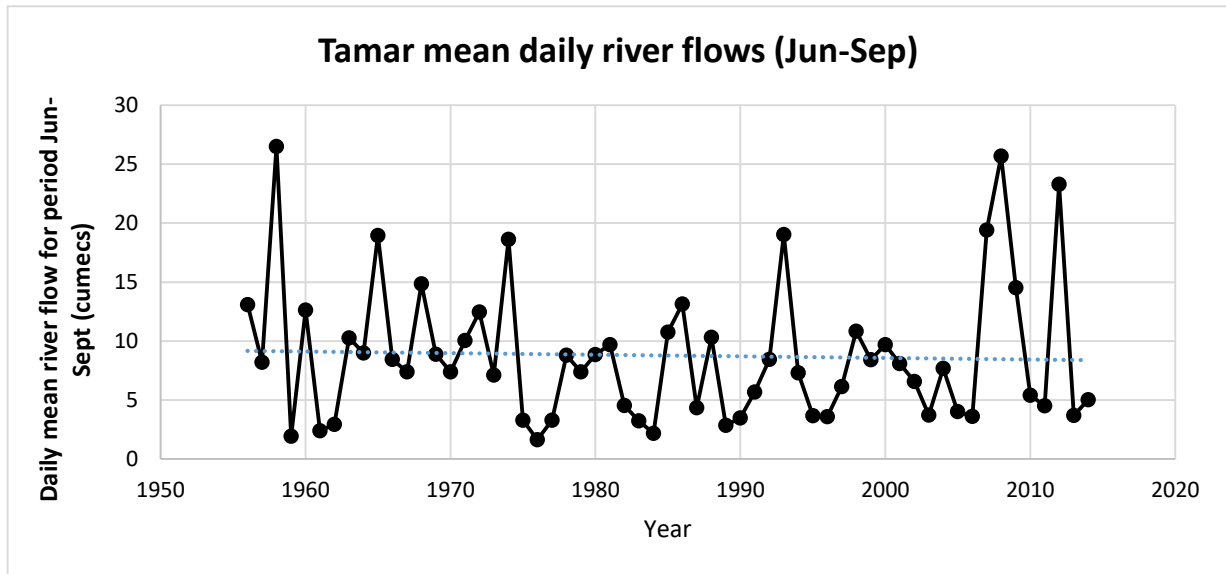


Figure 2.5 Annual mean daily river flows (summer; June-Sept) of the Tamar estuary.

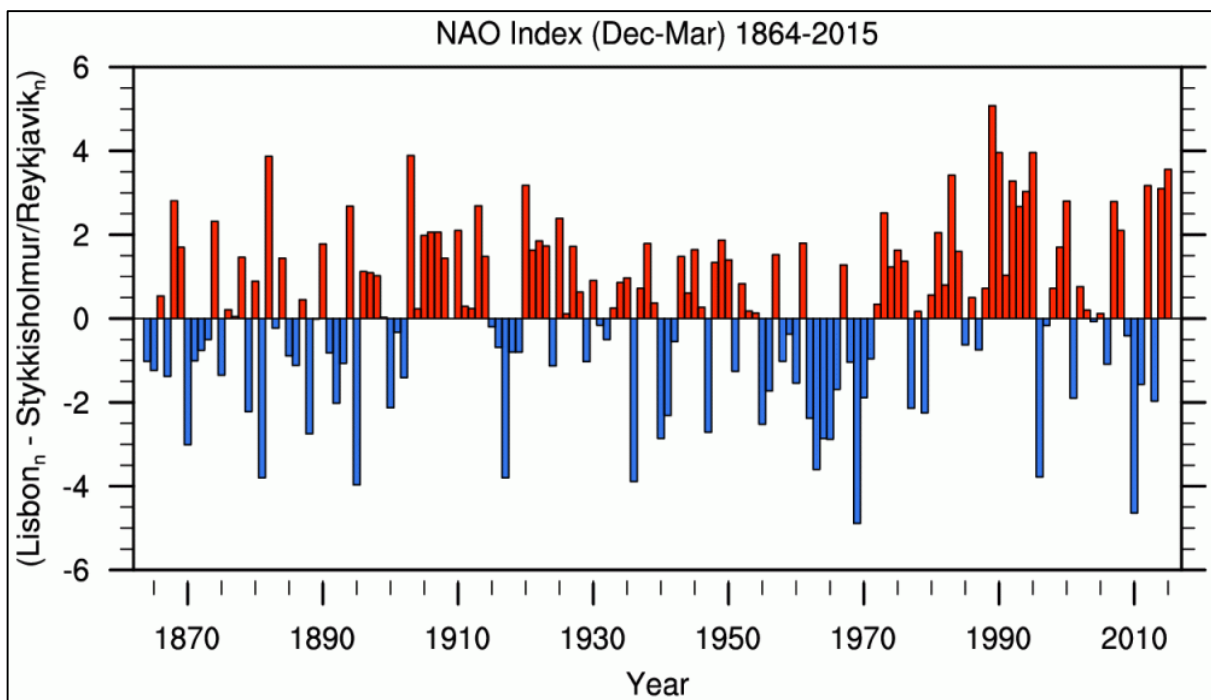


Figure 2.6 Winter (December through March) index of the NAO based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. The SLP values at each station were normalized by removing the long-term mean and by dividing by the long-term standard deviation.

Increasing the spatial resolution to the level of individual zones, supplementary data was also collected that could be used to characterise physiochemical changes at a more local scale (summary table 2.5). Surface salinity and sediment granulometry was available for comparison for the 1990-2005 period, at the level of the individual zones provided by the Environment Agency. 1937 period values for surface salinity were extrapolated from Percival (1929) and Milne (1938) and average sediment particle size was based on observations by Hartley, & Spooner, (1938). Additionally, data from the Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) and the Plymouth Harbour and Rivers Chart (Imray Chart C14) were used to estimate the (1990-2005) depth (at high tide), tidal currents and exposure for each survey site. Categorical approximations based upon these datasets concurred for similar sites reported for the 1937 period data (e.g. Hartly, 1936: Milne, 1940) and hence were used to estimate relative depth, exposure and tidal current values for these sites.

Table 2.5 Summary of annual average concentrations of selected environmental variables for each zone of the Tamar estuary (1937-2005).

Variable	Year	Source
Salinity (ppm)	1937;1990-1992;2005	Percival (1929); Milne (1938); Environment agency
Site Exposure	1937;1990-1992;2005	Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) and the Plymouth Harbour and Rivers Chart (Imray Chart C14)
Tidal streams (knots)	1937;1990-1992;2005	Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) and the Plymouth Harbour and Rivers Chart (Imray Chart C14)
Granulometry (mm)	1937;1990-1992;2005	Hartley, & Spooner (1938);Environment agency
Depth (m)	1937;1990-1992;2005	Tidal Stream Atlas for Plymouth Harbour and Approaches (1991) and the Plymouth Harbour and Rivers Chart (Imray Chart C14)

2.4.2 Tamar macro-benthic invertebrate data collection

Macro-fauna data were examined from over fifteen different published and unpublished sources with five studies allowing some inter-comparisons to be made at the species to estuarine scale (see Table 2.6). These surveys were selected on the basis that the samples taken were in the same places at similar times of the year and provided data with reasonable coverage of the Tamar's mudflats. All field work was carried out between the months of May and August. While every effort has been made to standardise the data as far as possible, owing to different sampling methodologies by different researchers over the years, variations in sampling effort, such as sampling different areas of sediment; to different depths; sieving samples though different mesh sizes (0.8 and 0.5mm) while extracting and identifying organisms using different expertise, meant complete uniformity was unattainable.

Table 2.6 Sources of data relating to macrofaunal communities in the Tamar estuary examined in the course of this thesis

Data set title	Originator	Temporal reference	Original sample information	Protocols/standards used to collect the data
The ecology of the Tamar Estuary VI. An account of the macrofauna of the intertidal muds.	Spooner & Moore (1940). Journal of the Marine Biological Association of the United Kingdom, 24(01), 283-330.	1937	11 Sample stations	0.25m ² quadrats marked out with a wooden frame and dug to a depth of 15-30cm at low tide. Converted to 0.1m ² . Mesh size (0.8 mm)
Sediment-water contaminant exchange	Watson <i>et al.</i> , (1995) National Rivers Authority Report, Bristol, 185pp	1990	6 Sample stations	0.1m ² Drainpipe cores: : mesh size = (0.5 mm), low tide
Sediment-water contaminant exchange	Watson <i>et al.</i> , (1995) National Rivers Authority Report, Bristol, 185pp	1991	6 Sample stations	0.1m ² Drainpipe cores: : mesh size = (0.5 mm), low tide
South West Water (SWW) Tamar Estuary and Sublittoral Sediment Survey	JNCC Marine Recorder Database	1992	17 Sample stations	Day Grabs 0.1m ² : mesh size = (0.5 mm)
Differential responses of the estuarine macro-benthos to environmental factors: the role of vertical stratification within the sediment.	Dr Jeanette Louise Sanders doctoral Thesis (Unpublished) University of Plymouth in collaboration with PML. Obtained with permission from author.	2005	9 Sample stations	0.1m ² Drainpipe cores: : mesh size = (0.5 mm), low tide.

Having extracted the data from the literature, sample sites were spatially segregated into three separate biogeographical zones (upper, central and lower estuary) based on variations in salinity and wave exposure regimes (Table 2.7) based on criteria first described by Moore *et al.*, (1999). Within each of these zones three sampling sites, based on five replicate samples were used for the basis of further statistical and modelling analysis (Figure 2.15)

Table 2.7 Biogeographical zones used in delineating macro-fauna sample data

Location	Description
Zone A: Upper estuary	This zone extends from Cargreen to South Hooe and typically experiences very low salinity levels in the region of 5‰.
Zone B: Central estuary	This zone extends from the intersection of the River Lynher with the River Tamar and extends upstream to Cargreen. This area exhibits salinities between 25-15‰.
Zone C: Lower estuary	This zone extends up the Tamar River from Devil’s Point to the southern extent of the entrance to the River Lynher. Waters within this zone frequently exhibit high turbidity levels and reduced salinity (typically between 20-30‰).



Figure 2.7 Tamar macro-fauna sampling zones showing Zone A (upper estuary), Zone B, (central estuary) Zone C (lower estuary). Four point stars represent the selected 1937,1990,1991,1992 and 2005 sampling stations.

2.5 Description of the Eden data sets used

Pending the initial literature screening for the Eden, it was determined there was insufficient recent information to make a detailed comparison of biodiversity-function-service relationships at the community/ecosystem level and that additional data would need to be collected. Therefore in the summer of 2015, field-based measurements of macro-fauna and benthic primary producers were undertaken to supplement the available literature. This information was compared to a matching set of data collected previously during the summer of 1999 by the BIOPTIS programme (Assessing the Biological and Physical Dynamics of Intertidal Sediment Systems: a Remote Sensing Approach MAS3-CT97-0158) which aimed to couple ecologically significant variables with concomitant remote sensing data. More specifically the factors measured during the BIOPTIS project included: the analysis of sediment properties; the spatial distribution of organisms within sediments; pigment content and pigment fingerprinting. These measurements were then combined within a GIS program to allow visualisation and analysis of the target sites.

During the BIOPTIS campaign three sampling grids were established across three transitional areas of the estuary (Figure 2.16). Situated on the muddy-sandy Kincaple flats of the inner Eden estuary, Grid A (900m x 500m) consisted of 52 grid nodes, spaced 100m apart, running from the top shore down to the channel of the river Eden. The grid is dominated by a large *Enteromorpha* bed that is located in the mid to low shore region of the grid. Situated further upstream, on a muddy tidal flat at the mouth of the River Eden, Grid B (800m x 500m) consisted of 46 grid nodes spaced 100m apart, with the channel of the river Eden running through a portion of the grid, running east to west. Finally Grid C (200m x 300x) consisted of 12 grid nodes spaced 100m apart, situated on the exposed sandy region known as West Sands at the mouth of the estuary. Using these grids as a template, in 2015, ground based measures were collected along a single vertical transect of the original BIOPTIS sampling grids. Transects were chosen objectively based on the collective stations having high numbers of invertebrate individuals and chlorophyll *a* measures (e.g. Figure 2.17) to increase the statistical reliability of subsequent comparisons.

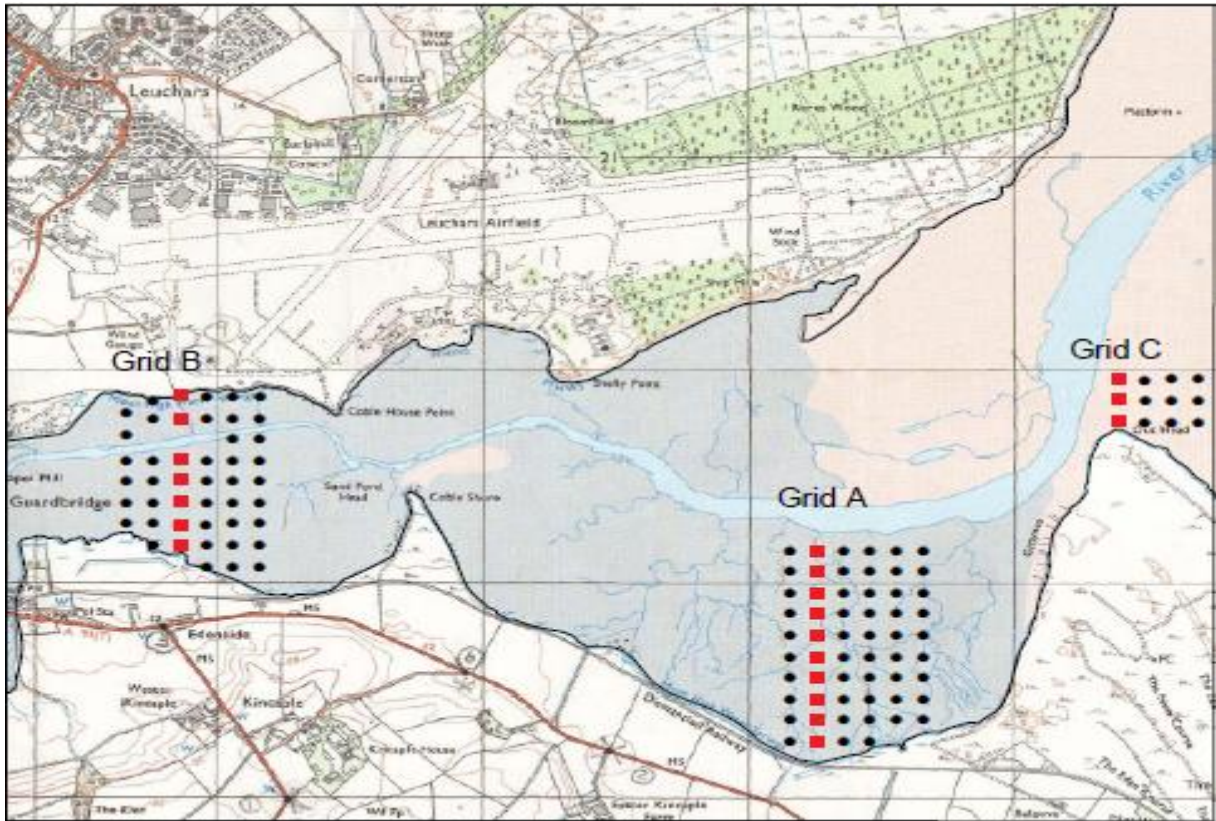


Figure 2.8 BIOPTIS sampling stations showing Grid A, Grid B, Grid C. Black circles represent the 1999 sampling stations, while the red squares represent the stations sampled during the 2015 campaign.

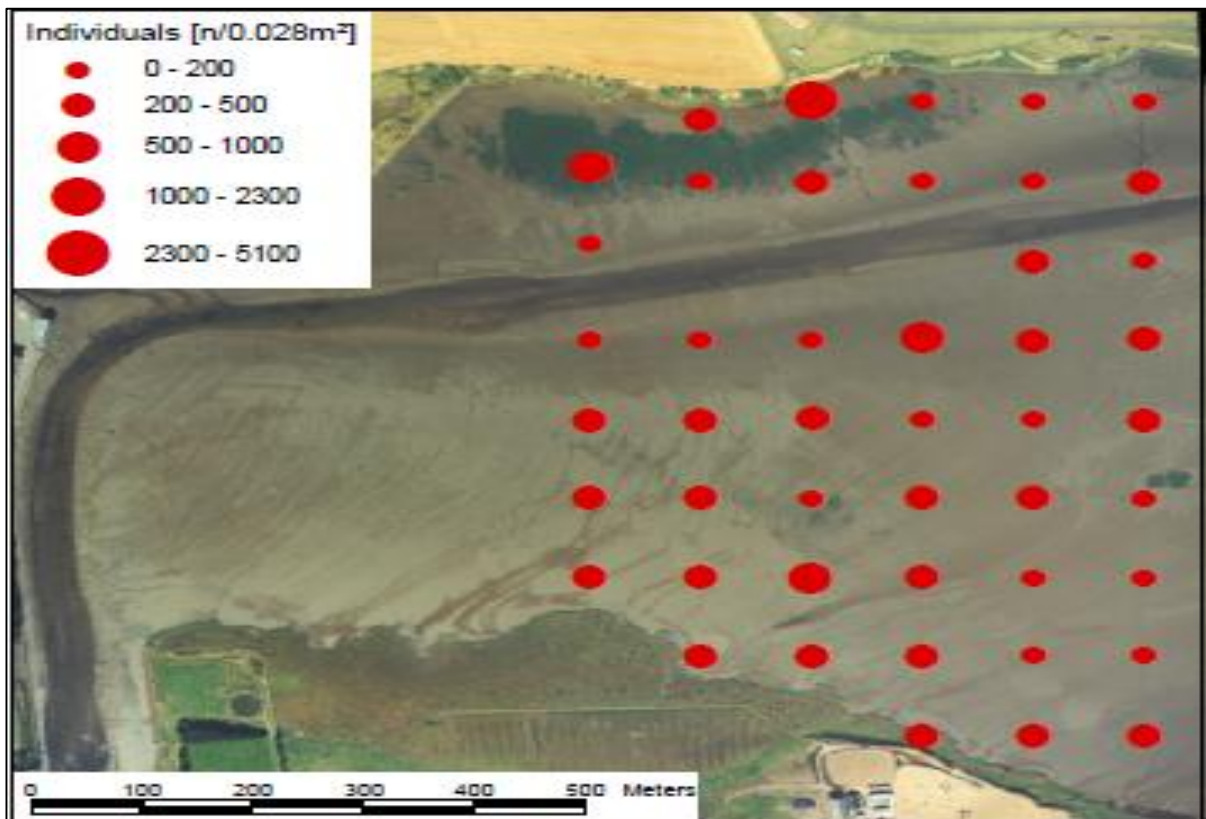


Figure 2.9 GIS representation of Macro-fauna (Total Individuals) collected during the BIOPTIS campaign at Eden Grid B

2.5.1. Eden physicochemical data collection

Few historical records exist that record the physiochemical nature of the Eden estuary as a whole and hence it is difficult to assess accurately any long term changes or trends within the selected time periods. However a small number of data sources were identified that could be used to provide a general indication of change between the late 1990's and the 2010-2015 period.

With regards to salinity, two comparative studies undertaken at Guardbridge in September 1990 (Loutit, 1991) and 2010 (Chocholek, 2013) where recorded over different tidal cycles and these were used to provide an indirect but potentially sensitive indication of detecting changes in precipitation, evaporation and/ or river runoff (see summary table 2.8).

Table 2.8: Summary of selected environmental variables for the Eden Estuary as a whole (1990-2015).

Variable	Year	Source
Temperature (°C)	1990 -2014	Scottish Environment Protection Agency (SEPA)
pH	1990-2014	Scottish Environment Protection Agency (SEPA)
Surface salinity (psu)	1990 vs 2010	Loutit, (1991),Chocholek, (2013)
Dissolved oxygen (mg l ⁻¹)	1990-2014	Scottish Environment Protection Agency (SEPA)
Ammonium (mg l ⁻¹)	1990-2014	Scottish Environment Protection Agency (SEPA)
Nitrite (mg l ⁻¹)	1990-2014	Scottish Environment Protection Agency (SEPA)
Nitrate (mg l ⁻¹)	1990-2014	Scottish Environment Protection Agency (SEPA)
Filterable reactive phosphorus (mg/L)	1990-2014	Scottish Environment Protection Agency (SEPA)
River flow (m ³ /s)	1990-2015	The National River Flow Archive (NRFA)
North Atlantic Oscillation index	1990-2015	Hurrell, (1995)* updated <i>via</i> the associated website
Depth (m)	2002-2009	Chocholek, (2013)
Granulometry (mm)	1999 vs 2010	BIOPTIS ,Chocholek, (2013)

Surface water quality data in the form of monthly ammonium, nitrite, nitrate, phosphate and dissolved oxygen (all mg l⁻¹) concentration data was provided by the Scottish Environment Protection Agency (SEPA) from the main gauging station (Kemback) located on the River Eden (SEPA Location code 8157), for the 1990-2014 period. Additional information regarding pH and temperature changes during the study period were also inferred from the same dataset.

Data for river flow entering the catchment was acquired from the National Rivers Archives website (www.nerc-wallingford.ac.uk/ih/nrfa/index.htm) for the River Eden also from the Kembeck station gauging station (NO415158) for the 1980-2015 period (Figure 2.18). As with the Tamar, the most recent (1864-2015) copy of the North Atlantic Oscillation (NAO) winter index (December–March) illustrated in Figure 2.15 was extracted from Hurrell (1995, updated on Hurrell’s website) to compare inter-annual surface sea-level pressure across estuary.

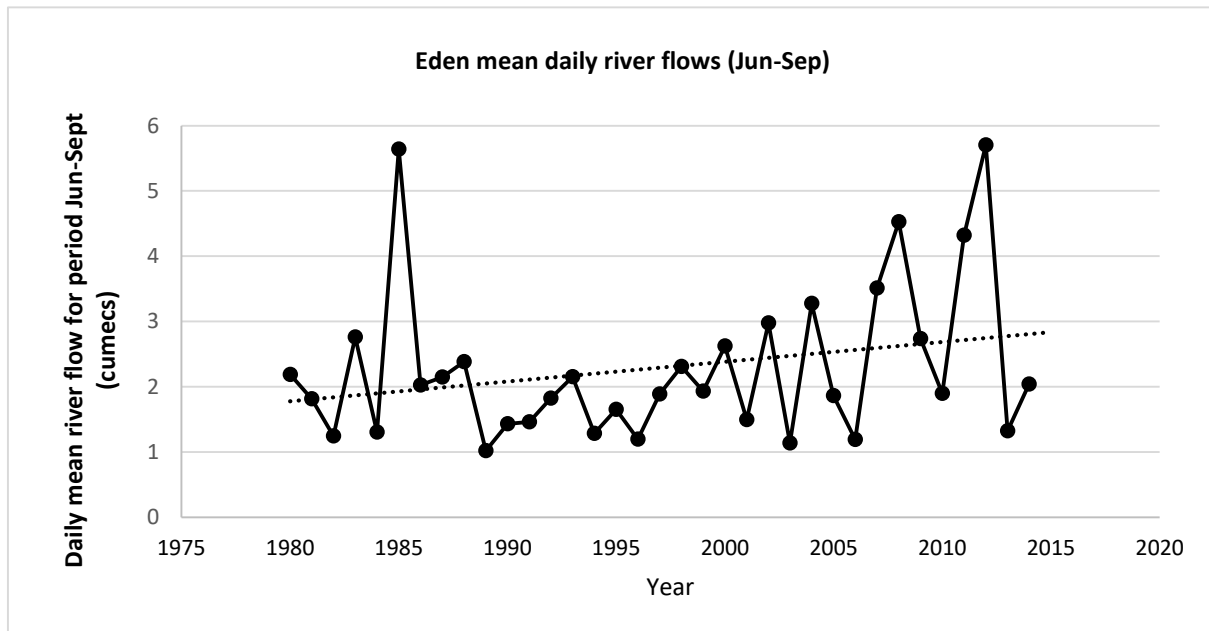


Figure 2.10 Annual mean daily river flows (summer; June-Sept) for the river Eden. (1980-2015 period)

Although particle size analysis was not carried out during the 2015 sampling campaign, a detailed study by Chocholek (2013) in 2010 on a similar sub-set of the BIOPTIS data used in this study was used to infer changes in sediment granulometry. During the same study, bathymetry profiles were undertaken on the main channel of the estuary (between the 2002-2009 periods), and were used to infer relative changes in depth and sediment dynamics of the estuary.

2.5.2 Eden benthic primary producer data collection

During the BIOPTIS and 2015 sampling campaign, contact cores (Honeywill *et al.*, 2002) were used to estimate mitophytobenthic biomass ($\text{chl } a \text{ mg m}^{-2}$). At each station five replicate cores were taken (diameter 56 mm, depth 2-3mm), by being frozen in liquid nitrogen and stored in foil at -80°C . Upon removal the frozen sediments were first freeze dried and homogenised, then exposed to acetone for 48 hours to extract algal pigments. Chlorophyll determinations were then made spectrophotometrically using a Cecil 3000 scanning spectrophotometer, at the following wavelengths: 662 Chlorophyll *a*: 647 Chlorophyll *b*: 750 turbidity correction. Chlorophyll *a* ($\mu\text{g g}^{-1}$) was then determined using the following equation (as in HIMOM, 2003):

$$\text{Chlorophyll concentration (mg l}^{-1}\text{)} = \frac{[A662] - [A750]}{E} \times 1000$$

Equation 2.1

2.5.3 Eden macro-benthic invertebrate data collection

During the BIOTIS sampling campaign, a single replicate macro-fauna sample was taken at each of the selected stations using an 18cm \emptyset stovepipe core. Respectively, during the 2015 sampling campaign 3 replicate, 9cm \emptyset cores were taken at each site, before being averaged and standardised to the BIOPTIS protocols. To standardise the number of replicates between the studies, the single BIOPTIS cores were compared to adjacent transects. All samples were taken within 5m either side of the sampling location from undisturbed sediment, to a constant depth (15cm) with the location of each sample point determined during the 2015 campaign using a Garmin eTrex hand held GPS device. The depth of the cores was based on, a small-scale depth study undertaken concurrently with the original BIOPTIS macro-faunal sampling, with the results suggesting that the vast majority of organisms (>95%) were located in the upper 15cm across all sampling sites. Exceptions to this rule included deep burrowing organisms such as *Arenicola marina*, *Mya arenaria* and in some cases *Corophium volutator* (perhaps as an anti-predator response; MacDonald *et al.*, 2014) all of which were recorded at depths of over 20cm. Once the samples were taken, they were put into separate pre-labelled bags, with the site code, replicate number and date. Any residue on the outside of the core was removed before the sample was placed in its container.

Samples were then returned to the laboratory and gently sieved through a 1mm-grade mesh sieve within 24 hours of sampling and immediately fixed with a 10% buffered formalin solution stained with 1% Rose-Bengal. Prior to sorting, samples were then washed through a 0.355mm sieve with seawater to remove any residual formaldehyde solution with samples stored in 70% industrialised methylated spirit (IMS).

Sub-samples of each replicate were then sorted systematically by eye in concentric rings using a binocular microscope, forceps and a fine pipette to extract specimens. All extracted material was stored in pre-labelled containers with 70% IMS and a third of sample residues were re-checked to increase the validity of the results. Macro-fauna were identified to species level where possible, with all fauna in tubes extracted for identification. Although no living *Arenicola marina* were collected, their presence at Grid C was apparent by numerous coiled castings and therefore this species was enumerated by an alternative method. Cast counts from each replicate were averaged, normalised to core size and used to estimate the average number of active *Arenicola marina sensu* Ford & Honeywill (2002). In the case of oligochaetes, samples were initially classed as oligochaetes but closer investigation of the sub-samples identified the majority of species to belong to the *Tubificodes* family.

Chapter 3 Review and evaluation of estuarine biotic indices to assess benthic structure and functioning under the influence of differing nutrient regimes in two UK estuaries.

Chapter Summary

Following different legislative mandates to assess the status of marine ecosystems (e.g. the European Marine Strategy Framework Directive, MSFD, 2008/56/EU and Water Framework Directive WFD, 2000/60/EC), benthic monitoring programmes tend to collect basic data on species abundance/biomass patterns over spatial and temporal scales (Rice *et al.*, 2010). However despite a wealth of methods currently proposed to assess benthic health (see Van Hoey *et al.*, 2012; Rice *et al.*, 2012), determining environmental status and assessing coastal and marine ecosystems health in an integrative way is still one of the biggest challenges in marine ecology research and management (Borja, 2014).

The purpose of Chapter 3 therefore was to test a number of commonly used benthic indicators used in UK research and monitoring programmes for their effectiveness to detect changes in biodiversity-functioning responses following restorative management efforts aimed at reducing the impacts of nutrient enrichment. As the Tamar (England, UK) and Eden (Scotland, UK) estuaries have been under severe environmental pressures in the past, temporal trends in water quality and in the inter-tidal benthic community over a 68-year interval (Tamar) and 16-year interval (Eden) were investigated with the aim of assessing changes in environmental quality and ecological status in response to nutrient related stress and subsequent restoration efforts. Data on inter-tidal macro-benthic communities and environmental variables, covering a (historic 1937), high nutrient (1990-1991), pre-management (1992) and post management period (2005) were used to assess restoration effectiveness of the Tamar, while a pre –management (1999) and post-management (2015) period was used respectively in the case of the Eden. Firstly, temporal differences in the structure and composition of the macro-benthic assemblages between periods were assessed. Secondly, the relative performance of different ecological indicators (Shannon–Wiener, Margalef, Pielou, Simpson, AMBI, IQI, taxonomic distinctness and diversity) to capture potential ecological changes between periods was analysed. Lastly, to assess the relative link between biodiversity and the environmental functioning and the processing of organic material (e.g. carbon and nutrients) under the impact of changing nutrient regimes, two functional indicators Biological Traits Analysis (BTA; Bremnar *et al.*, 2006) and Community Bioturbation Potential (Bpc) (Queirós *et al.*, 2013) were assessed. Indicator testing was implemented using a nested hierarchical approach (Jorgensen & Fath, 2014) whereby predefined subsystems (or zones) of each estuary were assessed before being combined together to form larger systems. In this way the

examination of the relationship between biodiversity and ecosystem service flows across coastal margins can be better addressed (EPBR, 2011), with different measurement scales providing complementary information about each system. Following implementation, each indicators' performance was compared with the information given by the analysis of macro-fauna composition and structure to distinguish their usefulness for addressing specific management objectives.

3.1 Introduction

Understanding how changes in biodiversity can lead to changes in the functioning of ecosystems is a critical step for tracing the consequences of human activities through to the impacts on ecosystem services (Crowe, 2015; Strong *et al.*, 2015). As defined and described in Chapter 1, there is a general consensus that marine biodiversity and ecosystem function (BEF) relationships do exist, and that positive and negative consequences of biodiversity have been observed on several marine ecosystem functions (Emmerson *et al.*, 2001; Worm *et al.*, 2006; Cardinale *et al.*, 2012; Harrison *et al.*, 2014). However, given that it may never be possible (or practical) to study all marine ecosystems individually to sufficiently predict the consequences of biodiversity loss on ecosystem function(s), environmental decision makers need cost-effective indicators of how multiple local pressures, combined with climate change are affecting ecosystems and their delivery of ecosystem services (Arkema *et al.*, 2015; Hyder *et al.*, 2015).

This need to ensure the future sustainable functioning of the marine environment and evaluate BEF relationships succinctly is increasingly being recognised in many marine policy obligations, either explicitly (e.g. the European Marine Strategy Framework Directive, MSFD, 2008/56/EU), or indirectly by addressing structural aspects which can be related to functioning (e.g. Water Framework Directive WFD, 2000/60/EC, and Habitats Directive, 1992/43/EEC). Furthermore, these policies have to fit within the current philosophy of the Ecosystem Approach requiring the development and use of Ecological Quality Objectives and Standards. While the MSFD is closely linked to the WFD and Habitats Directive only the latter two are relevant to transitional systems such as estuaries. The WFD for example ties in with the goal of Good Environmental Status under the MSFD, by setting a goal of achieving Good Status for all EU surface and groundwaters by 2015 (or failing that 2021). 'Good status' means both 'good ecological status' and 'good chemical status', implying a different emphasis between these two major pieces of legislation (see Borja *et al.* (2010) for differences between both concepts). Regardless of such differences both the MSFD and WFD directives now include descriptors that relate to the structure and functioning of ecosystems which if upheld would allow ecosystems to maintain their resilience to human induced environmental change and, although not explicitly mentioned, would allow associated ecosystem services and benefits to be delivered.

Many of the aforementioned directives particularly acknowledge benthic invertebrate assemblages as useful indicators of environmental status in the marine coastal environments since they have limited mobility, closely reflect local environmental conditions and contribute strongly to the maintenance of regulatory ecological processes. This importance is exemplified in several management objectives including descriptor 6 of the MSFD framework, which identifies that the structure and functions of benthic ecosystems should be safeguarded and also by the WFD, where various multi-metrics containing several indicators have been developed to give a measure of the ecological state of the benthic ecosystem in coastal and transitional waters as a reaction to human pressures.

As evaluating existing indicators for soft-bottom habitats can be considered highly useful in the implementation of supporting existing and new legislation (Diaz *et al.*, 2004; Veríssimo *et al.*, 2012b), the first objective of this chapter was to test the effectiveness of several commonly used structural benthic indicators (e.g. species abundance/biomass) currently being used within UK WFD monitoring schemes, under the impact of changing nutrient conditions. This was followed by a second objective to investigate two more novel functional diversity indicators primarily involved with the maintenance of benthic supporting and regulatory ecosystem services that could potentially be used in benthic monitoring programmes to evaluate BEF relationships. A synopsis of the indicators chosen along with their applicability to be used to evaluate ecosystem status and BEF relationships is given below.

3.1.2 Structural indicators of biological compositions of ecosystems

To date, most practical marine monitoring programmes have focused on structurally-based biodiversity assessments (i.e. taxonomically based classification of organisms) as opposed to functional aspects (i.e. ecological and evolutionary processes, including gene flow, disturbances and nutrient cycling). This is because structural indicators such as species richness and species diversity are well established, cost-effective to measure and have proven effective as surrogate indicators of ecosystem condition (Strong *et al.*, 2015). In this chapter, structural indicators are assigned to five separate categories and are used to summarise and communicate broad trends about the health of the species, populations, communities and habitats of the each ecosystem.

3.1.2.1 Abundance, size and age indicators

At the most basic level, species-level effects can influence ecosystem functioning by the number of individuals present (i.e. species abundance), where large assemblages of individuals can act to underpin the stability of ecosystems under change from environmental conditions (Doak *et al.*, 1998; Henderson & Magurran, 2014). This form of stability can be variable however, depending on the size (biomass) or age structure (maturity) of a population, with an abundance of smaller individuals may indicate a more pressured system (Warwick, 1986; 1994). Overall density (i.e. number of individuals

per unit area), for example, has been shown to be particularly sensitive to many natural and anthropogenic pressures, such as seasonal temperatures, eutrophication and dredging (Dekker, 1989; Bergman & Hup, 1992; Gilkinson *et al.*, 1998; Snickars *et al.*, 2015).

While abundance, body size and age class indicators provide a useful starting point for environmental monitoring assessments, size and age class distributions of populations are not always measured as part of standard environmental monitoring programmes. Another major disadvantage of these indicators is that they are very dependent on the sample size in question (Clarke & Warwick, 2001). To overcome this, species abundance information is often used to commutate more complex indicators.

3.1.2.2 Diversity indicators

As natural communities are made up of numerous taxa living together, the presence of multiple species in a system can also enhance its stability because different species respond to environmental change in different ways or at different scales such that the aggregate components of a system are maintained (Rosenzweig, 1995). In practice this works because many species within systems perform similar ecological functions. This overlap between species provides a level of functional redundancy within the community as a whole meaning that the loss of a single species does not necessarily mean a loss of ecosystem function (Naeem, 1998; Walker, 1992). As a result, in environmental monitoring assessments, high diversity indicators are often used as a proxy of good ecological or environmental status with communities with high levels of diversity assumed to have higher levels of redundancy and thus a greater capacity to lose species and still maintain ecosystem functions (Loreau *et al.*, 2003). Typically species diversity (or heterogeneity *sensu*, Peet, 1974) indicators are univariate in nature and are often grouped into two main categories: species richness and species evenness.

Species richness (S) is the most basic of the diversity indicators, most often measured as: the number of species per sample counted using a standardised sampling area, allowing values of richness that can be compared in a meaningful way (Stirling & Wilsey, 2001). Thanks to this intuitive approach and ease of calculation (only presence absence data are required), S has become a fundamental stability indicator that has been used in almost all studies on the effects of disturbance and benthic quality. Building on the concept of species as a viable component of biodiversity, a number of other indices such as the Shannon Wiener (H'), Simpson's dominance (D_s), Margalef's species richness (D_m), and Pielou's evenness (J) attempt to combine species richness and evenness (i.e. the relative abundance of the different species making up the richness of an area) into a single index. These indicators differ in the degree to which they emphasize richness versus evenness (Magurran, 2004) but all incorporate

them to some degree. By doing so, these indicators have been found to respond more rapidly to human disturbance than species richness measures (Hillebrand *et al.*, 2008).

Although species richness and evenness indicators are often correlated with ecosystem function (Cardinale *et al.*, 2002) and tend to decline at high levels of disturbance (Johnston & Roberts, 2009), there are a number of factors that interfere with their performance. Firstly, under certain circumstances many diversity indicators may be relatively insensitive to disturbance, often showing little change despite considerable human influence (Lu, 2003; Johnston & Keough, 2005) particularly in naturally stressful environments such as estuaries where many species have adapted to harsh conditions. A second disadvantage of some diversity indices is that rare species contribute as much to these indicators as common species (Grassle & Smith, 1976) and hence the evenness or the density distribution of a sample is not always taken into account. Despite these shortcomings, several studies have found that analyses of diversity indicators using multivariate analyses to be more sensitive and powerful means of detecting ecological impacts than studies which consider diversity indicators alone (Warwick & Clarke, 1991; Schratzberger *et al.*, 2000; Magurran, 2004 Gong *et al.*, 2005). Therefore, despite decades of cautions against the use of these metrics (e.g. Hulbert, 1971 or Gray *et al.*, 1990), they remain a cornerstone of almost all environmental monitoring assessments.

3.1.2.3 Phylogenetic indicators

An alternative approach to address some of the problems identified with species richness and other diversity indicators is to consider the phylogenetic diversity or taxonomic distinctness of an assemblage, which captures the evolutionary histories or relatedness of different species. Although these indices are not regularly used in environmental monitoring assessments, a small number of these indices have now been successfully applied in the marine context (Warwick & Clarke, 1995; Clarke & Warwick, 2001; Tweedley *et al.*, 2015) and have proven to be relatively insensitive to natural changes in environmental conditions, but are sensitive to anthropogenic disturbance (Leonard *et al.*, 2006). This makes them useful baseline tools to investigate anthropogenic change over a broad range of historical and environmental contexts including comparing data sets from different studies (e.g. Goodsell *et al.*, 2009).

3.1.2.4 Sensitive/opportunistic species indicators

Sensitive/opportunistic species indicators are an essential part of environmental monitoring assessments for all areas of the marine environment, because a major aspect of environmental policy is to decrease the amount of human pressures and restoring “good conditions” by promoting GES. One of the most widely used and cited tools in this regard is the AZTI Marine Biotic Index (AMBI e.g. Borja *et al.*, 2009; Warwick *et al.*, 2010), which was designed to assess the environmental quality of

European coastal waters by classifying the resident benthic macro-invertebrate species into five ecological groups on the basis of their known sensitivity to environmental stress (Borja *et al.*, 2000; 2003). Many previous studies have highlighted the ability of AMBI to discriminate between pressures, both anthropogenic and natural in origin, either alone or in combination with other metrics, such as species richness and Shannon–Wiener diversity (e.g. Blanchet *et al.*, 2008; Borja *et al.*, 2004; 2007).

3.1.2.5 Composite metrics

While individual structural indicators clearly have particular benefits, single indicators used in isolation typically calculate only one measurable characteristic of an assemblage. As such there has been a recent tendency to move from single metric to multi-metric assessments, as a combination of metrics enables reference and degraded samples to be distinguished more effectively than one metric alone (Gibson *et al.*, 2000; Borja *et al.*, 2011).

These multi-metric indicators are commonly based on quantitative calculations based on other structural indicators such as species composition (e.g. abundance, biomass), diversity (e.g. H, Ds) and species sensitivity data (e.g. AMBI), with the aim to produce an Ecological Quality Ratio (EQR) expressed as a decimal value between zero and one, with ‘high’ status represented by values close to one and ‘bad’ status by values close to zero. The most common of these metrics is a Multivariate version of AZTI Marine Biotic Index (M-AMBI), where EQR is based on the proportions of sensitive and stress tolerant benthic invertebrate species (AMBI), number of species (S) and Shannon–Wiener diversity (H).

Another less well cited, but commonly used WFD compliant metric is the Infaunal Quality Index (IQI Phillips *et al.*, 2012). Developed by the WFD the IQI classifies the ecological health of a benthic invertebrate assemblage according to the extent to which chosen measures of ecological health have departed from their expected state under levels of anthropogenic disturbance. The multi-metric is composed of three individual components AMBI, Simpson’s Evenness ($1-\lambda'$), and number of species (S) and unlike M-AMBI, requires appropriate environmental reference conditions to be defined according to the specific habitat associated with each biological sample, rather than at an ecosystem level. In practice this allows suitable reference conditions based on physiochemical conditions and sampling methodologies to be derived (Connor *et al.*, 2004) and *a priori* tailored to the heterogeneous conditions associated with transitional ecosystems.

To date both MAMBI and IQI have been shown to detect the impact of various pressures on benthic invertebrates including those relating to; hazardous substances (Phillips *et al.*, 2012), organic enrichment (Fitch & Crowe., 2010) and general disturbance (Kennedy *et al.*, 2011).

3.1.3 Functional indicators

When considered in more detail, the attributes of species, or their “traits” have the potential to form a much more effective basis for predicting an ecosystems response to stressors, than simply the number of individuals or identities of species (Crowe & Russel, 2009). The main difference between trait diversity and taxonomic or phylogenetic based diversity is that trait diversity emphasises phenotypic differences among taxa while discounting phylogenetic differences (Weiher, 2011). As such, species data can be converted to trait data which may be more informative in terms of the functional capacity of the system because it ignores regional taxonomic differences, centring on what species do rather than their identities (Naeem & Wright, 2003; Hooper *et al.*, 2005; Petchey & Gaston, 2006). Functional traits are described as being observable or operationally defined phenotypic characteristics that influence species performance or ecosystem processes (Poff *et al.*, 2006) including aspects of demography, feeding strategies or morphology (Steneck & Dethier, 1994). As such, trait diversity is synonymous with functional diversity and is defined as the degree to which coexisting species vary in terms of their functional traits (Weiher, 2011).

One critical reason that functional diversity might link organisms and ecosystems is that it implicitly contains information about how species will compensate for the loss of another when multiple species exhibit similar traits. This functional redundancy or ‘biological insurance’ effect (Naeem & Li, 1997; Yachi & Loreau, 1999), is a well-supported phenomenon, both theoretically (Folke *et al.*, 2004) and empirically (Loreau & Mazancourt, 2013; Downing *et al.*, 2014) and stipulates that the resistance of ecosystem functions to stressors will be greater in assemblages that have differing responses to environmental perturbations (Mouillot *et al.*, 2013; 2014) as long as organisms with the same traits also don’t have the same sensitivities to a specific stressor.

Analogously to structural indicators, an ever increasing number of functional diversity indicators are now being developed that attempt to link traits to ecosystem functioning in the marine environment (Petchey *et al.*, 2009). Once such group of metrics that has proven useful when trying to categorise and understand ecosystem function conducted by benthic communities, are bioturbation potential related indices (e.g. Solan *et al.*, 2004). At ecosystem scales, the use of these indices are one of the only a few readily available options to investigate the contributions of individuals (Bpi), populations (Bpc) or entire communities (Bpc) to key biogenic processes such as carbon and nutrient cycling (Queirós *et al.*, 2015). At these scales however challenges remain in understanding both the underlying mechanics in community bioturbation and how the response of macro-fauna to environmental stimuli might impact on bioturbation (Queirós *et al.*, 2013). Furthermore although

useful, these methodologies give a reductionist view of functioning given that they focus in only one or a small number of functional traits (Verissimo *et al.*, 2012a).

An alternative framework to describe functional diversity that takes a more multidimensional approach is the multi-trait approach, Biological Traits Analysis (BTA). Having now been translated for use in the marine environment (Bremner *et al.*, 2003; 2006b) BTA has proven to be a flexible approach, by allowing the potential to select specific traits that underpin particular ecosystem functions (effect traits) and those that determine a species response to environmental change (response traits). In doing so, it allows the prediction of specific consequences of community changes on ecosystem functioning (and indeed services) but also a method to inform conservation and management towards specific objectives (Bremner *et al.*, 2006a; Bremner, 2008). The approach has also proven to be more stable than taxonomic composition, by accounting for species that may not have impacts on functioning by using a specialised “fuzzy coding” scheme (Chevenet *et al.*, 1994) allowing an improved comparability among regions with different species.

One concern raised about the application of trait-based approaches however, is that the process of selecting traits is often arbitrary and influential. For instance, if decisions on trait inclusion are subjective, then the investigator can have undue influence on the outcome. Another limitation of this method is that trait information is not readily available for a large number of species or for certain traits (Tyler *et al.*, 2012) although there have been valuable initiatives made in this direction for marine systems (e.g. Marlin’s BIOTIC database www.marlin.ac.uk/biotic). A particular knowledge gap is therefore is how to select traits repeatedly for inclusion, taking account of the availability of trait information.

3.1.4 Study aim and hypothesis

This chapter aims to assess the effectiveness and value of the previously mentioned structural and functional indicators on two contrasting case study areas: the Tamar and Eden Estuaries. In both instances, the ability of indicators to assess benthic ecological change following management interventions (primarily causing a reduction of nutrients into the catchments) was determined for the periods: Tamar (1992-2005) and Eden (1999-2015). In particular, I searched for differences in ecological condition covering two periods (pre- and post-management). Additionally for the Tamar, structural and functional indices were compared during a known eutrophic period (1990), with those of the following year (1991) and a historic reference period (1937). Formal hypothesis tested were as follows:

H1 Faunal composition and/or structural indicators of each case study will differ significantly following nutrient remediation actions.

H2 Faunal composition and/or structural indicators of each case study will differ spatially (i.e. between upper, central and lower zones).

H3 Functional indicators of each case study will differ spatially (i.e. between upper, central and lower zones).

H4 The relative ecological functioning linked to the provisioning of the ecosystem services carbon sequestration and waste remediation will improve following nutrient remediation actions.

3.2 Materials and methods

The sample sites and collection methods used in the acquisition of macro-benthic data from the Tamar and Eden estuaries are described in Chapter 2, Section 2.4 & 2.4.2 (Tamar) – 2.5 & 2.5.3 (Eden). Prior to statistical analysis, macro-fauna data were segregated into three separate zones (upper, central and lower estuary) based on case study specific variations (see Chapter 2, sections 2.4.2 (Tamar) & 2.5 (Eden) for a more detailed description of the zones). In addition to zones, replicates and stations were also pooled from all three zones to look at the estuaries as a whole.

3.2.1 Sampling and analytical procedures

All macro-fauna samples collected from the sites were identified to the lowest possible taxonomic level, which was usually species (>90% of individuals). In addition to classifying the fauna into species, classification individuals were assigned to major taxonomic groups for a general assessment. These groups were Polychaetes, Crustaceans, Molluscs, and Oligochaetes; while individuals from a number of other small groups including Echinoderms, Holothurians, Nemertean, Cnidarians, Bryozoans and Sipunculids were classified as 'Others'. Prior to calculations, both macro-fauna abundance and biomass data were standardised to ind.m⁻² and g AFDWm⁻² respectively. Where necessary wet weight biomass was converted to AFDM using published conversion factors in Brey's (2001) Virtual Handbook on Population Dynamics, version 4 (Brey.,2012, (www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.htm)) and calculated using case study specific relationships (e.g. for the Tamar: Dashfield & McNeill; 2014 & Biles *et al.*, 2002 for the Eden).

In association with the macro-benthic sampling, complementary environmental parameters were collected to represent average water quality during the sampling years (see Chapter 2 section 2.4.1 (Tamar) & 2.5.1 (Eden) for details of collection and calculation). These included temperature (°C), pH (log scale), dissolved oxygen (mg l⁻¹), salinity (SS, psu), biochemical oxygen demand (BOD, mg l⁻¹), ammonium (mg l⁻¹), nitrite (mg l⁻¹), nitrate (mg l⁻¹), filterable reactive phosphorus (FRP, µg l⁻¹), chlorophyll *a* (mg l⁻¹), sediment grain size (mm), water depth (m), river-flow (m³/s⁻¹), tidal streams (knots), site exposure and surface sea-level pressure (NAO index).

3.3 Statistical analysis

3.3.1 Structural indicators: description and computation.

Three basic proxies for the macro-benthic community structure were initially considered and quantified. These were the total density (no. m²), biomass (g m²) and species richness (S) in each macro-invertebrate assemblage. As sample area was initially different prior to the pre-treatment of samples, species richness was estimated using the rarefaction methods proposed by Sanders (1968) and Hulbert (1971), which under the strict assumption that individuals arrive in the sample independently can be used to project back from the counts of total species (S) and individuals (N), how many species would have been “expected” had the observations come from a smaller number of individuals. It should be noted however that while the data were manipulated to standardise them as far as was possible, it was accepted that no post hoc mathematical manipulations could adequately compensate for differences in sampling methodology. As species naturally exhibit some form of spatial clustering (Clarke & Warwick, 1994), the species estimates here are likely to represent an overestimation of the expected number of species present. Despite the associated caveats, the diversity and overall health of each system were then assessed by reducing the multi-species complexity of assemblage data into a small number of indices (see Table 3.1 for details).

Besides estimated species richness (S), the univariate diversity indices used in this study were the Shannon Wiener (H), Simpson’s Dominance (Ds), Margalef’s Species Richness (Dm), and Pielou’s Evenness (J) indices all calculated from the benthic density matrix using the DIVERSE routine in the PRIMER (Plymouth Routines in Multivariate Analysis of Variance) package version 7 (Clarke *et al.*, 2014a).

Using the same PRIMER package a number of phylogenetic indices first proposed by Warwick & Clarke (1995) were also estimated using a hierarchical Linnean classification system with the average taxonomic diversity (Δ), average taxonomic distinctness (AvTD) and total taxonomic distinctness (TTD) indices used as a proxy for the relatedness between individuals within an assemblage. This information was arranged in a species-by-sample matrix with a corresponding taxonomic aggregation data file provided across five taxonomic levels (species, genus, family, order and class) to aid calculation. Specifically Δ was used to represent the average taxonomic distance between every pair of individuals in the sample (Clarke & Warwick, 1999) while AvTD and TTD were used to represent the taxonomic breadth between pairs of species with a sample (Clarke & Warwick., 2001). The latter two indices were calculated based on presence/absence data, leaving measures closer to a pure reflection of taxonomic hierarchy, removing the bias of sampling effort and variation within the samples.

To determine benthic habitat quality or Ecological Status (ES) *sensu* the WFD, outputs of two multi-metric indices: Multivariate AMBI (M-AMBI) and the Infaunal Quality Index (IQI) were calculated. As a prerequisite to both indices AZTI'S Marine Biotic Index (AMBI) was first calculated using the AMBI 5.0 software tool available from AZTI'S webpage (<http://www.azti.es>). Under the recommendations outlined by the authors (Borja & Muxika, 2012). M-AMBI was then used to ordinate samples based on the values of: number of species AMBI, and Shannon-Wiener diversity, followed by Factor Analysis to determine the distance of the sample from virtual "High" and "Bad" reference stations reported as a Benthic Ecological Quality Ratio (EQR). Secondly the UK and Irish Infaunal Quality Index (IQI) version 4 was also used to calculate an EQR using a proprietary tool in Microsoft Excel developed by the UK Environment Agency (Phillips *et al.*, 2012). The biological metrics incorporated into the IQI are; number of species, AMBI and Simpson's diversity. In both cases the EQR scale is divided into five ES classes (i.e. High, Good, Moderate, Poor, and Bad) by assigning a numerical value to each of the class boundaries allowing an EQR to be assigned to samples (Muxika *et al.*, 2007).

The relative performance of each indicator to detect ecological changes between each time period was assessed based on the classification proposed by the indicator developers (Table 3.1) and later by multivariate analysis (section 3.2.4.2). For instance, high values for Margalef, Shannon–Wiener, Pielou and taxonomically based indicators, are indicative of a high ecological status, while high values for MAMBI, IQI and Simpson's index suggest low ecological status.

Table 3.1 Structural indicators: algorithms and ecological classification

Structural indicators	Algorithm	Classification	Classification boundaries
Species Richness (S)	S is the total number of species in the dataset*calculated by rarefaction	Higher value, higher biodiversity	
Shannon–Wiener Index (H) (Shannon & Weaver, 1963)	$H = \sum p_i \log_2 p_i$ p_i : proportion of abundance of species i in a community where species proportions are $p_1, p_2, p_3, \dots, p_n$	Low diversity	0
		High diversity	≥5
Simpson Index (Ds) (Simpson, 1949)	$D = \sum p_i^2$ p_i is the proportion of individuals from species i in the community	Low diversity	1
		High diversity	0
Margalef Index (Dm) (Margalef, 1969)	$D = \frac{s-1}{\log eN}$ S: number of species found; N: total number of individuals	Low diversity	Low value
Pielou Evenness Index (J) (Pielou, 1969)	$J = \frac{H}{H_{max}} = \frac{H}{\log S}$ max: maximum possible value of the Shannon diversity	Low diversity	0
		High diversity	1
Average taxonomic diversity (Δ) (Warwick & Clarke, 1995)	$\Delta = \frac{\sum \sum_{i<j} \omega_{ij} x_i x_j}{n(n-1)/2}$ x_i abundance of the i th of the s species observed.	Higher value, higher biodiversity – on average species in the assemblage are not closely (phylogenetic) related	
Average taxonomic distinctness (AvTD) (Warwick & Clarke, 1995)	$\Delta^* = \frac{\sum \sum_{i<j} \omega_{ij} x_i x_j}{\sum \sum_{i<j} \omega_{ij} x_i x_j} n(\sum_i x_i^2)$ total numbers of individuals in the sample;		
Total taxonomic distinctness (TTD) (Warwick & Clarke, 1995)	$s\Delta^* \sum_i \left[\frac{\sum_{i \neq j} \omega_{ij}}{s-1} \right] \omega_{ij}$ “Distinctness weight” given to the path length linking species i and j in the taxonomy		
AZTI’s Marine Biotic Index (AMBI) 5.0. (Borja et al., 2000)	$AMBI = \frac{(0x\%GI) + (1.5x\%GII) + (3x\%GIII) + (4.3x\%GIV) + (6x\%GV)}{100}$ G I: species very sensitive to organic enrichment and present under unpolluted conditions. G II: species indifferent to enrichment, always present in low densities with non-significant variations with time. G III: species tolerant to excess organic matter enrichment. These species may occur under normal conditions; however, their populations are stimulated by organic enrichment. G IV: second-order opportunistic species, adapted to slight to pronounced unbalanced conditions. G V: first-order opportunistic species, adapted to pronounced unbalanced situations	Ecological Status (EQS)	0.0-1.2 1.3-3.3 3.4-4.3 4.4-5.5 5.6-7.0
Multivariate AMBI (MABI) Muxika et al. (2007)	M-AMBI is calculated by factor analysis (FA) of : AMBI: AZTI Marine Biotic Index H Shannon–Wiener Index S number of species	Ecological Quality Ratio (EQR)	0.85 0.55 0.38 0.20
Infaunal Quality Index (IQI) version 4 (Phillips 2012)	$IQI = \frac{\left(0.033x \left(\frac{1 - \left(\frac{AMBI}{7} \right)}{1 - \left(\frac{AMBI_{ref}}{7} \right)} \right) \right) + \left(0.08x \left(\frac{1 - \lambda}{1 - \lambda_{ref}} \right) \right) + \left(0.54x \left(\frac{S}{S_{ref}} \right) 0.1 \right) - 0.4}{0.6}$ AMBI: AZTI Marine Biotic Index 1- λ : Simpson’s Evenness S number of species	Ecological Quality Ratio (EQR)	0.75 0.64 0.44 0.24

3.3.2 Functional indicators: description and computation

To assess the relative ecological functioning of each system, two metrics; biological traits analysis (BTA) and bioturbation potential (Bpc) were calculated from the previously identified benthic taxa data sets.

The initial stages of the traits analysis involved the identification of key aspects of functioning in the ecosystem under consideration, along with the selection of suitable indicator traits. The procedure for identifying indicator traits comprised three stages (Figure 3.1) outlined in detail below.

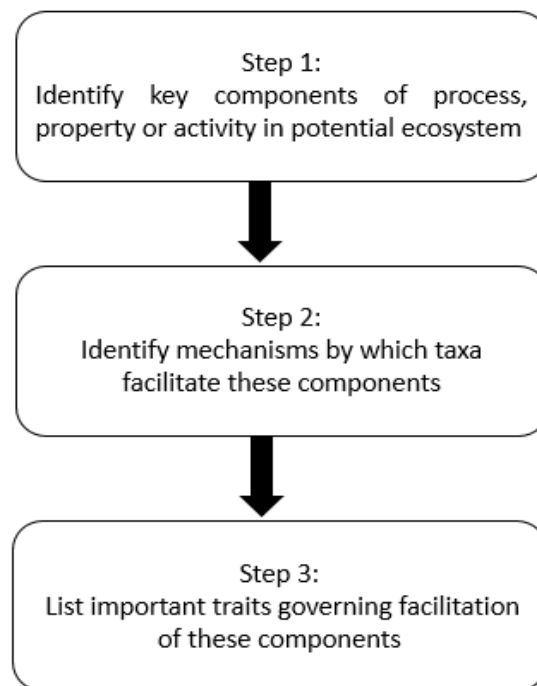


Figure 3.1. Procedure for identifying indicators of key ecosystem processes, properties and activities. From Bremner (2006a).

Step 1 Identify key components of process, property or activity occurring within the SAC

While macro-benthic components are important in providing a wide number of ecosystem functions (e.g. nutrient fluxes, carbon storage, benthic-pelagic coupling, secondary production) due to the nutrient related disturbances associated with both case study areas, it was decided to focus on key constituent processes that link functional mechanisms to the regulatory ecosystem services of Climate Regulation (Beaumont *et al.*, 2014) (specifically Carbon Sequestration and Storage) and Waste Remediation (Watson *et al.*, 2016) (with waste in this case being in the form of nutrients and organic matter). *A priori* the reasoning for this decision was that although the bulk of carbon and nutrient cycling and transformation processes are ultimately carried out by microbes or macrophytic plants in coastal marine systems, macro-fauna facilitate these processes both directly, as carbon and nutrient

reservoirs and indirectly as facilitators of benthic-pelagic coupling (Norkko *et al.*, 2001; Raffaelli *et al.*, 2003). Therefore given the intimate link between infaunal behaviour and elemental cycling pathways, any widespread effect on the efficiency of macro-benthic activity, is likely to have ecological consequences for ecosystem function in the chosen sediment systems (e.g. Solan *et al.*, 2004a; 2012).

The key steps (components) in the process of carbon cycling (and by association organic matter cycling) involve the supply of carbon into the marine ecosystem and the movement of carbon in its various forms between the pelagic and benthic compartments are shown in Figure 3.1.

Step 2: Identify mechanisms by which taxa facilitate these components

The carbon cycle illustrated in Figure 3.2 by Bremner (2008) has been simplified to show the steps in carbon cycling that are facilitated by benthic macro-organisms and does not detail the complex inorganic and microbial processes involved in the various carbon transformations. The mechanisms underlying each step are given below:

Pathway 1 - Direct fixation of carbon

- Benthic algae fix carbon directly from seawater.

Pathways 2-5 - Transport of carbon from pelagos to benthos

- Filter feeders consume pelagic primary producers, consumers, POC and microbes.

Pathways 6-14 - Transport of carbon within benthos

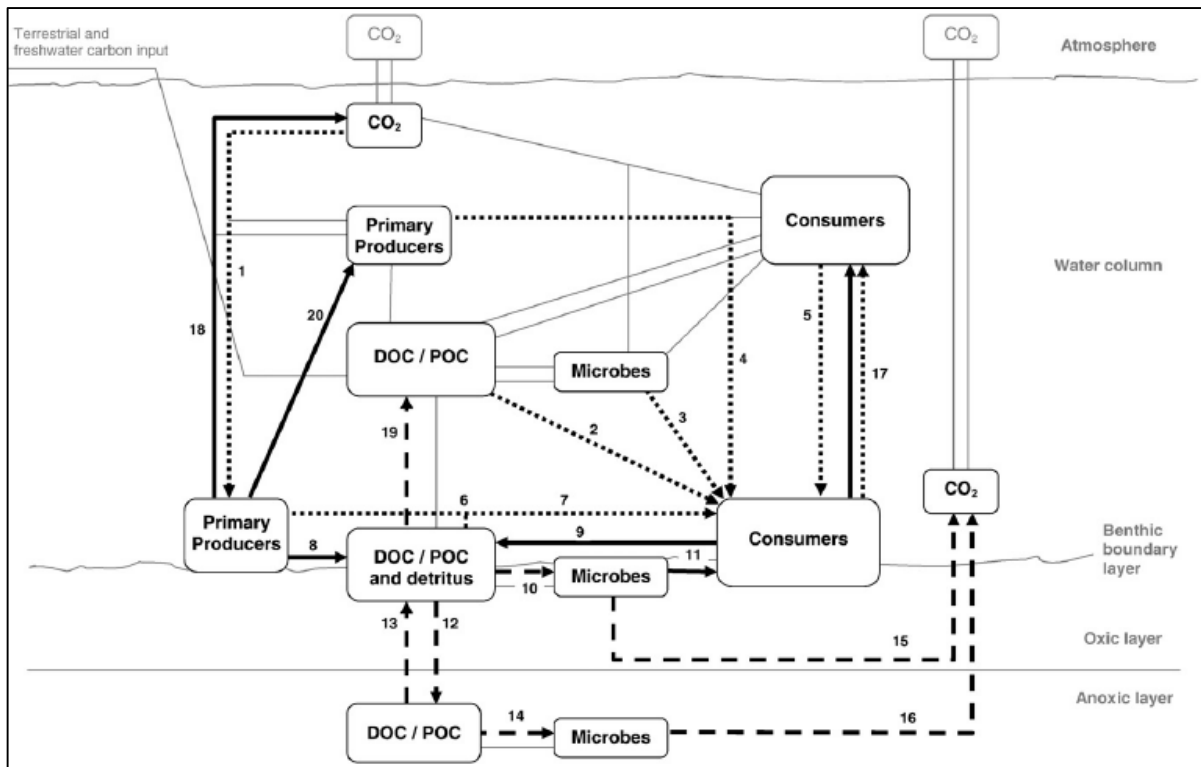
- Grazers and shredders consume benthic primary producers (macro- and microalgae).
- Deposit feeders and scavengers consume POC, detritus and microbes.
- Producers and consumers die and consumers defecate.
- Microbes decompose organic carbon; facilitated by deposit feeding and movement of fauna in top layers of sediments and by presence of tubes and burrows in upper sediments (break-up larger particles and transport oxygen).
- Deep-dwelling fauna transport carbon forms between aerobic and anaerobic layers.
- Microbes anaerobically decompose organic carbon; facilitated by deep-dwelling fauna that transport chemicals required.

Pathways 15-20 - Transport of carbon from benthos to pelagos

- Primary producers respire carbon into the water column.
- Primary producers produce planktonic propagules.
- Deep-dwelling fauna facilitate the transport of carbon released by microbes during anaerobic decomposition.

- Tubes and burrows facilitate the movement of decomposed carbon species from sediments to overlying waters, as do movements of fauna.
- Production of planktonic larvae, vertical feeding migrations and passive transport of individuals into the water column move carbon to the pelagos, as does the consumption of benthic organisms by pelagic fauna.
- Sediment re-working by fauna releases POC into overlying waters.

Figure 3.2 Simplified diagram of the marine carbon cycle, showing pathways facilitated by benthic



macro-organisms. Numbered pathways are detailed in step 2. Dotted lines represent pathways where macro-organisms have direct influence through resource capture, solid lines direct influence by other means and dashed lines indirect influence (Taken from Bremner, 2008)

Step 3: List important traits governing facilitation of these components

Traits governing the involvement of benthic organisms in each of the pathways outlined in step two can be utilised as indicators for their role in functioning as shown by the worked example below by (Bremner, 2006a),

Pathway 1 - Direct fixation of carbon

- Plant size, growth rate and longevity influence algal production.

Pathways 2-5 - Transport of carbon from pelagos to benthos

- Feeding methods govern capture of pelagic carbon by benthic macro-fauna.

Pathways 6-14 - Transport of carbon within benthos

- Feeding methods govern resource capture within benthos and break-up POC.
- Palatability and food preferences affect carbon transfer to consumers.
- Movement behaviours bring chemicals to microbes and break-up larger POC.
- Fauna living habits facilitate chemical transport within sediments.
- Living location affects transport of POC within sediments.

Pathways 15-20 - Transport of carbon from benthos to pelagos

- Reproductive method of algae and fauna transports carbon to pelagos.
- Living location and movement behaviour affects transport of POC to pelagos.
- Living habit and movement behaviour influences transport of chemicals to water.
- Morphology affects provision of food resources to pelagic fauna.

Identifying traits pertinent to a specific service in this manner, ensured a full consideration of different aspects ecosystem function that might have been missed by using a standard estuarine trait list. A summary of traits recommended for use as indicators of carbon and organic matter cycling are shown below (Table 3.2) with suggested trait categories. In addition to the traits identified above in step 3, two further traits were added to the traits list namely; salinity preference and species ecological group based on the previously calculated AMBI index. These traits were added due to their now known importance as environmental filtering traits in transitional ecosystems such as estuaries (Piscart *et al.*, 2006; Linden *et al.*, 2012).

Traits were divided into two categories, either to determine the organism's effects on ecosystem processes or services (effect traits) and/or its response to environmental change (response traits), such as disturbance, resource availability, management-related change or climatic shifts. In this respect, traits more associated with life history were classified as response traits while those reflecting behaviour and morphology were chosen to represent effects traits (*sensu* Bremner *et al.*, 2004; Tillin *et al.*, 2006) although the types sometimes coincided. Traits were subdivided into thirty-six categories that display the organisms' behaviour/strategy into more detail (e.g. the four considered categories of the trait 'feeding method' for benthic invertebrates were deposit, filter/suspension opportunist/scavenger and predator).

Table 3.2 Recommended biological traits that can be used as indicators of carbon cycling by are shown below with suggested trait categories (adapted from Bremnar *et al.*, 2006a):

Biological Traits	Description	Classification	Trait Categories
Maximum Size (mm)	The trait maximum size and longevity are representative of the movement of organic matter within the system.	Effect trait Response trait	Small(<1cm) Small-Medium(1-2cm) Medium(3-10cm) Large (11-20 cm)
Adult Longevity	Long-lived and large organisms hold matter within the system and short-lived small species contributing to higher turnover. These traits are also indicative of disturbance within the system.	Effect trait Response trait	Short (<2) Medium (2-5) Long (>5)
Growth Form (morphology)	Growth form and feeding method are descriptors of capture, palatability and movement of energy and matter through the food web (e.g. carbon).	Effect trait Response trait	Articulate A Bivalved/Turbinate BT Vermiform Segmented VS Tubicolous T
Feeding method		Effect trait Response trait	Deposit Filter/suspension Opportunist/scavenger Predator
Environmental Position	Deeper living species are potentially less subjected to hydrodynamic stress, but are more vulnerable to macroalgae blooms impacts, hypoxia and anoxia events.	Response trait	Hyperbenthic HB Epibenthic EPB Endobenthic ENB
Mobility in Sediment	Movement and development mechanisms capture energy/materials transfer pathways within the benthos. They also give insights on potential recovery patterns.	Effect trait Response trait	Fixed Tubes FT Limited Movement LM Slow free movement SFM Free Movement FM
Reproductive method		Effect trait Response trait	Gonochoristic Hermaphrodite
Bioturbation Functional Type	This trait can both indicate a change in energy and materials transfer, geochemical cycling related to environmental change and the functional effects of such a change.	Effect trait Response trait	Surface Modifier SM Biodiffusor B Upward conveyor UC Downward conveyor DC Regenerator R
Salinity preference	Describes species distribution depended on the species preference to salinity. An important environmental filtering trait in estuaries.	Response trait	<5 5–20 >20
Ecological group (AMBI)	Classifies species according to their tolerance of anthropogenic disturbance.	Response trait	Sensitive I Indifferent II Tolerant III Very Tolerant IV

Having identified important traits, actual computation of BTA required the construction of three different numerical matrices: (1) taxa density in each station (matrix 'taxa by stations'); (2) biological traits of the taxa (matrix 'taxa by traits'); and (3) a combination of the previous two, biological traits in each station (matrix 'traits by stations') (e.g. Bremner *et al.*, 2003). Data of taxa density were first sorted by year and zone, removing rare taxa; (defined as those present at less than an average of 0.5 individuals per core and those taxa that contributed to <1% of numerical biomass for any one site) on the basis that contributions made by these taxa towards functioning cannot be adequately quantified and would have particular implications for the analysis of ecological functioning. As biomass is often cited as the best measure of an organisms presence in a community (e.g Bremner, 2006a), the biological enumeration system used here was biomass (g m²).

To construct the second matrix 'taxa by traits', trait data were collected from a variety of published sources (see appendix 3A), mainly journal papers and websites of scientific institutions (e.g. the Biological Traits Information Catalogue developed by the Marine Life Information Network, <http://www.marlin.ac.uk/biotic/>) on the selected traits identified in Table 3.2. When reliable information was missing, expert judgment and/or data from the nearest phylogenetic neighbour were considered and when different information sources disagreed on the traits that are expressed by taxa *all* information was recorded. Using this information each taxon (i.e. species) was given a score from zero to three for the extent to which it exhibits each trait category, using a 'fuzzy coding' approach (Chevenet *et al.*, 1994) described below:

- 0 – No expression. The category is never exhibited by the taxon during its benthic existence.
- 1 – Low-level expression. The category is exhibited infrequently, weakly or there is a small amount of evidence that it is exhibited.
- 2 – Moderate expression. The category is exhibited moderately or there is a moderate amount of evidence that it is exhibited.
- 3 – High-level expression. The category is exhibited often, strongly or there is a large amount of evidence that it is exhibited.

Information from the 'taxa by stations' and 'taxa by traits' matrix were then combined to produce a 'trait by station' matrix (Table 3.3.). To do this, the trait category scores for each taxon present at each station were multiplied by their overall density at each station. To give the same weight to each taxon and each biological trait in further analysis, scores were standardized so that their sum for a given taxon and a given trait equals 1 (or 100%).

Table 3.3 Example of trait scores for taxa used to create the simulated biological traits dataset (trait category names are shown in Table 3.2). Full ‘taxa by traits’ for both Tamar and Eden are available in Appendix 3B & 3C.

Feeding Method				
	Deposit D	Filter/suspension FS	Opportunist/Scavenger OS	Predator P
<i>Ampharete grubei</i>	2	2		
<i>Ampharete acutifrons</i>	2	2		
<i>Arenicola marina</i>	3			
<i>Baltidrilus costata</i>	3			
<i>Capitella capitata</i>		3		
<i>Caulleriella killariensis</i>		3		
<i>Cerastoderma edule</i>		3		
<i>Chaetozone gibber</i>	3			
<i>Corophium volutator</i>	2	2		
<i>Cossura pygodactyla</i>	3			
<i>Cossura longocirrata</i>	3			
<i>Cyathura carinata</i>	3			
<i>Galathowenia oculata</i>	3	1		
<i>Gammarus locusta</i>	3			
<i>Hediste (nereis) diversicolor</i>	2	2	2	2
<i>Heterocirrus zetlandicus</i>	2	2		
<i>Macoma balthica</i>	3	3		
<i>Magelona johnstoni</i>	3			
<i>Manayunkia aestuarina</i>	1	3		
<i>Melina palmata</i>	3	1		
<i>Nephtys hombergii</i>			2	2
<i>Peringia ulvae</i>	3			
<i>Phyllodoce maculata</i>			3	3
<i>Polydora cornuta</i>	3	3		
<i>Pygospio elegans</i>	3			
<i>Retusa obtusa</i>				3
<i>Retusa truncatula</i>				3
<i>Scrobicularia plana</i>		2	2	
<i>Spio filicornis</i>	3			
<i>Streblospio shrubsolii</i>	3			
<i>Tubificoides amplivasatus</i>	3			
<i>Tubificoides benedii</i>	3			
<i>Tubificoides insularis</i>	3			

Following the BTA analysis, community Bioturbation Potential (Bpc thereafter) was calculated from infaunal benthic data (i.e. A= abundance, B = biomass and biological traits information of individual species) based on the methodology proposed by Solan *et al.*, (2004). The bioturbation formula is outlined below:

$$Bp_c = \sum_{i=1}^n \sqrt{\frac{B_i}{A_i} * A_i * A_i * M_i * R_i} \quad \text{Equation 3.1}$$

Where B_i and A_i are the biomass and abundance of a taxon (i) in a sample; M_i is their standardised score for mobility and R_i is their standardised score for sediment re-working mode derived according to the standardised scores for mobility and sediment reworking mode listed in Queirós *et al.* (2013). Overall calculations were conducted for individual species (Bp_i) and for the whole community (Bpc). This index is an indicator of bioturbation on the functional role of benthic infauna in relation to sediment turnover.

3.3.3 Multivariate data analysis

Initial statistical analyses regarding the macro-benthic and environmental data were performed covering the whole estuarine gradient, followed by posterior detailed analysis, focusing on each estuarine zone separately. In this way, the examination of the relationships between biodiversity and ecosystem service flows across coastal margins can be better addressed (EPBR .,2011), with different measurement scales providing complementary information about each system. All statistical analysis were performed using the PRIMER v7 statistical package (Clarke *et al.*, 2014a), together with the permutational multivariate analyses of variance (PERMANOVA) + PRIMER add-on package (Anderson *et al.*, 2008).

3.3.3.1 Environmental variables

In the case of the Tamar, environmental variables were analysed by means of a Principal Component Analysis (PCA) first coded for the temporal factor “year” and then to the spatial factor “zone” (Upper, Central and Lower). Prior to analysis, variables were normalised and transformed either by $\log(1 + x)$ or by square root, whenever data were not normally distributed. Initially PCA was performed considering the entire estuary. After that, a second PCA was carried out looking at each of the estuarine zones individually.

In contrast to the Tamar, due to the small number of temporal variables investigated for the Eden estuary, (i.e. two variables 1999 & 2015) visual Exploratory Data Analysis (EDA) was used instead of PCA, by plotting historic data (1990-2015) as a time series in Microsoft Excel (2013) to identify general trends in physiochemical variables. Although not multivariate in nature, analysing the datasets in this way, allowed a visual summery to be made regarding the main changes to the estuary between the

late 1990's and early 2015 periods, giving a better representation of underlying physicochemical mechanisms of change, in contrast to comparing two data points.

3.3.3.2 Macro-benthic community structure

To investigate changes in macro-benthic community structure, PERMANOVA was employed to elucidate if changes in overall density (no. m²), biomass (g m²) and 11 of the previously calculated univariate biotic indicators were significantly different between years in each system. The 11 diversity indices used were, number of species (S), Shannon-Wiener (H), Simpson's Dominance (Ds), Margalef's Species Richness (Dm), Pielou's Evenness (J), Δ , AvTD, TTD, AMBI, MAMBI and IQI, were different between years and zones in each estuary and, if so which species were responsible for those differences.

Prior to the analysis, draftsman plots of the values at each site were examined visually to assess whether the values were heavily skewed and, if so, which type of transformation would satisfy the assumption of homogeneity of variances. These plots demonstrated that the data required a square root transformation prior to constructing a similarity matrix based on a Bray-Curtis coefficient to down-weight the contributions of taxa with relatively high values.

PERMANOVA analyses were conducted in a two-step approach. The first approach (i) was performed considering the data from all estuarine zones together in a two-way, PERMANOVA design: with 'year' (temporal factor) and 'zone' (spatial factor) as fixed factors. For the Tamar the temporal factors spanned 5 levels (1937, 1990, 1991, 1992 & 2005) and 3 spatial levels (lower, central and upper), while the Eden covered 2 temporal levels (1999, 2015) and 3 spatial levels (lower, central and upper). Respectively a second approach (ii) was accomplished for the whole estuary and each estuarine zone separately using a one-way pair-wise, PERMANOVA design using the same factors. For the tests, 9999 random permutations were used and the method of permutation chosen was the 'Permutation of residuals under a reduced model' for the multi-factorial design. The null hypothesis that there was no significant difference was rejected if the significance level (P) was <0.05.

Following the PERMANOVA tests, the same data matrix was subjected to ordination by nMDS (Clarke, 1993) in order to visually assess variations in the distribution of community composition. Initially, a general nMDS ordination was carried out taking into account all estuarine zones together followed by a more detailed comparison of nMDS ordinations of each zone separately.

3.3.3.3 Biological traits analysis

Using the same experimental design as described above (same number of permutations, permutation method and significance level), the 'traits by station' data matrix resulting from BTA was subject to PERMANOVA and nMDS in order to statistically and visually assess variations in the distribution of traits composition of both systems. Prior to analysis, data were square root transformed and a similarity matrix based on Bray–Curtis coefficient was calculated.

3.4 Tamar results

Overall, a total of 59, 767 individuals from over 125 different taxa were identified from the 42 samples (no. m²) taken from the Tamar estuary over the 1937-2005 period. The macro-faunal abundance was dominated by Polychaetes (23 families), followed by Molluscs (19 families), Crustaceans (19 families), Oligochaetes (1 family) and others (5 families).

3.4.1 Tamar environmental variables

A summary of the annual average concentrations of selected environmental variables for the Tamar Estuary as a whole (1990-2005) and by individual zones (1937-2005) is shown in Table 3.4 and 3.5 respectively.

Table 3.4: Summary of annual average concentrations of selected environmental variables for the Tamar Estuary (1990-2005).

Year	1990	1991	1992	2005
Temperature(°C)	12.10	10.67	11.08	11.95
pH	7.33	7.50	7.70	7.59
Surface salinity (psu)	17.56	14.69	16.30	6.91
Dissolved oxygen (mg l ⁻¹)	10.00	10.86	10.76	10.29
Biochemical oxygen demand (mg l ⁻¹)	2.11	1.59	1.52	1.10
Ammonium (mg l ⁻¹)	0.07	0.05	0.04	0.02
Nitrite (mg l ⁻¹)	0.03	0.02	0.02	0.008
Nitrate (mg l ⁻¹)	11.65	12.62	12.10	12.61
Filterable reactive phosphorous (µg l ⁻¹)	110	78	63	47
Chlorophyll <i>a</i> (mg l ⁻¹)	29.55	8.78	6.98	6.32
River flow (m ⁻³ /s)	3.48	5.36	8.65	4.01
North Atlantic Oscillation index	5	4	1	-0.5

Table 3.5 Summary of selected environmental variables for each zone of the Tamar Estuary (1937-2005). Categories: **salinity** 2=Reduced/low (0.5-30), 3=Variable (18-35); **exposure** 2=extremely sheltered, 3=very sheltered, 4=sheltered; **tidal stream** 2 = <1 knot, 3 = 1-3knots; **Granulometry** 1 = <0.063, 2= 0.025-0.5mm, 3 =>2mm **depth** 1 = <5m, 2 =<10m, 3 =<15m and 4 = >15m.

Year/Zone	Salinity	Site Exposure	Tidal stream	Granulometry	Depth
1937 Upper	2	2	3	2	1
1990 Upper	2	2	3	2	1
1991 Upper	2	2	3	2	1
1992 Upper	2	2	3	2	1
2005 Upper	2	2	3	2	1
1937 Central	3	3	3	2	3
1990 Central	3	3	3	2	3
1991 Central	3	3	3	2	3
1992 Central	3	3	3	2	3
2005 Central	3	3	3	2	3
1937 Lower	3	2	3	1	4
1990 Lower	3	2	3	1	4
1991 Lower	3	2	3	1	4
1992 Lower	3	2	3	1	4
2005 Lower	3	2	3	1	4

With regard to the PCA ordinations embracing the whole estuarine gradient (Figure 3.3), the first two components accounted for 91% of the variability in the data set. Therefore, the PCA 2-D plot provided a very good summary of the sample relationships. From the observation of the PCA plots coded for the entire estuary, clear distinctions could be seen among the samples from the different years. The 1990 (eutrophic) period was separated, mainly by high nutrients (ammonium, nitrite, nitrate, filterable reactive phosphorus), alongside high levels of chlorophyll *a*, BOD and sea surface pressure (NAO). Following the eutrophic period, the 1991 and 1992 periods were categorised by an increase in river flow as well as dissolved oxygen. Successively, the 2005 period was separated from the pre-management period (1992) by a slight increase in sea surface temperature, nitrates and pH, but coinciding with a decline in all other variables.

Differences between the zones (Table 3.5) showed that both the central and upper zones to be different from the lower zone, with higher values of salinity and larger sediment sizes. Starting in the lower estuary, a clear horizontal decreasing depth gradient was also apparent while the central estuary proved to be more sheltered than the upper and lower regions of the estuary. Tidal currents

had a similar structuring influence across all zones. In summary, the outcomes reflected a dynamic changing spatial gradient from the estuary's mouth toward its inner parts along with distinct temporal variations in the environmental variables between the time periods.

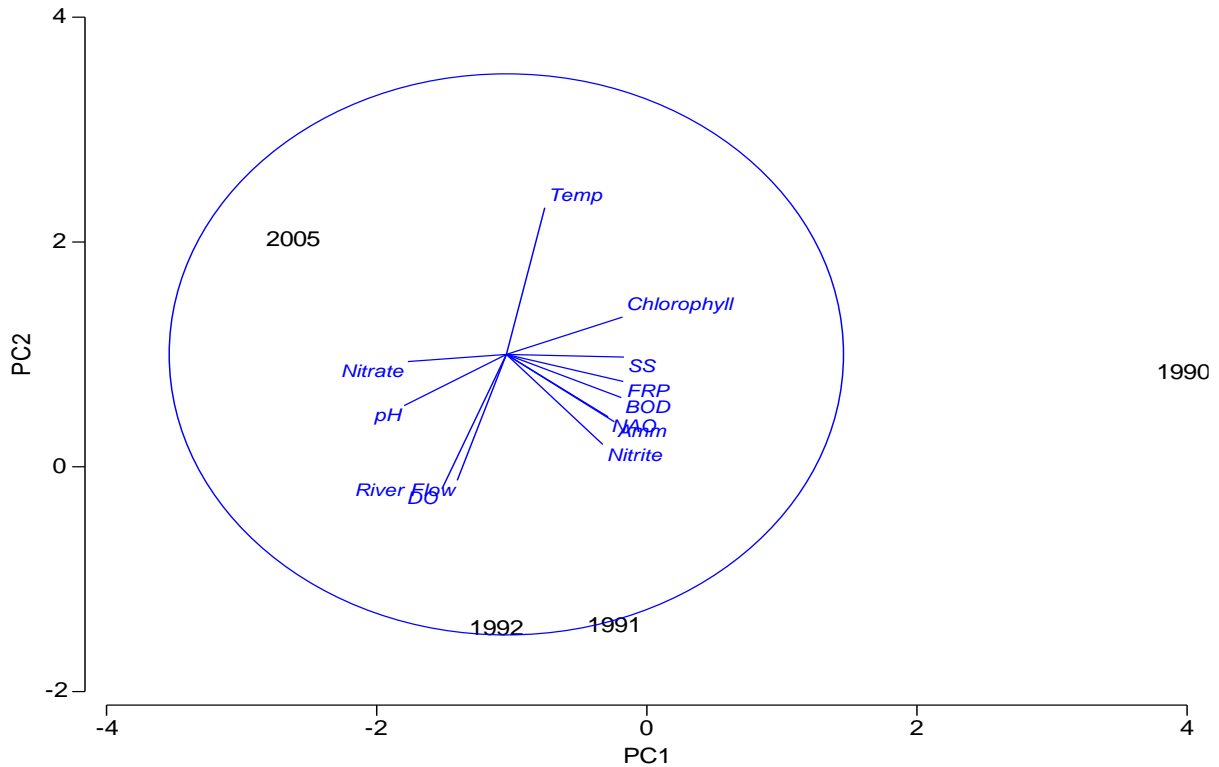


Figure 3.3 Ordination diagram for the first two axes of the principal component analysis of environmental variables, coded for the temporal factor (year).

3.4.2 Tamar abundance and biomass

Abundance and biomass showed clear differences between sites over the period of the study (Table 3.6). The highest values for both abundance (10430 individuals) and biomass (17.30g m²) were found between during the eutrophic (1990), post-eutrophic (1991) and pre-management (1992) periods, in the upper reaches of the estuary. During these periods the upper estuary accounted for ~50% of the total abundance (31420) and biomass (49.43g m²), encountered in this study. Concurrently, the lowest numbers of individuals (1000-1710) were also found during the same 1990-1992 period, but in the central and lower regions of the estuary. The lowest biomass recorded was 1.35g m² during the 1937 sampling period in the lower estuary.

Table 3.6 Total density (N) and biomass (AFDW g) recorded at each site during the study period.

	Site	Number of stations	1937	1990	1991	1992	2005
Abundance (N m ²)	Upper	3	2745	10430	10980	10010	1347
	Central	3	3726	1000	1450	1710	3034
	Lower	3	5023	1140	2560	1290	3320
Biomass (AFDW g m ²)	Upper	3	3.38	15.10	17.03	17.30	2.43
	Central	3	10.28	2.66	2.61	2.63	2.32
	Lower	3	1.35	6.85	7.25	6.35	2.64

A summary of mean values for the number of individuals and biomass at each site during the study period is given (Figure 3.4). When considering the abundance and biomass composition data from all estuarine zones together throughout the study period, a significant interaction ($p < 0.05$) for the

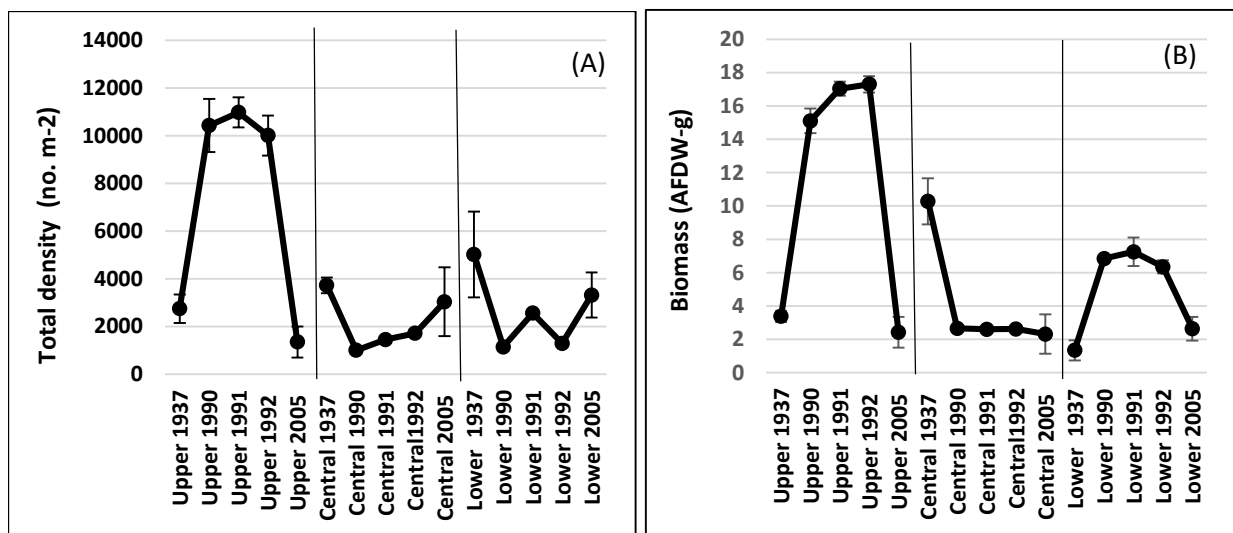


Figure 3.4 Summary of means and 95% confidence intervals of (A) total density and (B) biomass (AFDW) factors 'Year' and 'zone' was detected by a two-way PERMANOVA analysis (Table 3.7), indicating the existence of significant temporal and spatial differences over the 1937-2005 periods. A significant difference ($p < 0.05$) was also detected between the two factors (Year x zones) when considering the size of individuals (biomass), but not their overall densities ($p > 0.05$).

Table 3.7 Pseudo-F (pF) values and significance levels (P) for two-way PERMANOVA tests, employing separate Euclidean distance resemblance matrices constructed from the (pre-treated) data for total density and biomass data, collected on the Tamar estuary across each of the 1937, 1990,1991,1992,2005 periods. df= degrees of freedom. Significant differences ($p = <0.05$) are highlighted in bold.

	Density		Biomass	
	pF(df)	P	pF(df)	P
Year	61.029(4)	0.001	3.7425 (4)	0.002
Zones	6.2988(2)	0.002	25.841 (2)	0.001
Year x zones	1.6747(8)	0.128	5.5537(8)	0.001

Posterior detailed analysis of these trends, indicated that the reason for the variability between the factor ‘Year’ at was due to significantly different ($p<0.05$) overall densities and biomasses of fauna between the 1990, 1991 and 1992 vs the 1937 and 2005 periods (table 3.8 one-way PERMANOVA all $p<0.05$). These trends were also expressed in a similar manner when the resolution was increased to assessing individual zones, suggesting all zones were impacted significantly during the high nutrient periods. One exception to this was in the central estuary where no significant different biomass results were identified between the 2005 vs 1990, 1991 and 1992 periods.

Table 3.8 One-way PERMANOVA pair-wise post hoc comparisons among years for the whole estuary and each estuarine zone. Values in bold were significant at ($p < 0.05$).

Year	Density				Biomass			
	Whole	Upper	Central	Lower	Whole	Upper	Central	Lower
1937, 1990	0.025	<0.05	<0.05	<0.05	0.029	<0.05	<0.05	<0.05
1937, 1991	0.027	<0.05	<0.05	<0.05	0.032	<0.05	<0.05	<0.05
1937, 1992	0.021	<0.05	<0.05	<0.05	0.001	<0.05	<0.05	<0.05
1937, 2005	0.993	>0.05	>0.05	>0.05	0.141	>0.05	>0.05	>0.05
1990, 1991	0.408	<0.05	<0.05	<0.05	0.541	<0.05	<0.05	<0.05
1990, 1992	0.416	>0.05	>0.05	>0.05	0.346	>0.05	>0.05	>0.05
1990, 2005	0.001	<0.05	<0.05	<0.05	0.003	<0.05	>0.05	<0.05
1991, 1992	0.408	>0.05	>0.05	>0.05	0.567	>0.05	>0.05	>0.05
1991, 2005	0.004	<0.05	<0.05	<0.05	0.005	<0.05	>0.05	<0.05
1992, 2005	0.017	<0.05	<0.05	<0.05	0.001	<0.05	>0.05	<0.05

Table 3.9 One-way PERMANOVA pair-wise post hoc comparisons among zones for the whole estuary using the t-statistic. Values in bold were significant at $p < 0.05$.

Zone	Density	Biomass
Lower, Central	0.54597	2.7329
Lower, Upper	3.353	5.5368
Central, Upper	4.1762	5.6685

Additional one-way PERMANOVA results (table 3.9) looking at the factor 'zone' over the entire estuary indicates there were significant changes in the biomass of individuals between all zones in the case of the biomass data (all <0.05). Similarly overall density of individuals was found to have p values of less than (<0.05) between the upper vs lower and upper vs central sampling periods.

Multidimensional Scaling (MDS) ordinations of samples, based on density and biomass data display a fairly similar distribution (Figures 3.5 and 3.6). Four general groupings could be identified based on 80% hierarchical clustering analysis. Clear distinctions can be made between the eutrophic (1990), post eutrophic (1991) and pre management (1992) time periods in both graphs; concurring with the previous findings in Table 3.7. In particular the upper zones during the 1990-1992 periods show a high degree of spatial segregation from the historic and post-management periods, which could account for the differences between the periods. There is also a clear overlap of samples from the historic (1937) and post-management period (2005) all at $\geq 80\%$ similarity. In contrast, distinctions between the pre (1992) and post- management (2005) periods for each of the central and lower zones are not clearly illustrated on the nMDS plots. This suggests a weak segregation among these samples and thus, temporal changes are weakly expressed.

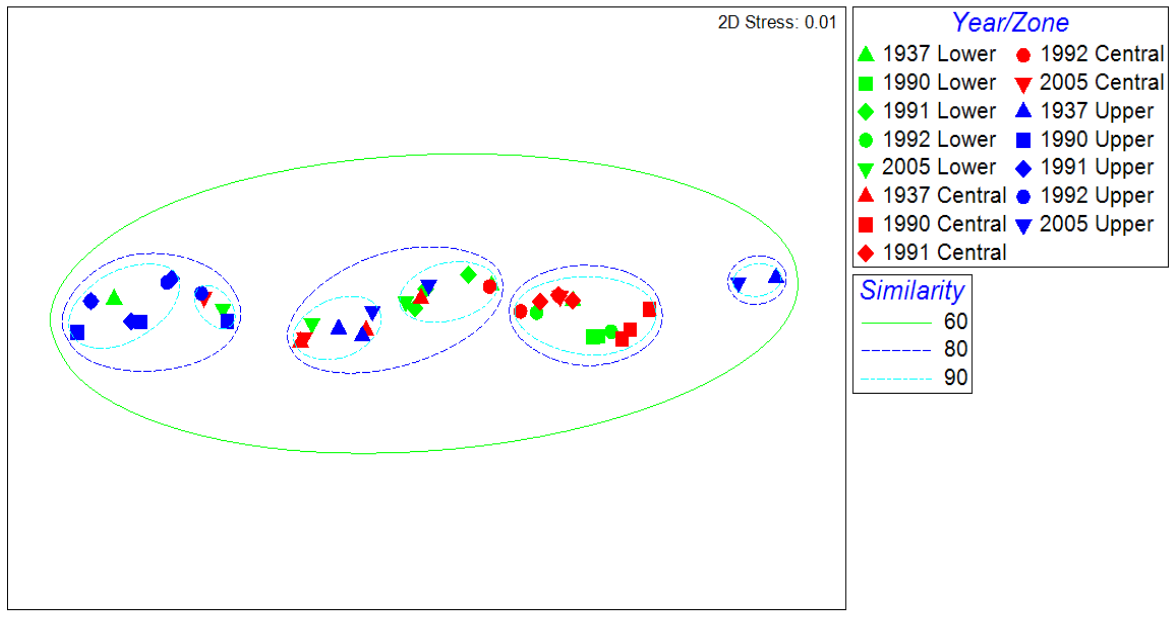


Figure 3.5 An nMDS plot based on square root transformed data of macro-benthic density data from all estuarine zones covering the five time periods defined by the intervention under study: Historic 1937 (Triangles), Eutrophic 1990 (Squares), Post-Eutrophic 1991 (Diamonds), Pre-management 1992 (Circles) and Post-management 2005 (Inverted triangles).

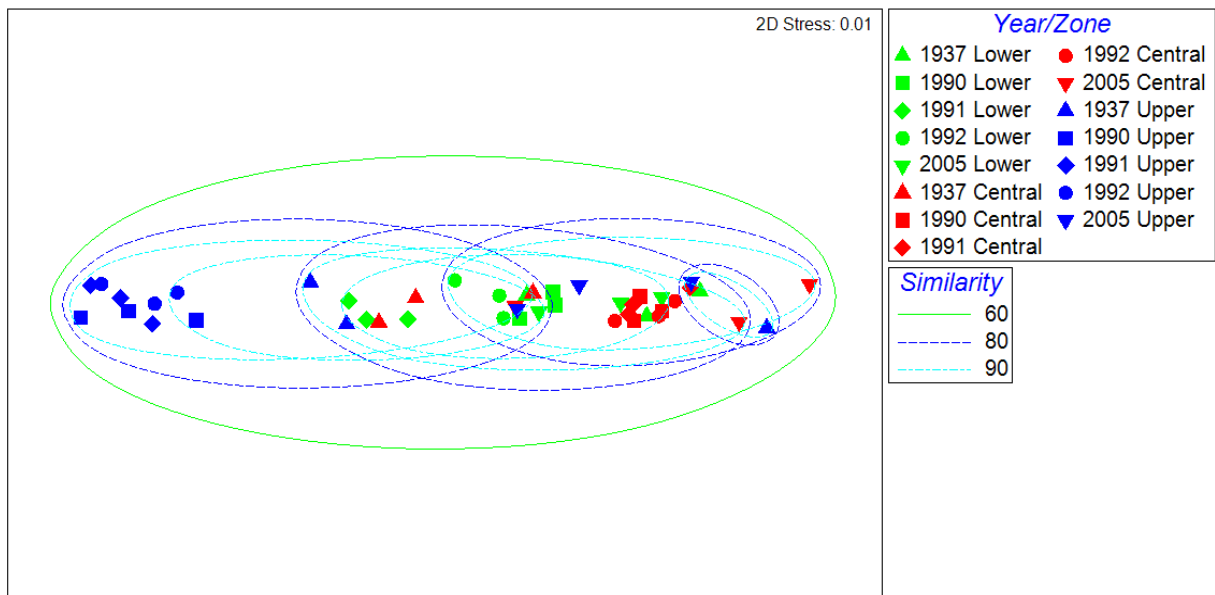


Figure 3.6 An nMDS plot based on square are root transformed data of macro-benthic biomass data from all estuarine zones covering the five time periods defined by the intervention under study: Historic 1937 (Triangles), Eutrophic 1990 (Squares), Post-Eutrophic 1991 (Diamonds), Pre-management 1992 (Circles) and Post-management 2005 (Inverted triangles).

3.4.3 Tamar species inventory and richness

The macro-faunal community structure of the Tamar estuary was dominated by the Polychaete taxa, representing over 87 % (52226 ind) of the total number of individuals found across all time periods (Table 3.10). Molluscs were second in the dominance order with 7% (4699 ind) of the total density, followed by Crustaceans and Oligochaetes which contributed 2.68% (2601 ind) and 2.08% (1241 ind.) of the total density respectively. The remainder of the total density was made up by the 'others' group including Echinoderms, Holothurians, Nemerteans, Cnidarians, Bryozoans and Sipunculids.

Table 3.10 Total density (N) of main taxa found during the study period

Year	Polychaetes	Crustaceans	Molluscs	Oligochaetes	Other
1937	7990	903	2540	57	1
1990	12281	176	210	9	0
1991	14860	20	113	0	0
1992	12410	440	160	0	0
2005	4685	65	1676	1175	17
Total individuals	52226	1604	4699	1241	18
% Total taxa	87.35	2.68	7.86	2.08	0.03

The order of the most abundant taxa by zone recorded a fairly similar trend, with Polychaetes recorded as the most abundant followed by Crustaceans, Molluscs and Oligochaetes (Figure 3.7). A slight difference was only recorded for 1937 central site where Molluscs were recorded as the most dominant taxa.

Polychaetes also comprised the highest number of species identified with 23 (32%) of the total of 73 species found during the course of this study (Table 3.11). With 19 species (26%) apiece, Molluscs and Crustaceans occurred as the second most diverse taxa. This was followed by Oligochaetes (7 species – 10%) and the 'others' group (5 species – 7%), which comprised mainly of Echinoderms and Nemerteans.

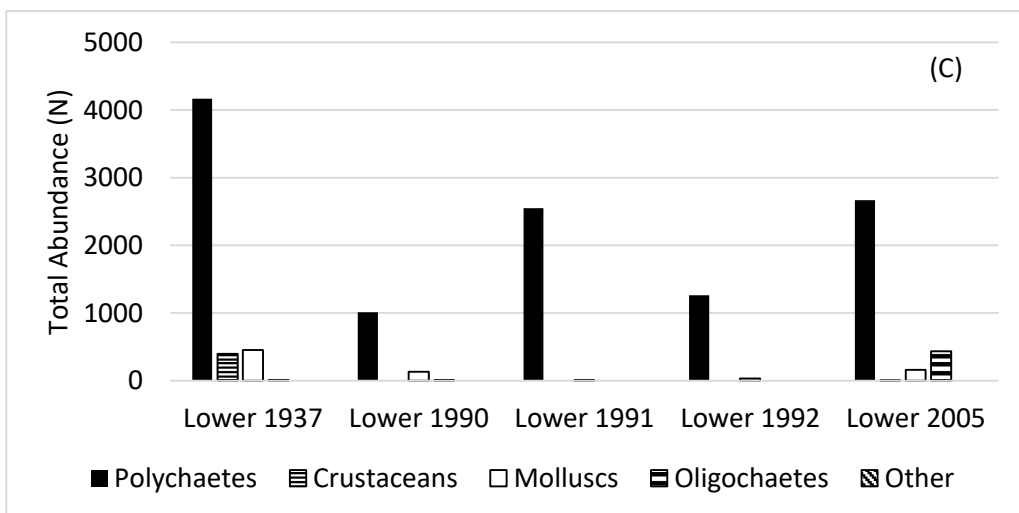
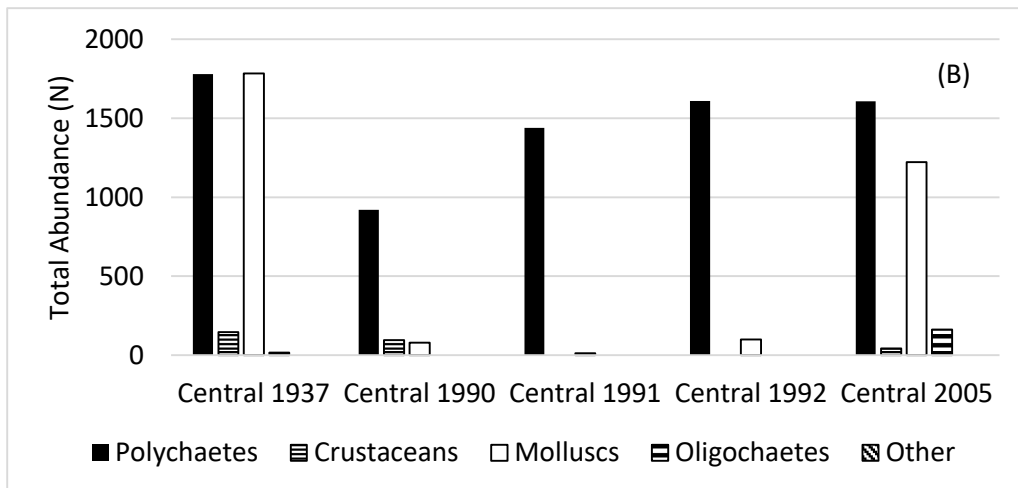
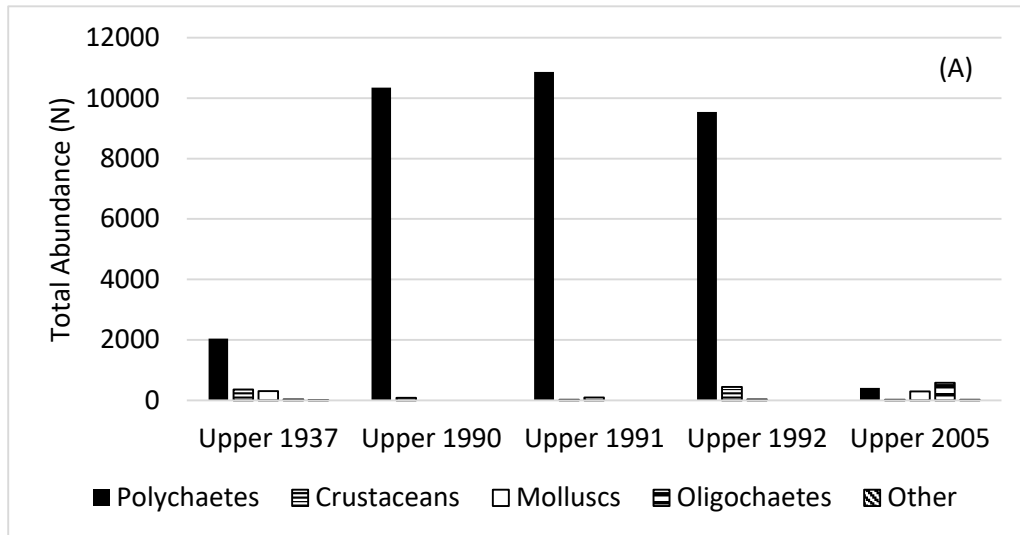


Figure 3.7 Total density of major taxa found in the (A) upper, (B) central and (C) lower regions of the Tamar estuary during the study periods.

Table 3.11 Species richness (S) of main taxa found during the study period.

Year/Zones	Polychaetes	Crustaceans	Molluscs	Oligochaetes	Others
1937 Upper	5	2	4	2	1
1990 Upper	3	1	2	0	0
1991 Upper	2	1	1	0	0
1992 Upper	2	1	1	0	0
2005 Upper	8	2	4	3	1
1937 Central	8	4	3	2	1
1990 Central	6	0	1	0	0
1991 Central	5	0	1	0	1
1992 Central	4	0	1	0	0
2005 Central	19	3	4	3	0
1937 Lower	10	9	9	1	0
1990 Lower	2	0	2	1	0
1991 Lower	3	0	1	0	0
1992 Lower	3	0	1	0	0
2005 Lower	19	2	5	6	0
Total No. Species Identified	23	19	19	7	5
%Total	32	26	26	10	7

Differences in the distribution of species richness were clearly shown between the 1990-1992 high nutrient periods when compared to the historic 1937 and post-management periods across all regions of the estuary (Figure 3.8).

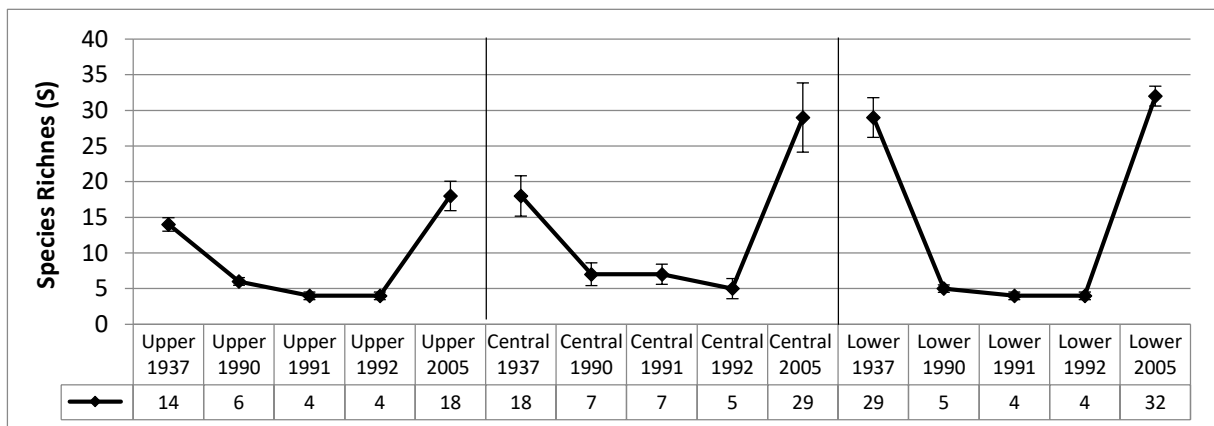


Figure 3.8. Summary of means and 95% confidence intervals for the number of species (S) across the 1937-2005 periods.

More detailed statistical analysis confirmed, there was a significant difference (one-way PERMANOVA all $p < 0.05$) between the 1937 vs 1990, 1991, 1992 and 2005 vs 1990, 1991 periods when considered at the whole estuarine scale (Table 3.12). Additionally a significant difference in species richness was also found between the 1990 vs 1992 periods. Similarly to the trends in total density and biomass

shown earlier (Table 3.5), similar patterns in significant differences were detected between years for species richness when the resolution was increased to assessing individual zones.

Table 3.12 One-way PERMANOVA pair-wise post hoc comparisons among years for the whole estuary and each estuarine zone using the t-statistic. Values in bold were significant at ($p < 0.05$).

Year	Species Richness		Zones	
	Whole	Upper	Central	Lower
1937, 1990	0.001	<0.05	<0.05	<0.05
1937, 1991	0.001	<0.05	<0.05	<0.05
1937, 1992	0.001	<0.05	<0.05	<0.05
1937, 2005	0.054	>0.05	>0.05	>0.05
1990, 1991	0.068	>0.05	>0.05	>0.05
1990, 1992	0.033	<0.05	<0.05	<0.05
1990, 2005	0.002	<0.05	<0.05	<0.05
1991, 1992	0.692	>0.05	>0.05	>0.05
1991, 2005	0.001	<0.05	<0.05	<0.05
1992, 2005	0.002	<0.05	<0.05	<0.05

Overall, the polychaete, *Hediste diversicolor* was the most numerically important species in the upper reaches of the estuary (Table 3.13), showing a marked increase in individuals (+ 8404) when compared with the 1937 historic reference period and a large decline (-9457) in individuals between the pre-1992 and 2005 post-management periods. Additionally, the number of species found in the upper zone when compared to the lower and central zones were found to be significantly different from each other (one-way PERMANOVA: $p < 0.05$) when comparing the factor 'zone' over the entire estuary (Table 3.14)

Across the other regions of the estuary, *Hediste diversicolor*, *Peringia ulvae* and *Nephtys hombergii* were consistently in the top 5 most dominant taxa at each site. The Polychaete *Melinna palmate* was noted to be a consistently important species in the lower reaches of the estuary. Other species such as *Cyathura carinata*, *Tubificoides benedii*, *Chaetozone gibber* and *Heterocirrus zetlandicus* also occurred in influential numbers during the 1937 and 2005 periods, but in a discontinuous pattern through the zones (Table 3.13).

Table 3.13 List of the 5 most dominant taxa (based on total density (N)) in each region of the Tamar estuary

Upper	Taxa	1937	1990	1991	1992	2005
<i>Cyathura carinata</i>	Crustaceans	356	-	-	-	-
<i>Hediste (nereis) diversicolor</i>	Polychaetes	1866	10270	10870	9540	83
<i>Peringia (hydrobia) ulvae</i>	Molluscs	118	230	94	253	285
<i>Polydora cornuta</i>	Polychaetes	47	-	-	-	-
<i>Tubificoides benedii</i>	Oligochaetes	-	-	-	-	470
Central		1937	1990	1991	1992	2005
<i>Chaetozone gibber</i>	Polychaetes	-	-	-	-	402
<i>Hediste (nereis) diversicolor</i>	Polychaetes	1071	118	87	178	43
<i>Nephtys hombergii</i>	Polychaetes	578	820	1210	1440	147
<i>Peringia (hydrobia) ulvae</i>	Molluscs	1464	46	39	40	1196
<i>Pygospio elegans</i>	Polychaetes	-	-	-	-	332
Lower		1937	1990	1991	1992	2005
<i>Hediste (nereis) diversicolor</i>	Polychaetes	84	580	2140	1030	188
<i>Heterocirrus zetlandicus</i>	Polychaetes	3010	-	-	-	-
<i>Melinna palmata</i>	Polychaetes	249	114	275	286	511
<i>Nephtys hombergii</i>	Polychaetes	317	430	410	230	243
<i>Peringia (hydrobia) ulvae</i>	Molluscs	232	43	107	89	68

Table 3.14 One-way PERMANOVA pair-wise post hoc comparisons among zones for the whole estuary using the t-statistic. Values in bold were significant at ($p < 0.05$).

Zone	Species Richness
Lower, Central	0.07
Lower, Upper	0.005
Central, Upper	0.01

3.4.4 Tamar structural indicators performance

Almost all of the univariate diversity indicators tested, presented the general behaviour expected (i.e. in line with the classifications proposed by the indicator developers) during both the eutrophic-post eutrophic (1990-1991) and pre-post management (1992-2005) scenarios, with almost all indicators portraying a low value (low ecological status) during (1990) and immediately after the eutrophic event (1991), and a higher value (better ecological status) after the management intervention (2005) (Figure 3.8). Simpson's Index also suggested the same trends with the variables in reverse, i.e. high value (low ecological status) under high levels of nutrients and low values (high ecological status) under reduced nutrients. These general trends were also detected in the phylogenetic indicators, average taxonomic distinctness ($\Delta+$) and total taxonomic distinctness ($s\Delta$) in the lower estuary, with the former remaining stable though the temporal periods and the latter suggesting species were more closely related during the pre-management period (1992) than the post management period. Pielou's Evenness however

deviated from the norm on one occasion, exhibiting higher values during the eutrophic event in the lower estuary than in both the historic (1937) and post-management periods (2005).

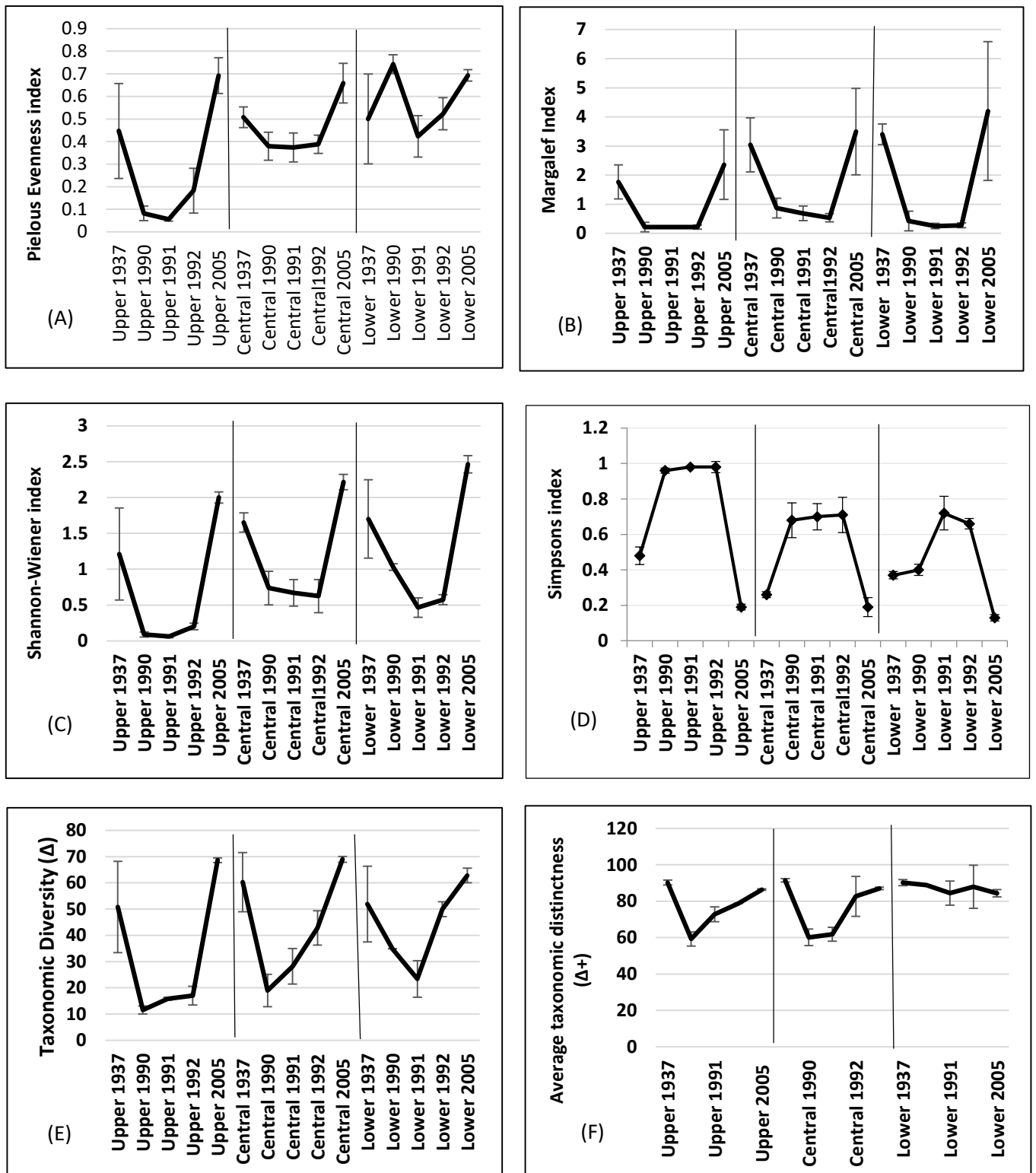


Figure 3.8. Temporal and spatial variation of the ecological indicators with 95% confidence intervals, based on inter-tidal macro- benthic communities for each zone (upper, central and lower) of the Tamar estuary (1937-2005). (A) Pielou; (B) Margalef; (C) Shannon–Wiener; (D) Simpson; (E) taxonomic diversity; (F) taxonomic distinctness.

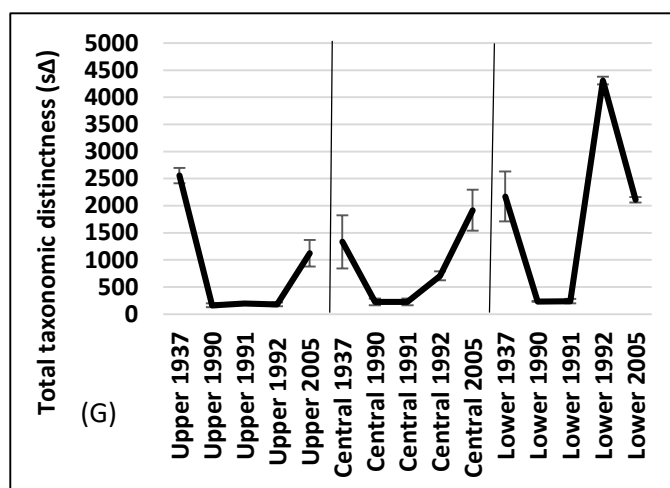


Figure 3.8 (continued). Temporal and spatial variation of the ecological indicators with 95% confidence intervals, based on inter-tidal macro- benthic communities for each zone (upper, central and lower) of the Tamar estuary (1937-2005). (G) Total taxonomic distinctness.

Spatial calibration of the composite metrics M-AMBI and IQI based on the disturbance of species within the sampling stations, showed a general decrease in ecological status between the historic (1937) and eutrophic period (1990) in all scenarios (Table 3.15) when EQRs were classified as ‘poor’ except in the central estuary which remained designated as ‘moderately disturbed’ by M-AMBI and ‘Good’ by IQI through the investigated period. Following the disturbance event (1991-1992), habitat quality was generally upgraded from ‘poor’ to moderate in all regions (except the central region) based on both M-AMBI and IQI. Neither indices could detect a positive or negative change in habitat quality between the pre- and post-management periods.

Table 3.15 M-AMBI and Infaunal Quality Index (IQI) EQR scores from the Tamar estuary 1937-2005. Different colours represent environmental status; High (Blue), Good (Green), Moderate (Orange) and Poor (Yellow).

M-AMBI					
	1937	1990	1991	1992	2005
Whole	Moderate	Poor	Moderate	Moderate	Moderate
Upper	High	Poor	Moderate	Moderate	Moderate
Central	Moderate	Moderate	Moderate	Moderate	Moderate
Lower	Good	Poor	Poor	Moderate	Moderate
IQI					
	1937	1990	1991	1992	2005
Whole	Good	Moderate	Moderate	Moderate	Moderate
Upper	High	Poor	Moderate	Moderate	Moderate
Central	Good	Good	Good	Good	Good
Lower	Good	Moderate	Moderate	Moderate	Moderate

3.4.5 'Multivariate' analysis of structural indicators

Results of the PERMANOVA analysis (Table 3.16) were in general agreement with trends expressed by the indicators, both when the indicators from all three zones were pooled to represent the estuary as a whole and within individual zones of the estuary. Altogether five of the seven (Pielou, Margalef, Shannon–Wiener, Simpson and taxonomic diversity) indices tested exhibited significant (one-way PERMANOVA all $p < 0.05$) negative temporal differences between the historic (1937) and high nutrient periods (1990-1992). The same indices also expressed a significant (one-way PERMANOVA all $p < 0.05$) corresponding trend of increased ecological status between the high nutrient periods (1990-1992) and the post-management period (2005). Immediately following the eutrophication event (1990), significant ($p < 0.05$) negative differences in species composition, were detected in the year following the eutrophic symptoms (1991), by Pielou's, Shannon–Wiener and Simpson's index.

When comparing the historic (1937) period with its contemporary counterpart (2005) five of the seven indices (Pielou, Margalef, Simpsons, taxonomic diversity and total taxonomic distinctness) tested with no degree of temporal difference (one-way PERMANOVA all $p < 0.05$). In contrast the Shannon–Wiener index displayed a significant positive increase ($p < 0.05$) during this period, while average taxonomic distinctness of species was significantly ($p < 0.05$) lower. Both of the taxonomic distinctness indices tested, were unable to detect temporal changes among years (all $p > 0.05$), except between the 1937 vs 1991 and 1937 vs 2005 periods. During this time both indices presented lower mean values, except for the 1937 vs 2005 period where total taxonomic distinctness exhibited similar mean values.

	Ecological indicator						
	Pielou	Margalef	Shannon–Wiener	Simpsons	Taxonomic diversity	Taxonomic distinctness	Total taxonomic distinctness
1937 vs 1990	↓	↓	↓	↑	↓	p > 0.05	p > 0.05
1937 vs 1991	↓	↓	↓	↑	↓	↓	↓
1937 vs1992	↓	↓	↓	↑	↓	p > 0.05	p > 0.05
1937 vs 2005	p > 0.05	p > 0.05	↑	p > 0.05	p > 0.05	↓	-
1990 vs1991	↓	p > 0.05	↓	↑	p > 0.05	p > 0.05	p > 0.05
1990 vs1992	↑	-	p > 0.05	-	p > 0.05	p > 0.05	p > 0.05
1991 vs 1992	↑	p > 0.05	-	-	p > 0.05	p > 0.05	p > 0.05
1990 vs 2005	↑	↑	↑	↓	↑	p > 0.05	p > 0.05
1991 vs 2005	↑	↑	↑	↓	↑	p > 0.05	p > 0.05
1992 vs2005	↑	↑	↑	↓	↑	p > 0.05	p > 0.05

Table 3.16 Synopsis of the ecological indicators trends obtained for the Tamar Estuary. Arrows in an upward (Green) and downward (Red) direction represent an increase and a decrease in the indicators mean values between each period, respectively. Horizontal lines (Yellow) indicate similar indicators mean values between periods. No significant statistical differences (Orange) in indices values among years and thus, between periods, showed by ($p > 0.05$), considering a significance level of 0.05. Results represent the whole estuary including changes in the upper, middle and lower zones.

3.4.6 Biological traits of the Tamar benthic community.

When considering the biological traits composition data from all of the estuarine zones together throughout the study period (Table 3.17), a significant interaction for the factors ‘year’ and ‘zone’ was detected by the two-way PERMANOVA analysis (two-way PERMANOVA, all zones: $p < 0.05$) indicating the existence of spatial and temporal differences.

Table 3.17 Pseudo-F (pF) values and significance levels (P) for two-way PERMANOVA tests, employing separate Euclidean distance resemblance matrices constructed from the ‘traits by station’ matrix, across each of the 1937, 1990,1991,1992,2005 periods. df= degrees of freedom. Significant differences ($p = < 0.05$) are highlighted in bold.

Whole estuary	pF(df)	p
Year	10.754(4)	0.001
Zone	38.991(2)	0.001
Yearxzones	8.334(8)	0.001

Visual assessment, by considering the nMDS for the spatial factor ‘year’ (Figure 3.9) suggests that there was a clear separation between the high nutrient periods (1990-1992) and the relatively lower nutrient periods (1937 & 2005) most likely providing the significant differences from the two-way analysis. Based on hierarchical clustering analysis, the high nutrient periods were all determined to be 80% similar, in terms of benthic community functioning. Spatial segregation of the community traits coded by the factor ‘zone’ also indicated distinct differences between the traits expressed by taxa in each of the three zones over the time periods.

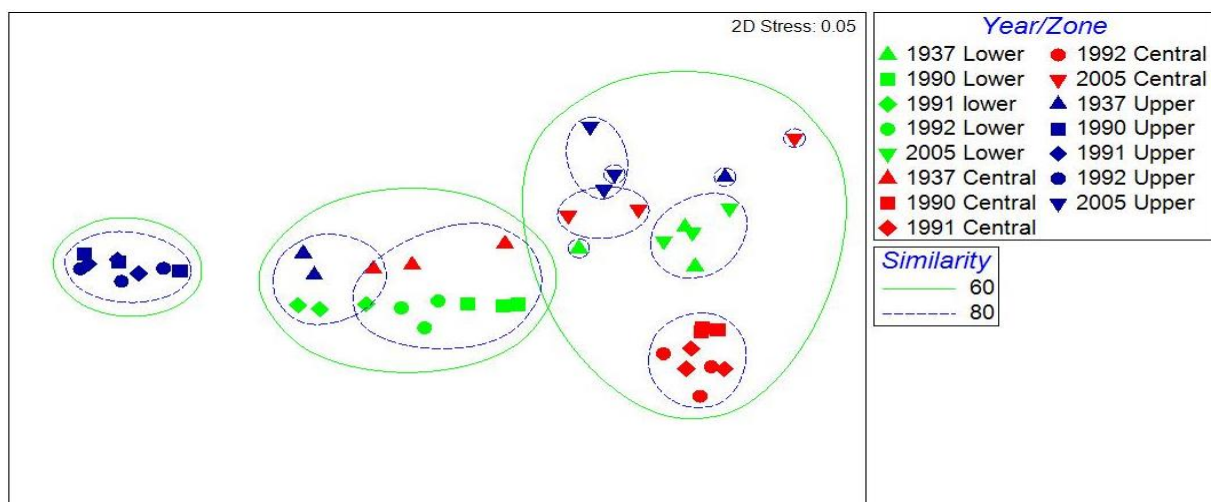


Figure 3.9 nMDS ordination plots of biological traits composition data considering data from all estuarine zones together over the time periods defined by the intervention under study: Historic 1937 (Triangles), Eutrophic 1990 (Squares), Post-Eutrophic 1991 (Diamonds), Pre-management 1992 (Circles) and Post-management 2005 (Inverted triangles).

With regard to the main trait categories characterising the Tamar Estuary during the time periods (Figure 3.10):

Body Size: Generally the Tamar Estuary, was dominated by individuals with large body sizes (11-20cm), with a >80% representation of these individuals, during the 1937-1992 period. During the eutrophic and high nutrient periods (1990-1992), there was reduction in the numbers of very small (<1cm), small (1-2cm) and medium (3-10cm) taxa and a relative increase in the numbers large bodied individuals. In the post- management period (2005) the system graduated back towards a system composed of diverse body sizes, with a particular abundance of medium (3-10cm) sized individuals.

Life Span: Species with long life spans (or K strategists) were found in the greatest numbers during the historic (1937), and post-management (2005) periods. Short lived species (or r strategists) dominated the majority all of the periods, representing over 80% of the biomass at any given period.

Growth form: Veriform segmented species were the most representative species, found in the Tamar across all periods. During the eutrophic period (1990) there was a reduction in the biomass of articulate, tubicolous, bivalved and turbinata individuals. In the period following the management intervention (2005), tubicolous, bivalve and turbinata individuals once again increased in prominence.

Reproductive method: Species with a gonochoristic reproductive-technique were prevailing across all time periods. During the post-management period (2005) there was a substantial increase (40 %) in hermaphrodite species biomass.

Resource capture method: Feeding strategies were largely distributed evenly among the four groups across the time periods. Only during the post-management period (2005) was there any change in species behaviour to resource acquisition, with an increase in the numbers of deposit feeding species.

Mobility in the sediment: Free moving species contributed the most to overall biomass across of the estuary during the 1937 -1992 periods. During the 2005 period free moving species were replaced by slower free moving individuals and an increase in more sessile species. During the high nutrient periods (1990-1992) there was a decrease in stationary, tube building species and slow free moving individuals corresponding with an increase in free movement individuals.

Environmental position: Endobenthic species were the dominant species across all years. Only during the 1937 and 2005 periods did hyperbenthic species increase in total biomass.

Bioturbation functional type: Infaunal behaviour was mainly categorised by organisms with activities that mix sediment homogeneously over short distances *i.e.* bio-diffusers. Between the historic (1937) and high nutrient (1990-1992) periods there was a decrease in the diversity of relative sediment reworking modes of individuals, including upward, downward conveying and surface modifying

individuals . During the post-management period (2005) there was recorded increase in upward and downward conveyors of material.

Salinity preferences: Species tolerance to salinity was largely analogous between tolerance boundaries and periods. The only exception being, a slight decrease of tolerance to low salinity individuals (<5) during the post-management period (2005).

Ecological group: According to initial AMBI ecological groupings, the mainstay of taxa residing within the Tamar were classified as tolerant to ecological change. All four tolerance classifications were expressed in the historic period (1937) with a slight drop in sensitive species found during the high nutrient periods of 1990-1992. The greatest difference, however occurred during the post-management period (2005), with a sizable increase in very tolerant individuals.

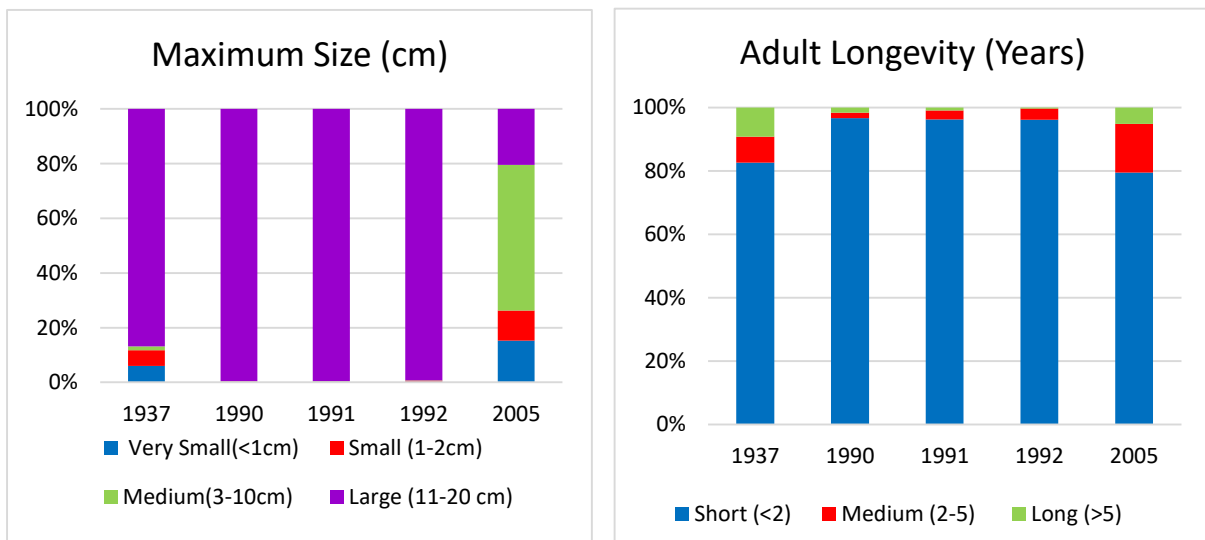


Figure 3.10: Biological traits patterns for the Tamar estuary over the study period (1937–2005)

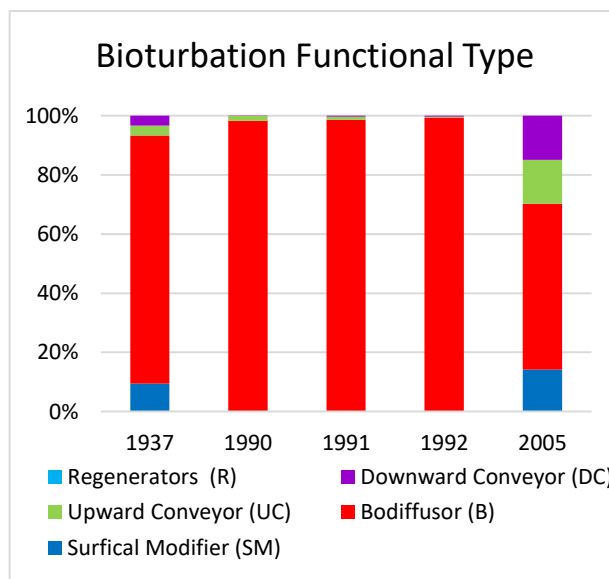
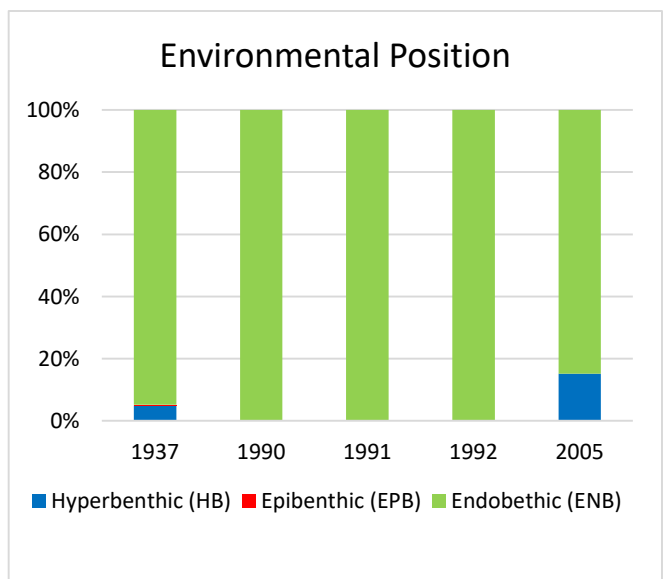
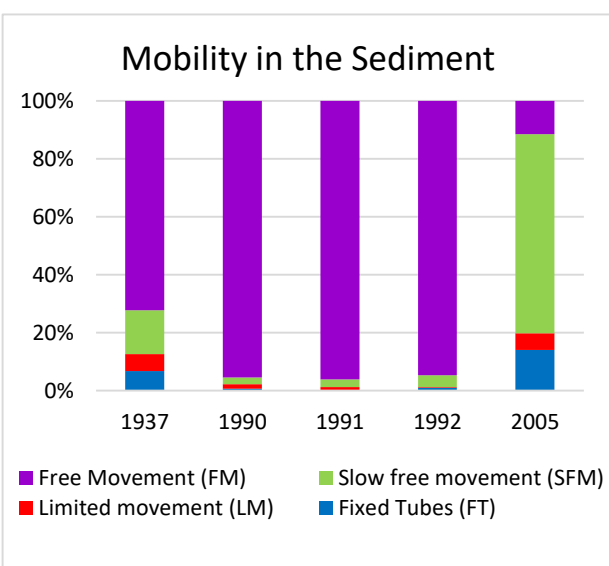
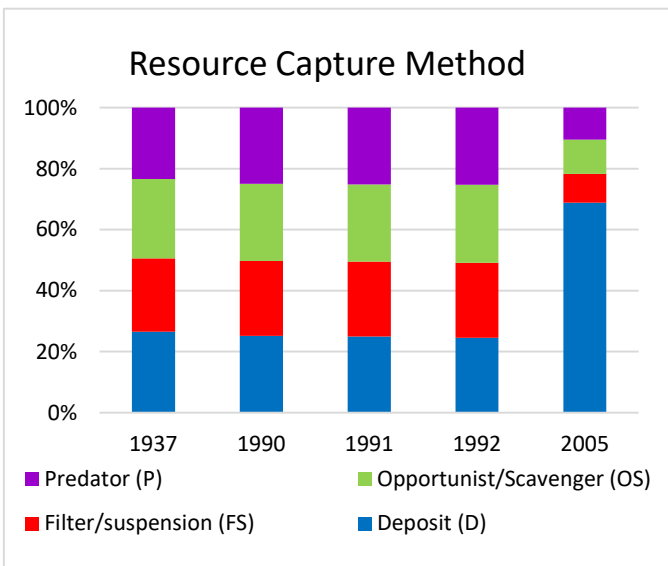
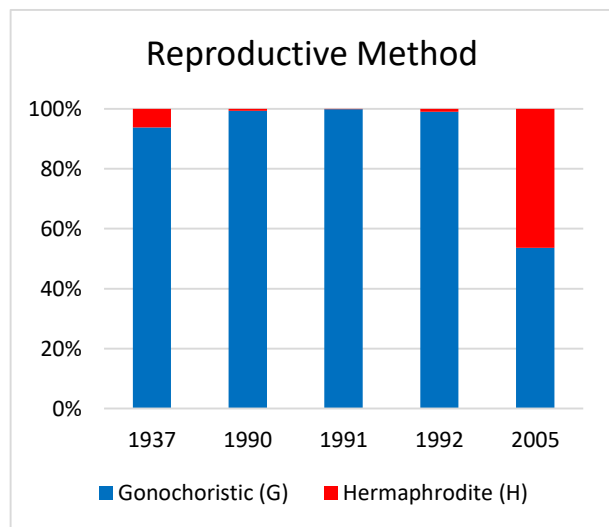
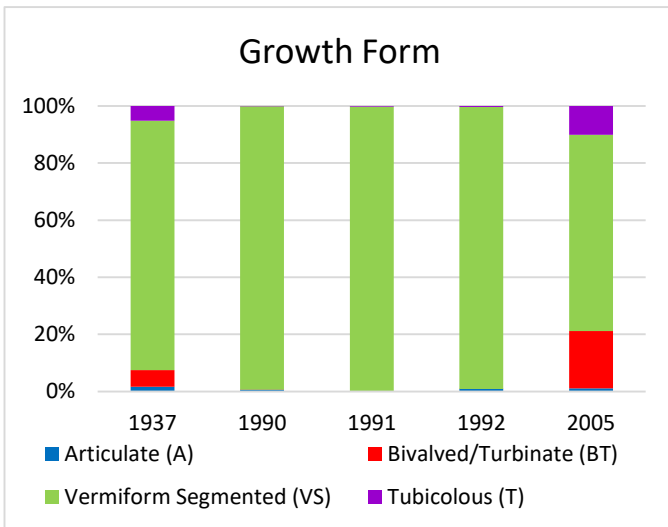


Figure 3.10 (continued): Biological traits patterns for the Tamar estuary over the study period (1937–2005)

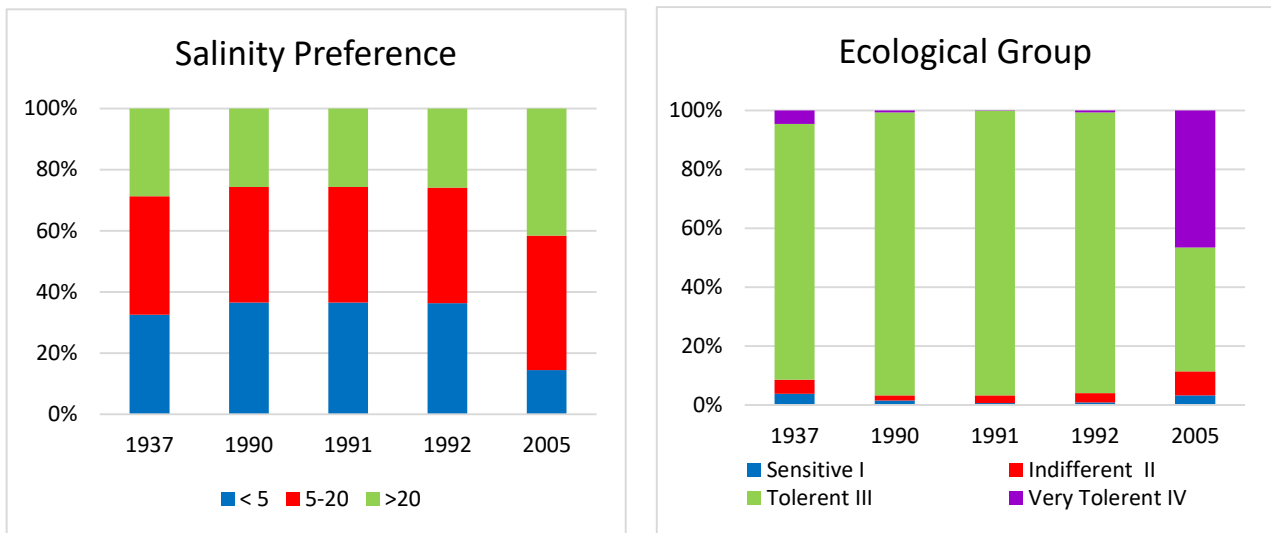


Figure 3.10 (continued): Biological traits patterns for the Tamar estuary over the study period (1937–2005).

When each estuarine zone was assessed individually, clear temporal trends in traits composition were visible on the nMDS plots across all zones (Figure 3.11). Generally the high nutrient periods (1990-1992) displayed a high degree of hierarchical clustering and therefore ecological functioning across all zones, while the historic (1937) and post-management (2005) periods were also functionally similar.

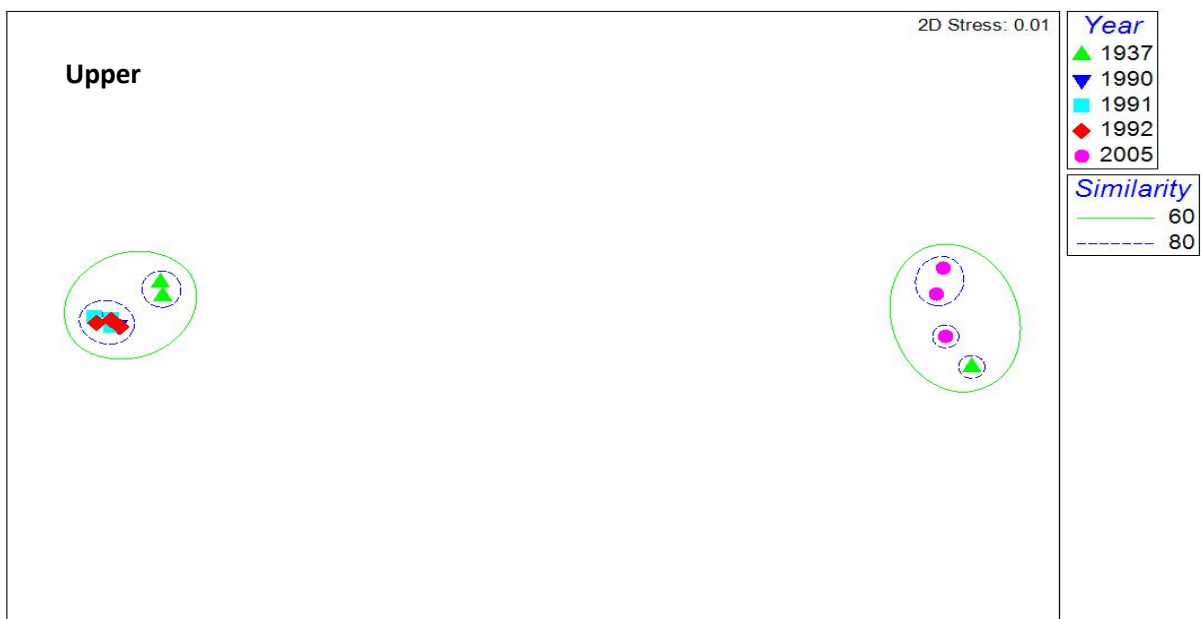


Figure 3.11: nMDS ordination plots based on macro-benthic biomass trait data for the three individual zones (Upper, Central and Lower), and coded for the temporal factor 'year'.

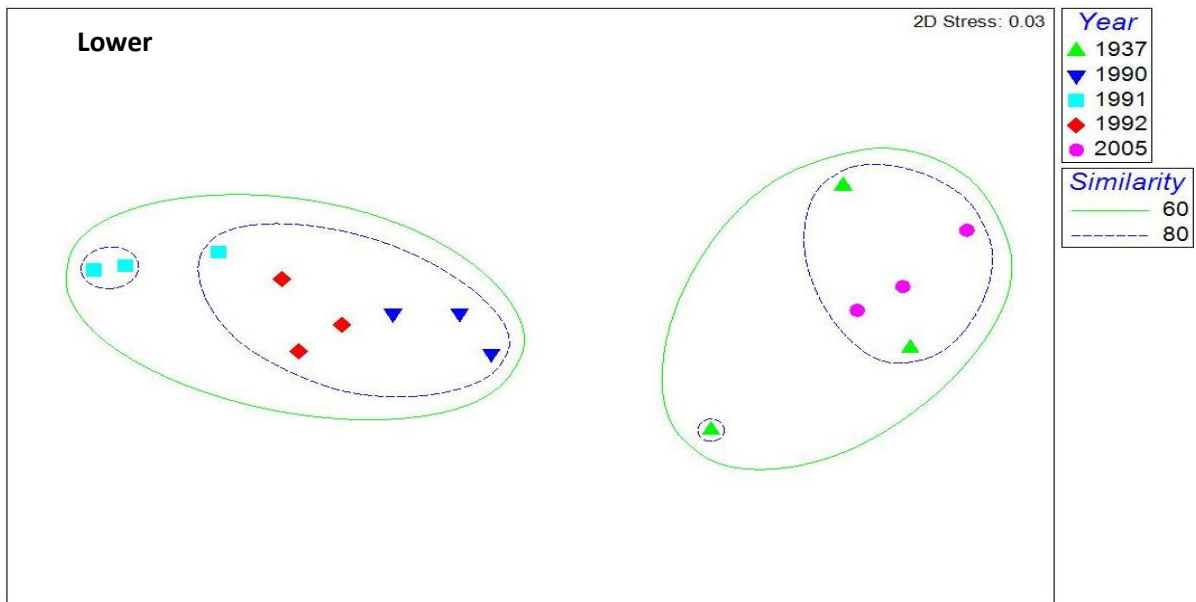
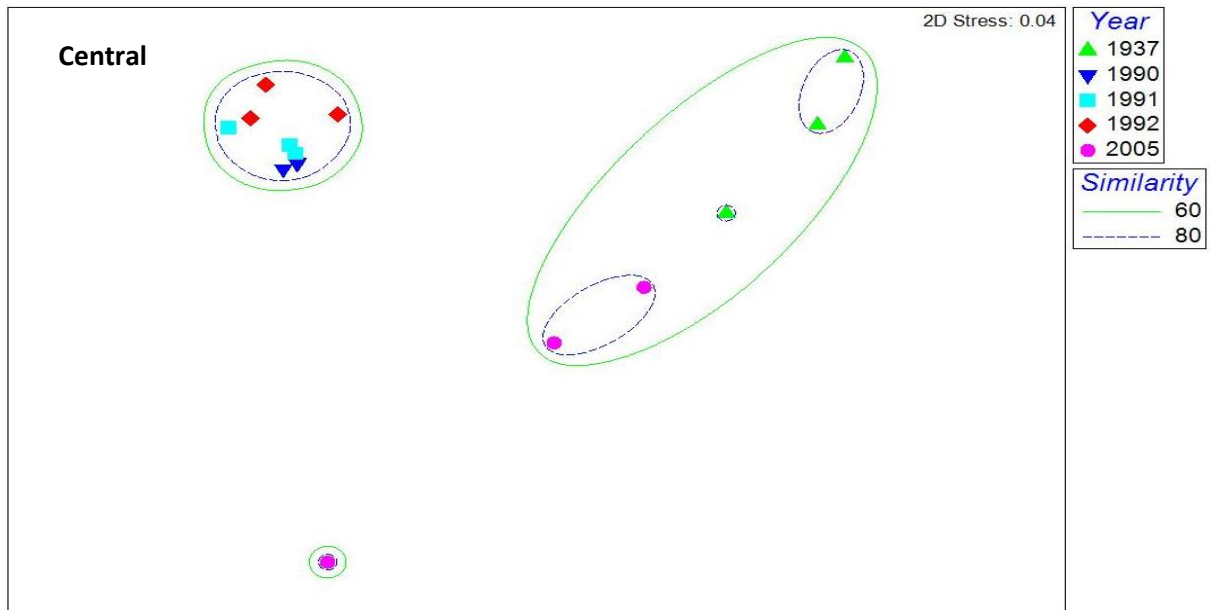


Figure 3.11 (continued): nMDS ordination plots based on macro-benthic biomass trait data for the three individual zones (Upper, Central and Lower), and coded for the temporal factor ‘year’.

Corresponding with the visual separation of traits expressed in the nMDS plots, significant differences could be detected statistically (one-way PERMANOVA, all $p < 0.05$) in inter-tidal benthic community functioning between the 1990, 1991 and 1992 vs 1937 or 2005 (Table 3.18) years at the whole estuary scale and at the level of individual zones. Significant changes in ecological function also were detected in the central and upper zones 1937 vs 2005, when all zones were considered separately (one-way PERMANOVA, all $p < 0.05$).

Table 3.18 Community traits one-way PERMANOVA pair-wise post hoc comparisons among years for the whole estuary and each estuarine zone. Values in bold were significant at ($p < 0.05$).

Year	Zones			
	Whole	Upper	Central	Lower
1937, 1990	0.023		<0.05	<0.05 <0.05
1937, 1991	0.028		<0.05	<0.05 <0.05
1937, 1992	0.032		<0.05	<0.05 <0.05
1937, 2005	0.134		<0.05	<0.05 >0.05
1990, 1991	0.675		>0.05	>0.05 >0.05
1990, 1992	0.493		>0.05	>0.05 >0.05
1990, 2005	0.035		<0.05	<0.05 <0.05
1991, 1992	0.243		>0.05	>0.05 >0.05
1991, 2005	0.276		<0.05	<0.05 <0.05
1992, 2005	0.342		<0.05	<0.05 <0.05

With regard to the biological trait changes thought the study period observed for the aforementioned zones, trait changes typically mirrored those of the estuary as a whole (Figure 3.12). Major changes in trait dominance, were only evident during the high nutrient periods (1990-1992) of the central estuary. During this timeframe functional differences of traits that differed from the whole estuary and other zone trends were especially evident: with a shift in dominance to short (<2) and medium (2-5) lived species (life span); removal of free moving species to slow or limited moving species (mobility); slight increase in articulated species (growth form); increase in upward and downward conveyors, during the 1990 and 1991 period only (bioturbation functional type); removal of low salinity tolerant (<5 ppm) species (salinity preference) and a general increase in sensitive or intolerant individuals (ecological group).

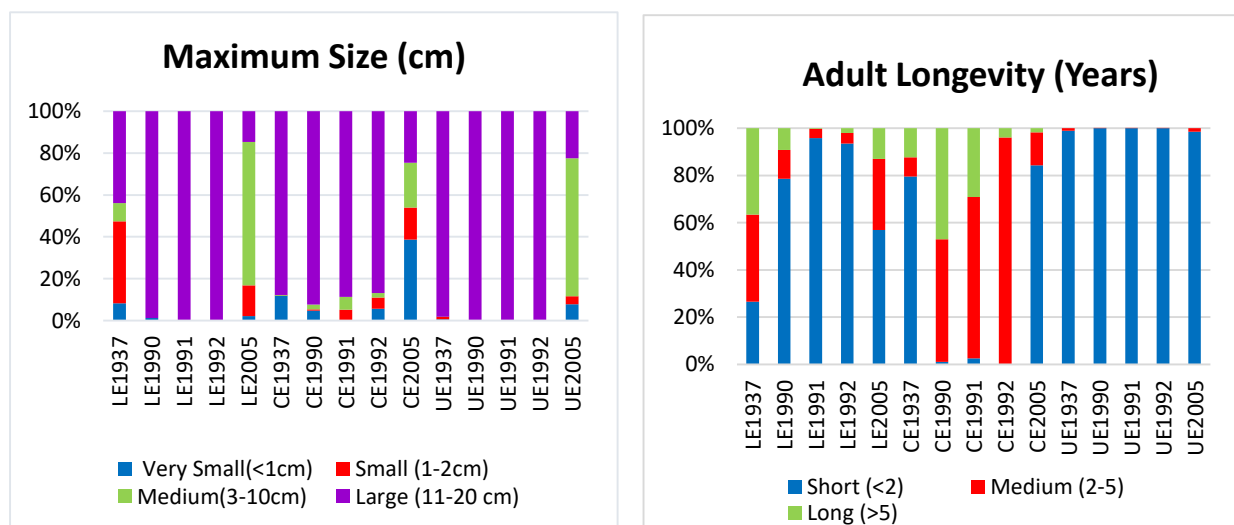


Figure 3.12: Biological trait patterns for the Tamar estuary over the study period (1937-2005)

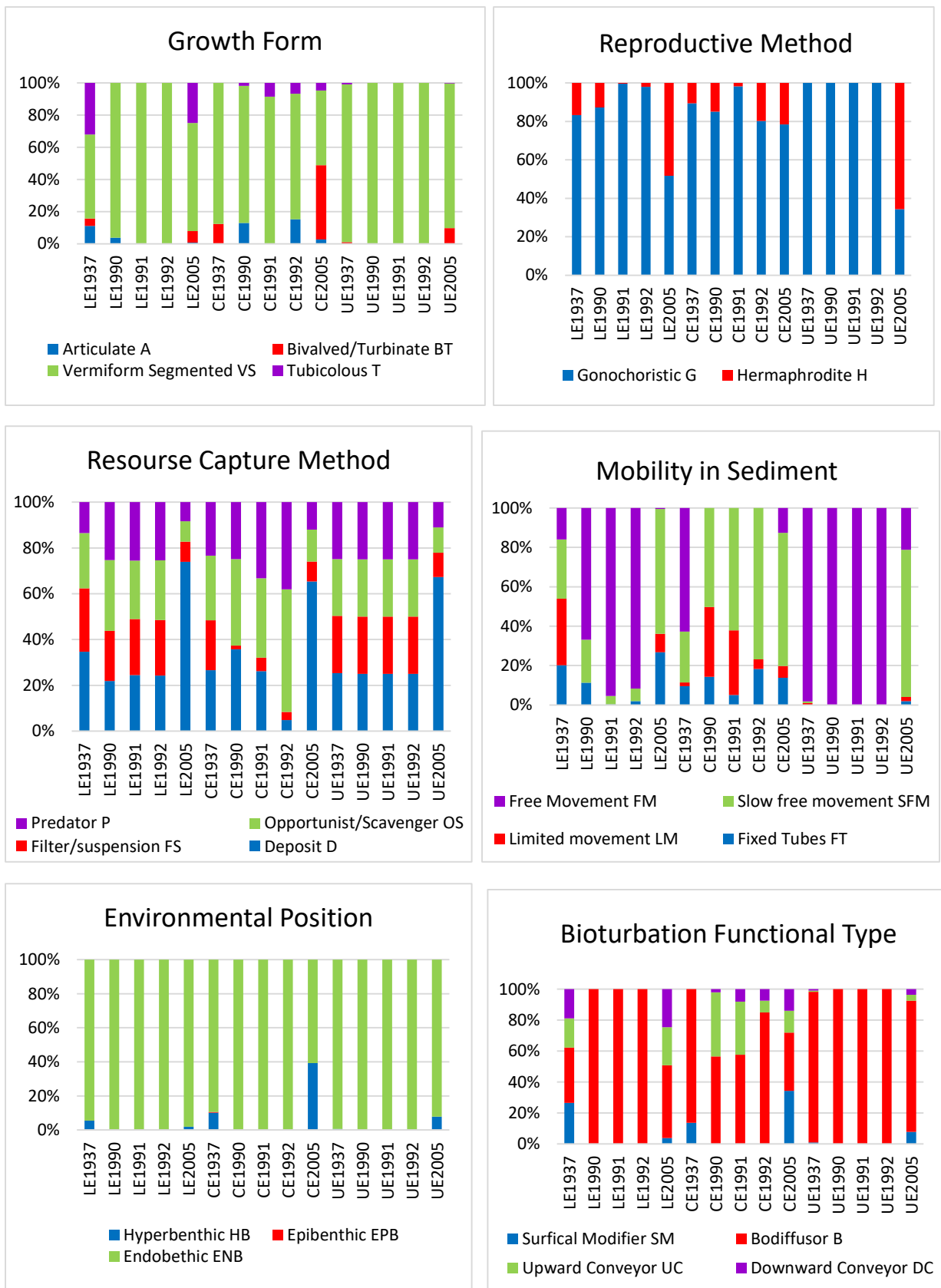


Figure 3.12 (continued): Biological traits patterns for each zone of the Tamar estuary over the study period (1937–2005).

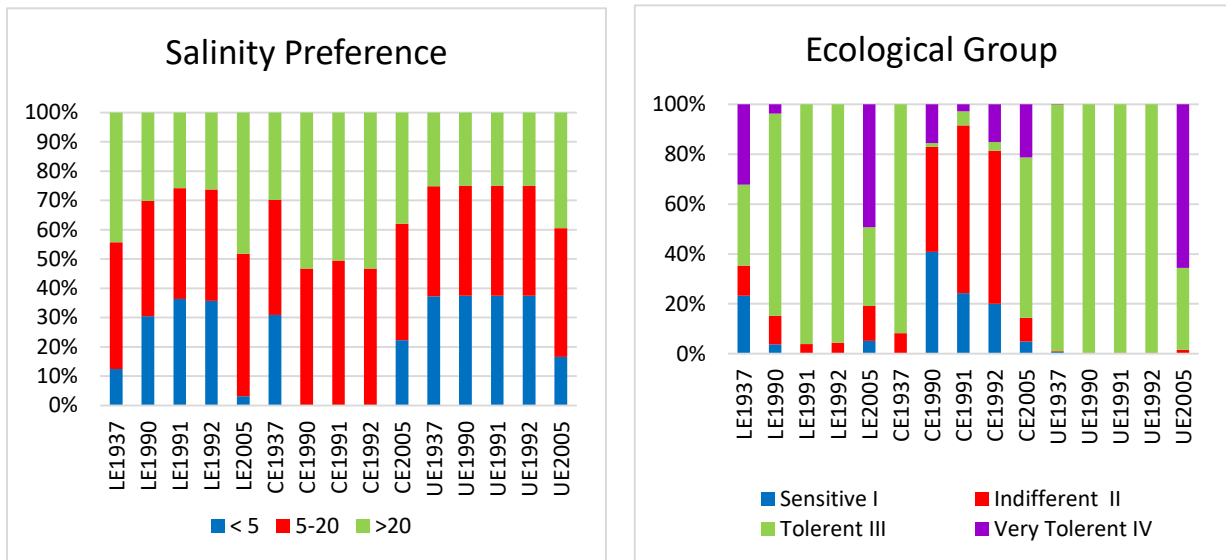


Figure 3.12 (continued): Biological traits patterns for each zone of the Tamar estuary over the study period (1937–2005).

3.4.7 Tamar Bioturbation potential (Bpc) results

Bpc calculations for the estuary as a whole, ranged from 365 to 615 (Figure 3.13). The highest Bpc values were observed in the high nutrient periods (1990-1992) when the community at this site was mainly dominated by motile deep burrowing polychaetes, such as *Nephtys hombergii* and *Hediste diversicolor*. The lowest Bpc values were found in the post-management period.

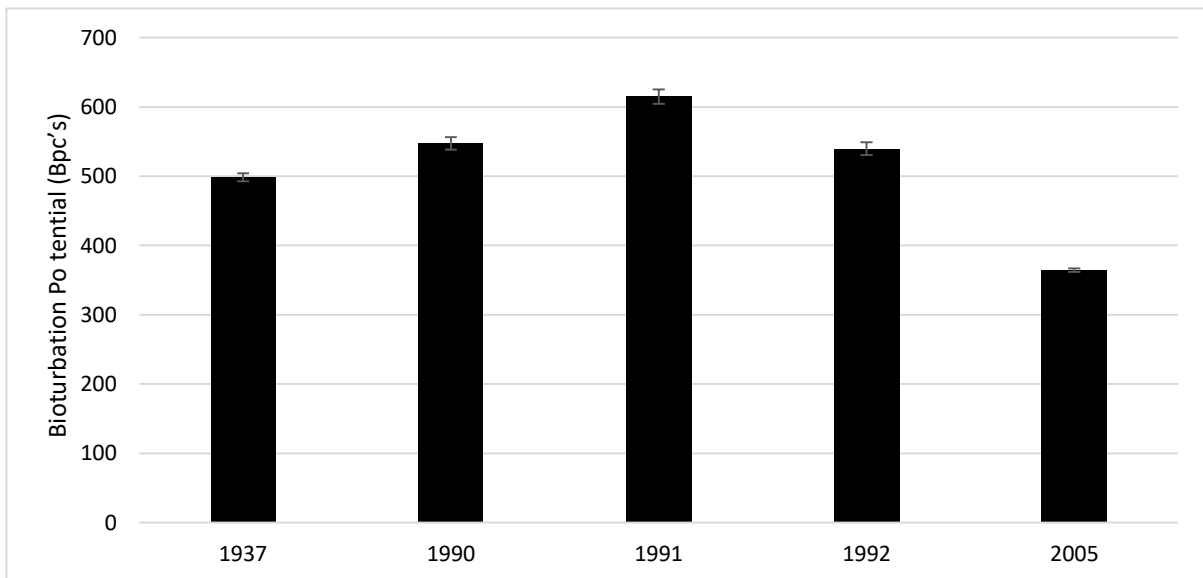


Figure 3.13 Bioturbation potential (Bpc) values for the Tamar estuary (1937-2005) with 95% confidence intervals.

When Bpc calculations were conducted at all individual sites (Figure 3.14), the values ranged from 81 to 345. The highest values of Bpc were found in the upper region of the estuary, with over a 100% increase in functioning of individuals during the high nutrient periods (1990-1992). In comparison, Bpc in the low nutrient period (2005) in this zone was much lower. In the central and lower estuary, trends were more stable. The central estuary exhibited the opposite trends to the upper estuary, with a fall in Bpc during the high nutrient periods, while in the lower estuary similar Bpc values were observed.

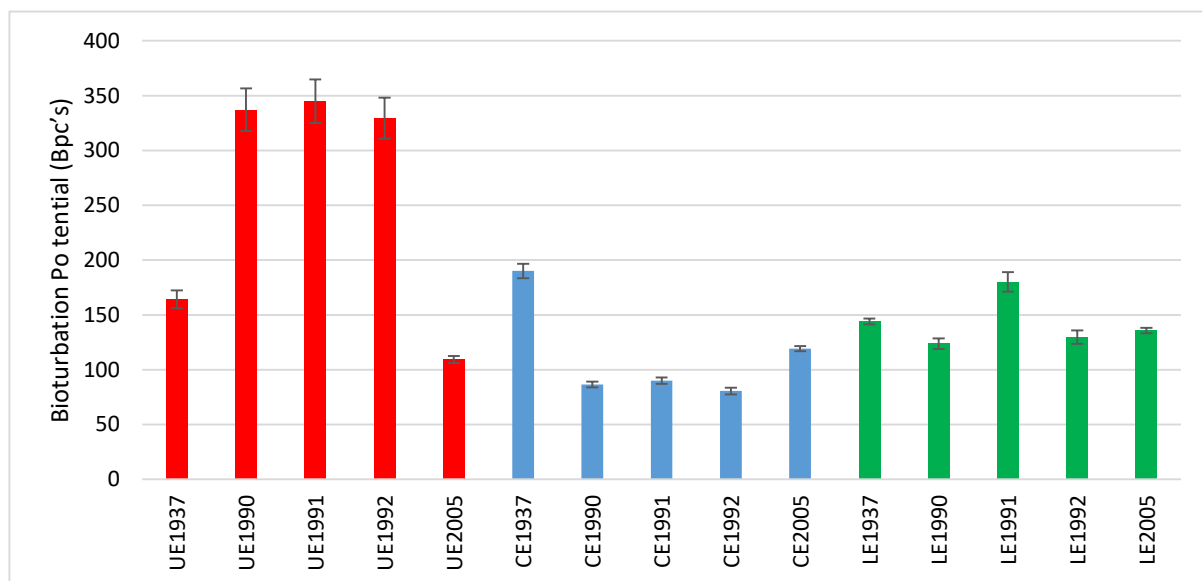


Figure 3. 14 Bioturbation potential (Bpc) values for the Tamar estuary by year (1937-2005) and zone; upper (red), central (blue) and lower (green) with 95% confidence intervals.

3.5 Eden results

Overall, a total of 43,050 individuals from over 27 different taxa were identified, from the 60 samples taken from the Eden estuary over the 1999 and 2015 periods. The macro-faunal abundance was dominated by Polychaetes (9 families), followed by Molluscs (8 families), Crustaceans (6 families), Oligochaetes (1 family) and others (1family).

3.5.1 Eden environmental variables

A summary of the physiochemical trends found during the Exploratory Data Analysis (EDA) are shown in Table 3. 19. Available historic data regarding changes in salinity was too limited in quantity to make any statistical correlations, but the data are still valuable to infer broader patterns over time. For instance the indication of a much lower salinities during the 2010 period would correlate well with the increases in the far more robust datasets, i.e. NAO and river flow suggesting changes in salinity regimes could be driven by increased river discharges often associated with positive NAO periods.

Table 3.19 Trends of selected physiochemical determinants for the Eden estuary (1990-2015).

Variable	Year	Observed trend
Temperature (°C)	1990-2014	Very little change
pH	1990-2014	Increasing towards more alkaline conditions
Surface salinity (psu)	1990 vs 2010	Decrease 9 psu
Dissolved oxygen (mg l ⁻¹)	1990-2014	Very little change
Ammonium (mg l ⁻¹)	1990-2014	Decreasing
Nitrite (mg l ⁻¹)	1990-2014	Decreasing
Nitrate (mg l ⁻¹)	1990-2014	Decreasing
Filterable reactive phosphorus (mg l ⁻¹)	1990-2014	Decreasing
River flow (m ³ /s)	1990-2015	Sequential increase in total flow and mean flow (cumecs)
North Atlantic Oscillation index	1990-2015	General trend towards a positive NAO in the twenty-first century
Depth (m)	2002-2009	Main channel has become shallower and slightly narrower
Granulometry (mm)	1999 vs 2010	Increase in fine muddy particles in the central estuary

More robust comparisons could be made with reference to the amount of nutrients entering the catchment (Figure 3.15) , with average ammonium, nitrite, nitrate and phosphate concentrations all showing a linear decline between 1990 & 2014. In contrast, a positive trend line based on the pH of water entering the catchment was observed between the 1990-2014 periods, suggesting a progressive trend to water becoming more alkaline. Mean trends in dissolved oxygen levels and water temperature were largely stable between the 1990-2014 periods, suggesting the waters entering the catchment to be well oxygenated and subject to typical inter-annual fluctuations in water temperature with no perceived pattern of change.

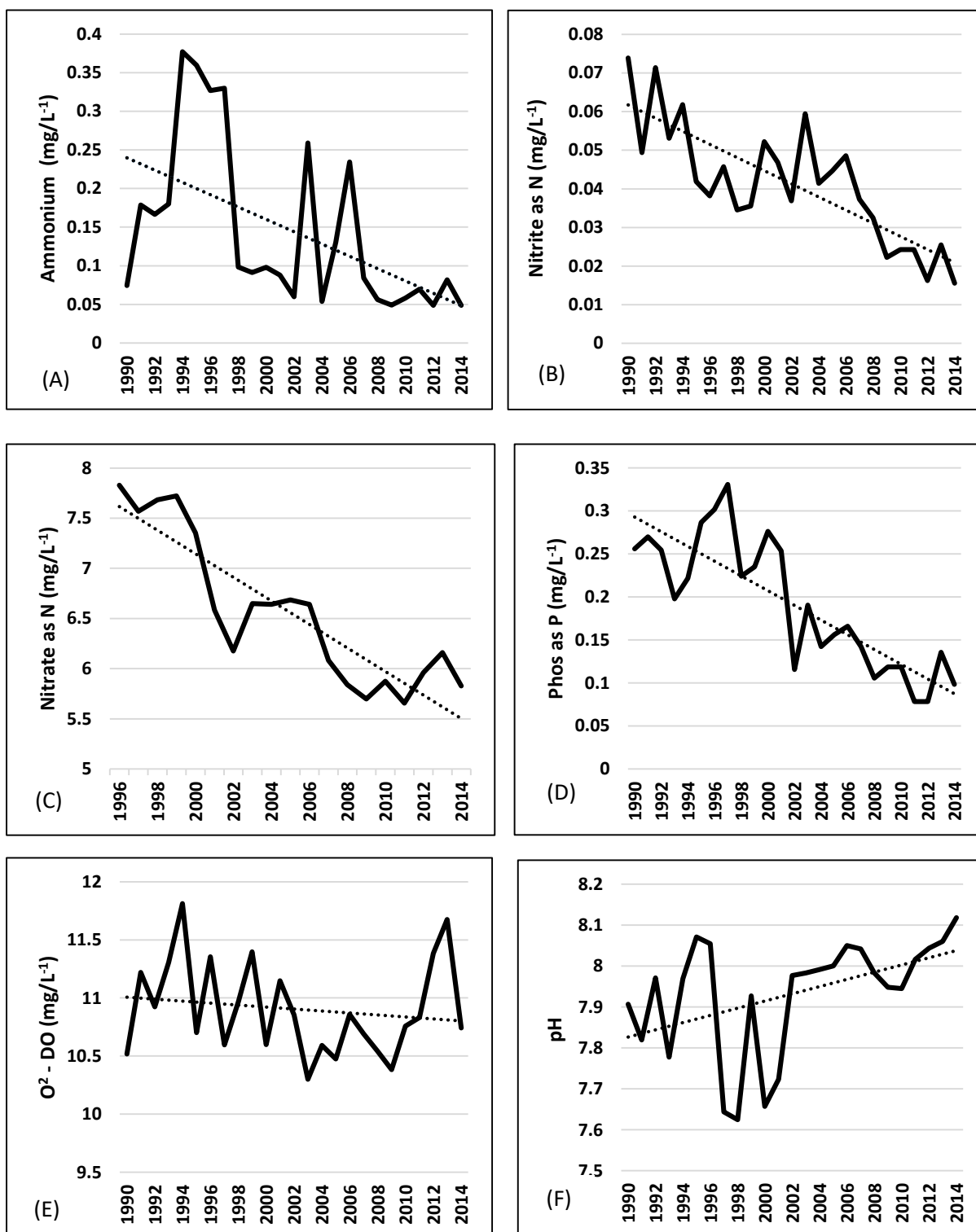


Figure 3.15 Selected physiochemical determinants; (A) ammonium (mg l^{-1}), (B) nitrite (mg l^{-1}), (C) nitrate (mg l^{-1}), (D) filterable reactive phosphorus (FRP, mg l^{-1}), (E) dissolved oxygen (mg l^{-1}) and (F) pH and for the Eden estuary (1990-2014) measured at the Kemback gaging station.

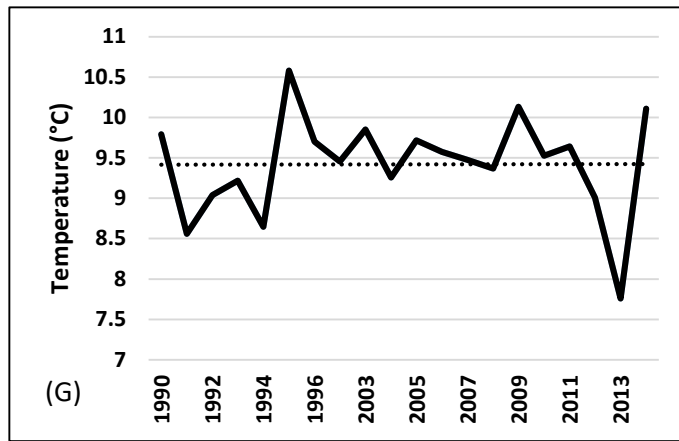


Figure 3.15 (continued) Selected physiochemical determinants; (G) temperature (°C) for the Eden estuary (1990-2014) measured at the Kemback gaging station.

EDA of the river Eden annual flow data (Figure 2.6) revealed a prevalent gradual increase in both total flow and mean flow (cumecs) over the time series. Investigating this apparent trend further, the linear regression for Figure 3.19 has a gradient which gives a rate of change per year at 3.05 cumecs averaged over the 1990-2014 period. However the R^2 value for the regression is low (0.2369) resulting from the variability in the time series.

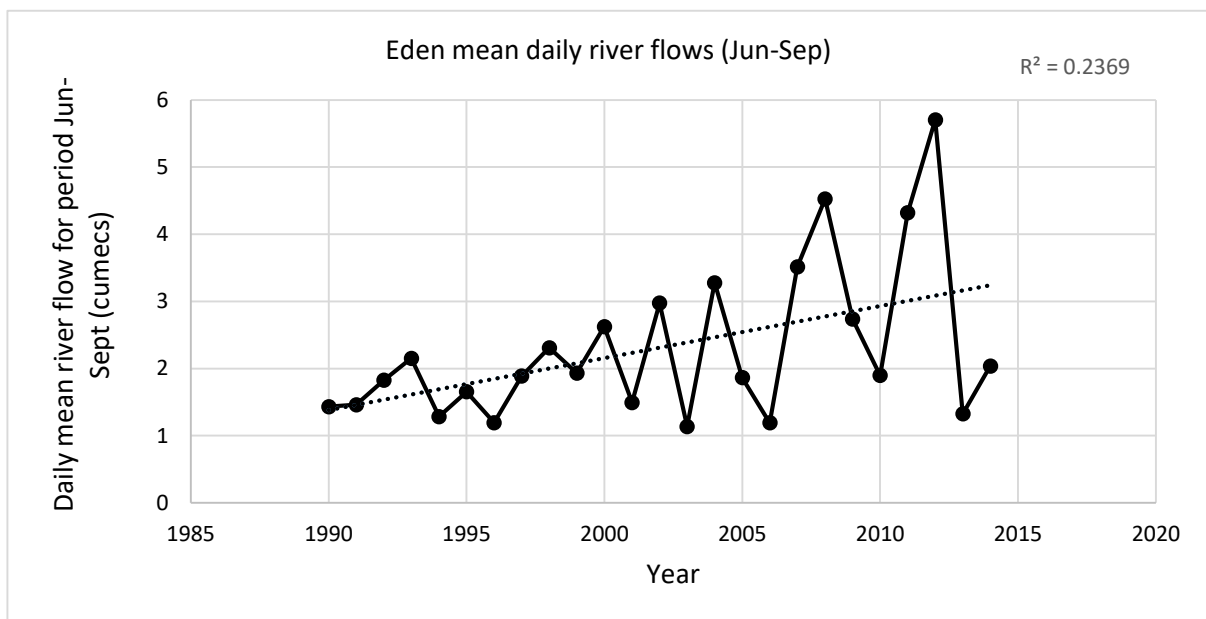


Figure 3.16 Annual mean daily river flows (summer; June-Sept) of the Eden Estuary (1990-2014)

Based on observations by Chocholek (2013) the morphology of the Eden Estuary was regarded to have changed markedly over the last decade. According to the author, the estuary has undergone an erosive phase during the period 2002 -2009 while bathymetry profiles show since 2002 the channel has become shallower and slightly narrower with the possibility of future loss of the central slot channel due to infilling by sediment, leading to an increased risk of floods within the estuary. During the same investigation, the author also observed an increase in finer mud particles in the central region of the estuary in comparison to the BIOPTIS 1999 sampling period.

Synoptic chlorophyll *a* measurements suggested an increase in microphytobenthic biomass across each of the zones between the 1999 BIOPTIS and 2015 sampling periods (Table 3.20), with the largest change occurring in the upper estuary.

Table 3.20 Mean benthic chlorophyll *a* measurements from contact cores for each zone of the Eden estuary.

Synoptic chlorophyll <i>a</i>	Zone		
	Upper	Central	Lower
1999	1639.11	2442.57	16.45
2015	2415.96	2702.95	21.68

3.5.2 Eden abundance and biomass

Abundance and biomass values for the Eden estuary differed markedly between the pre-management (1999) and post-management (2015) periods (Table 3.21). Abundance of individuals found in the upper and central regions of the estuary were lower in the 2015 period, represented by a drop individuals by a factor of -38.21% (6972 individuals) and -12.60% (3943 individuals) respectively. In contrast the numbers of macro-fauna found during in the 2015 period in the lower estuary was greater by ~57% (446 individuals), attributing to a 37.48% (0.55g m²) increase in total biomass. Conceding with lower abundance estimates in the central estuary for the 2015 period, representative biomass was also lower by ~37% (9.05g m²). The opposite of this trend was displayed when comparing the upper estuary, which despite showing the largest percentage drop in abundance, exhibited an increase of ~5% (0.48g m²) in biomass.

Table 3.21 Total density (N) and biomass (AFDW g) recorded at each site during the study period.

	Site	Number of stations (replicates)	1999	2015	Total
Abundance (N m ²)	Upper	7	12607	5635	18242
	Central	10	17614	13671	31285
	Lower	3	164	610	774
Biomass (AFDW g m ²)	Upper	7	4.02	4.51	8.54
	Central	10	16.74	7.69	24.44
	Lower	3	0.46	1.02	1.48

A summary of mean values for the number of individuals and biomass at each site during the study period is given (Figure 3.17). When considering the abundance and biomass composition data from all

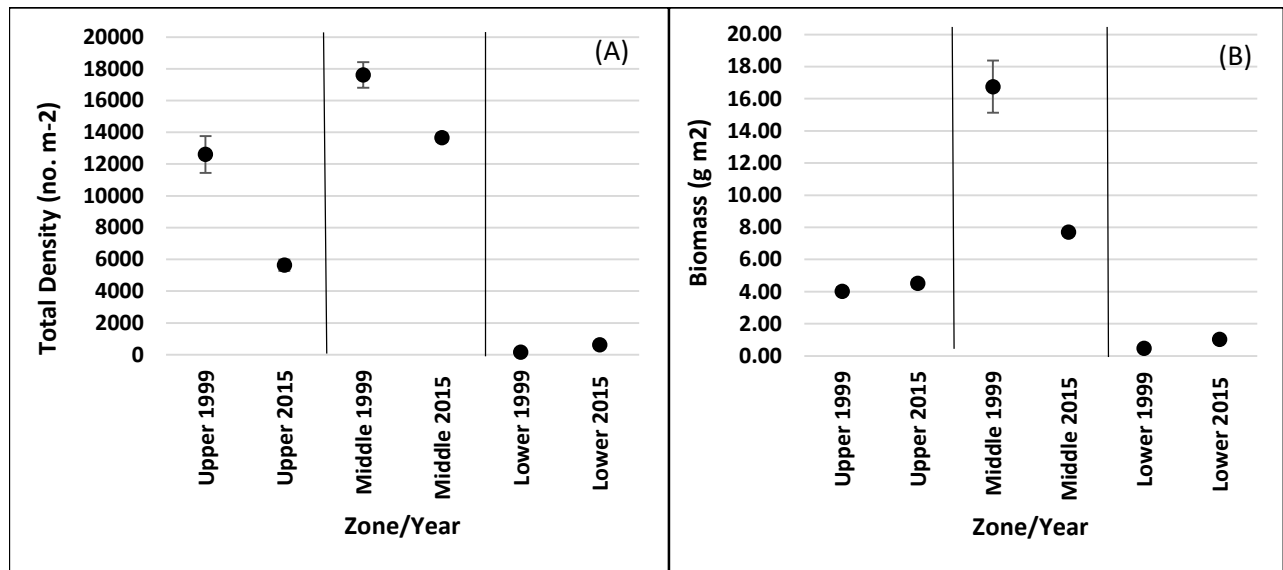


Figure 3.17 Summary of means and 95% confidence intervals of (A) total density and (B) biomass (AFDW)

estuarine zones together throughout the study period, a significant interaction ($p < 0.05$) for the factors 'Year' and 'Zone' was detected by a two-way PERMANOVA analysis (Table 3.22), indicating the existence of significant temporal and spatial differences between the 1999 and 2015 periods. A significant difference ($p < 0.05$) was also detected between the two factors (Yearxzones) when considering the abundance of individuals, but not their overall biomass ($p > 0.05$).

Table 3.22 Pseudo-F (pF) values and significance levels (P) for two-way PERMANOVA tests, employing separate Euclidean distance resemblance matrices constructed from the (pre-treated) data for total density and biomass data, collected on the Eden estuary across the 1999 and 2015 periods. df= degrees of freedom. Significant differences ($p = < 0.05$) are highlighted in bold.

	Density		Biomass	
	pF(df)	P	pF(df)	P
Year	3.9269 (1)	0.015	3.4322(1)	0.025
Zones	2.9875(2)	0.025	3.7798(2)	0.012
Yearxzones	3.8589(2)	0.007	0.68929(2)	0.612

When each estuarine zone was assessed individually, significant (< 0.05 one-way PERMANOVA) temporal differences were only detected in the upper estuary (Table 3.24) with regards to the density of individuals between the pre and post-management periods. These trends are well expressed in the nMDS ordinations shown in Figures 3.18 and 3.19, with the central sampling points showing a low degree of spatial segregation.

Spatial analysis of the data (table 3.22) by comparing only three stations in each zone, showed significant differences ($p < 0.05$) between the lower estuary and the central and upper regions both in terms of abundance and biomass although these trends were not clearly visible on the nMDS plots (Figures 3.21 and 3.22).

Table 3.23 One-way PERMANOVA pair-wise post hoc comparisons between years for the whole estuary and each estuarine zone using the t-statistic. Values in bold were significant at ($p < 0.05$).

Year	Density				Biomass			
	Whole	Upper	Central	Lower	Whole	Upper	Central	Lower
1999, 2015	1.9816	<0.05	>0.05	>0.05	1.8526	>0.05	>0.05	>0.05

Table 3.24 One-way PERMANOVA pair-wise post hoc comparisons among zones, using the t-statistic based on 3 stations in each region. Values in bold were significant at ($p < 0.05$).

Zone	Number of stations	Density	Biomass
Upper, Central	3	0.062	0.87563
Upper, Lower	3	2.11	2.5547
Central, Lower	3	2.53	2.4337

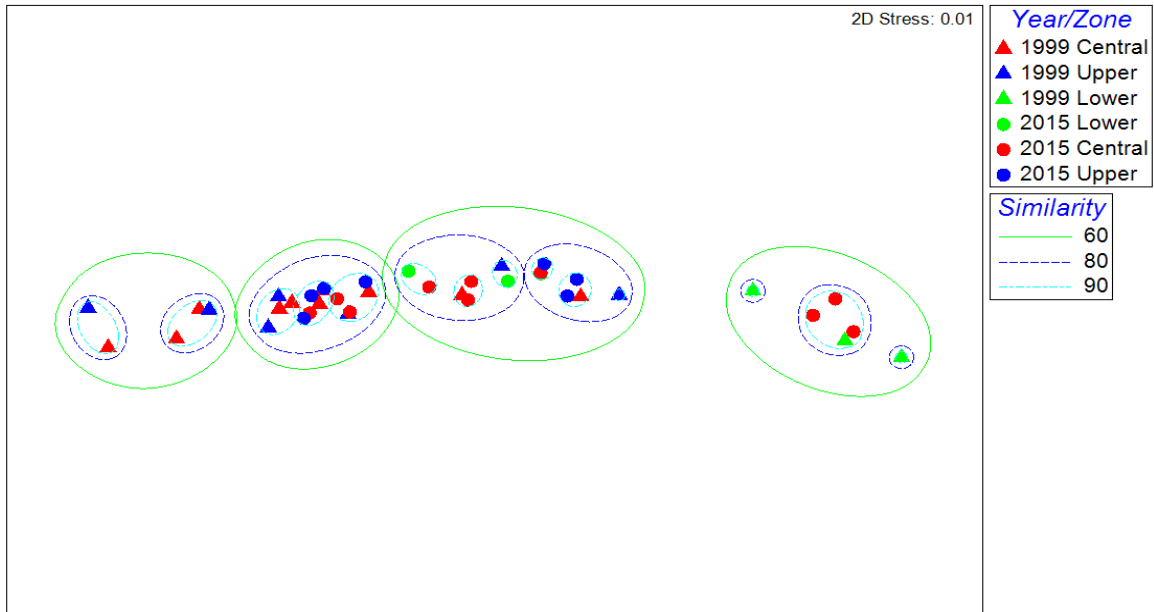


Figure 3.18 An nMDS plot based on square root transformed data of macro-benthic density data from all estuarine zones covering the two time periods defined by the intervention under study: Pre-management 1999 (Triangles) and Post-management 2015 (Circles).

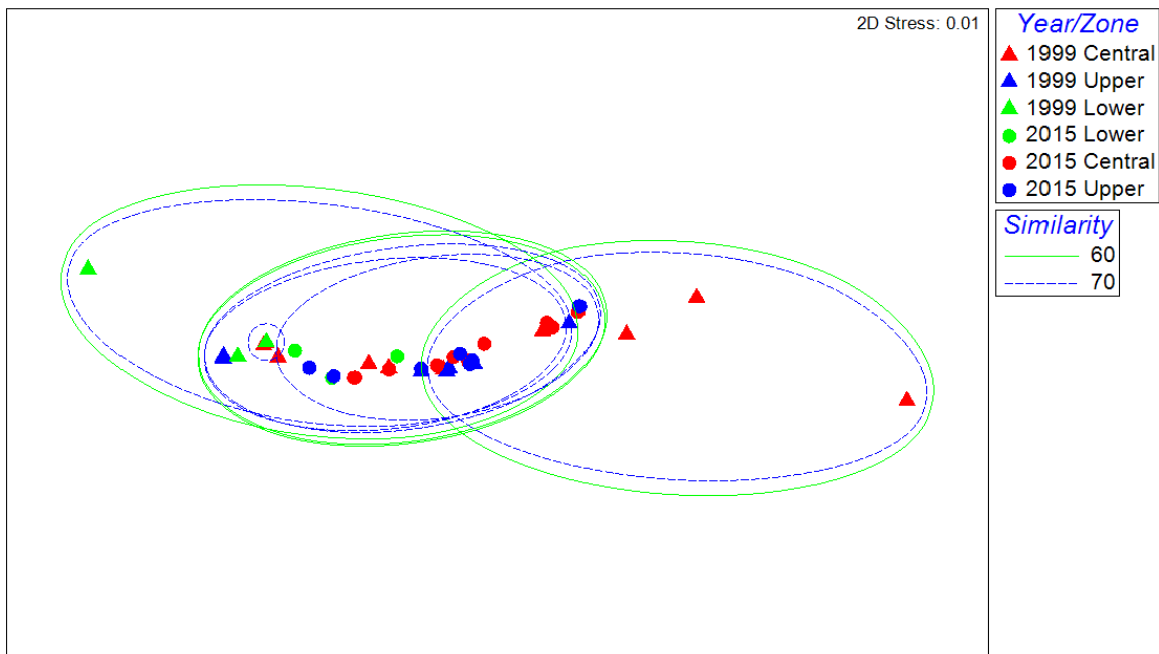


Figure 3.19 An nMDS plot based on square root transformed data of macro-benthic biomass data from all estuarine zones covering the two time periods defined by the intervention under study: Pre-management 1999 (Triangles) and Post-management 2015 (Circles).

3.5.3 Eden species inventory and richness

Macro-faunal community structure of the Eden estuary during the period of study was composed of four distinct taxa (Table 3.25), namely those of the Polychaetes, Crustaceans, Molluscs and Oligochaetes. The greatest total standing stock of individuals found across all time periods was represented by the Oligochaetes with 43% (18437 ind), followed Molluscs 33% (14445 ind), Crustaceans 14% (6069 ind) and finally Polychaetes with 10% (4224 ind) of the total density respectively.

Table 3.25: Total density (N) of main taxa found during the study period.

Year	Polychaetes	Crustaceans	Molluscs	Oligochaetes
1999	3185	4898	7332	14990
2015	1038	1171	7113	3447
Total individuals	4224	6069	14445	18437
% Total	10	14	33	43

Spatial distributions of taxa by zones, highlighted a similar trend to the estuary as a whole, with Oligochaetes and Molluscs recorded as the most abundant taxa (Figure 3.20). One discernible exception to this rule, was in the sandy region of the lower estuary, where community structure was clearly dominated by Crustaceans. Polychaetes were also recorded as the third most dominant taxa in the central region of the estuary across both periods and in the upper region during the 1999 period only.

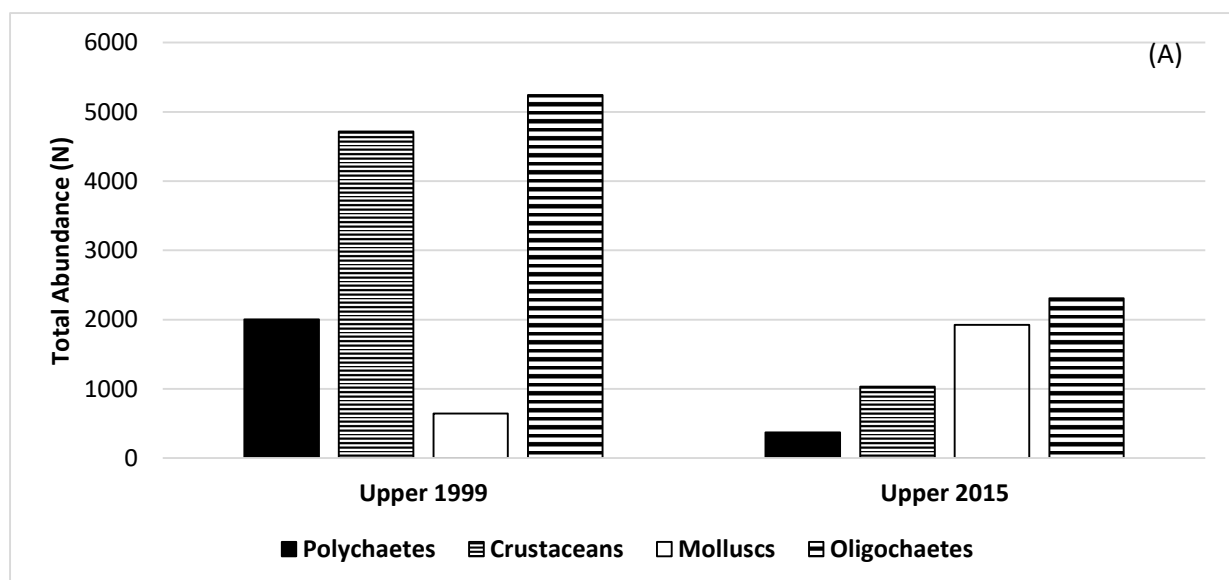


Figure 3.20 Total density of major taxa found in the (A) upper, (B) central and (C) lower regions of the Eden Estuary during the study periods.

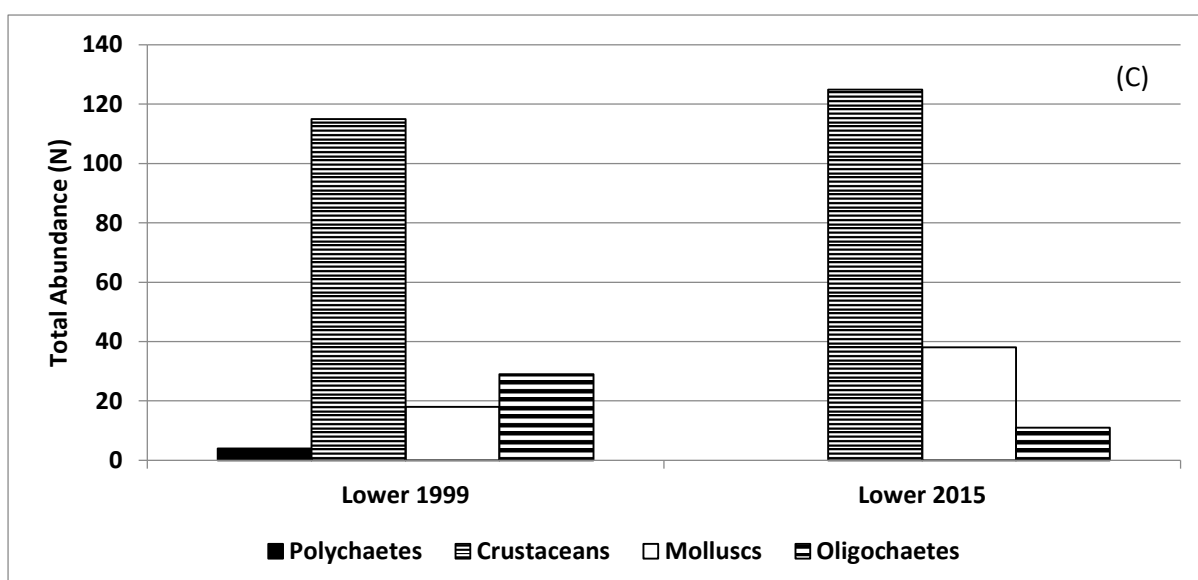
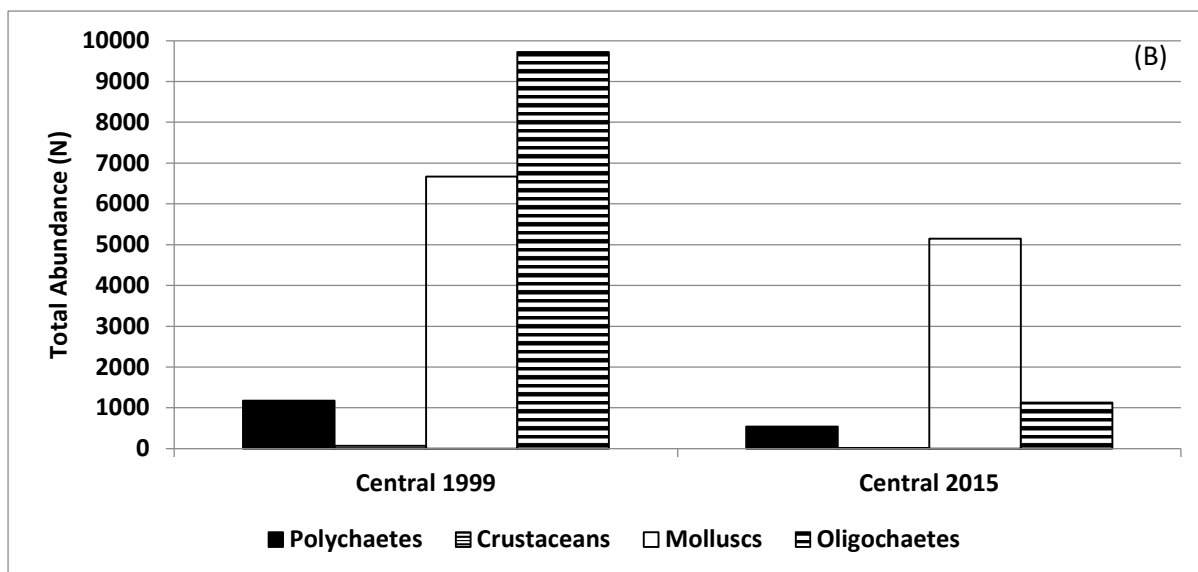


Figure 3.20 (continue) Total density of major taxa found in the (A) upper, (B) central and (C) lower regions of the Eden Estuary during the study periods.

With regards to the richness of species present across the time periods, Polychaetes comprised the greatest numbers of species identified (36%), followed in second place by the taxa Mollusca with 8 (32%) species (Table 3.26). This was followed by Crustaceans with 6 species (24%) and Oligochaetes with 2 (8%) representative species. When considered at the level of individual zones, Polychaetes were the most numerous taxa in both the upper and central regions of the estuary. Corresponding with the high number of individuals of Crustaceans found in the lower estuary, species diversity was co-dominant with the taxa Mollusca between the time periods.

Table 3.26 Total species richness (S) of main taxa found during the study period.

Year/Zones	Polychaetes	Crustaceans	Molluscs	Oligochaetes
1999 Upper	5	2	5	1
2015 Upper	7	2	6	1
1999 Central	8	4	8	1
2015 Central	8	2	7	1
1999 lower	1	3	2	1
2015 lower	0	2	6	1
No. Species Identified	9	6	8	2
%Total	36	24	32	8

When considered together, the total number of species present between the pre- and post-management periods was found to be fairly similar (Figure 3.21). Slightly higher values were recorded in the 2015 period in both the upper and lower regions of the estuary, concomitantly with a reduction in the number of species found in the central estuary.

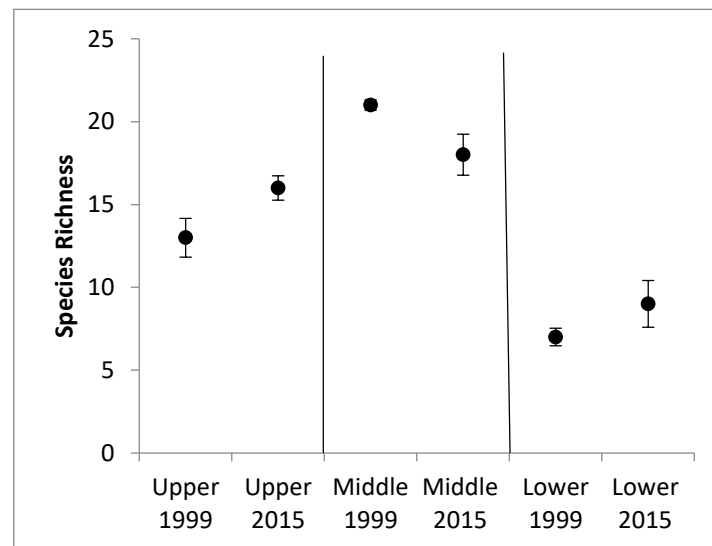


Figure 3.21 Summary of means and 95% confidence intervals for the total number of species (S) across the 1999-2015 periods.

Temporal variation of species richness between the periods were recognised (one-way PERMANOVA $p < 0.05$) both across the estuary as a whole and in the upper region only (Table 3.27). Taxonomic comparisons between mudflat regions, of the upper and central estuary (Table 3.28) revealed a similarity in four of the five most dominant taxa namely; the errant polychaete *Hediste diversicolor*, the deposit feeding polychaete *Spio filicornis*, the molluscan grazer *Peringia ulvae*, and the sub-surface deposit feeding oligochaete *Tubificoides benedii*. Differences between the sites were characterised by a decrease in density of the burrow-dwelling crustacean *Corophium volutator* in the upper estuary, relative to decreased numbers of the filter-feeding bivalve mollusc *Mytilus edulis* in the central estuary.

Table 3.27 One-way PERMANOVA pair-wise post hoc comparisons among years for the whole estuary and each estuarine zone using the t-statistic. Values in bold were significant at ($p < 0.05$).

Year	Species Richness		Zones	
	Whole	Upper	Central	Lower
1999, 2015	52.096	<0.05	>0.05	>0.05

Table 3.28 List of the 5 most dominant taxa (based on total density (N)) in each region of the Eden Estuary.

Upper	Taxa	1999	2015
<i>Hediste (nereis) diversicolor</i>	Polychaetes	314	271
<i>Spio filicornis</i>	Polychaetes	1575	180
<i>Peringia (hydrobia) ulvae</i>	Molluscs	521	1646
<i>Tubificoides benedii</i>	Oligochaetes	5242	2307
<i>Corophium volutator</i>	Crustaceans	4710	1029
Central			
<i>Hediste (nereis) diversicolor</i>	Polychaetes	146	250
<i>Spio filicornis</i>	Polychaetes	625	125
<i>Mytilus edulis</i>	Molluscs	1489	460
<i>Peringia (hydrobia) ulvae</i>	Molluscs	4717	4675
<i>Tubificoides benedii</i>	Oligochaetes	9717	1128
Lower			
<i>Arenicola marina</i>	Polychaetes	130	116
<i>Bathyporeia sarsi</i>	Crustaceans	78	121
<i>Eurydice pulchra</i>	Crustaceans	28	8
<i>Talitrus saltator</i>	Molluscs	14	4
<i>Peringia (hydrobia) ulvae</i>	Molluscs	-	475

Further spatial analysis (Table 3.29) identified that the lower sandy zone of the estuary had significantly different numbers of species present than the mudflat dominated central and upper zones (one-way PERMANOVA $p < 0.05$). These trends were clearly highlighted by the top five most dominant species present (Table 3.28), with the presence of the burrow dwelling polychaete *Arenicola marina* and the motile epibenthic crustaceans *Bathyporeia sarsi* and *Eurydice pulchra*, categorising the sandy nature of this zone.

Table 3.29 One-way PERMANOVA pair-wise post hoc comparisons among zones for the whole estuary. Values in bold were significant at ($p < 0.05$).

Zone	Number of Stations	Species Richness
Upper, Central	3	0.302
Upper, Lower	3	0.001
Central, Lower	3	0.001

3.5.4 Eden structural indicators performance

Most of the univariate indices tested suggested a general increase in species richness or evenness following the reduction of nutrient inputs to the estuary (Figure 3.22). Significant positive changes at the estuarine level were identified by the Margalef, Shannon-Wiener, Simpson and taxonomic diversity indices (Table 3.30). Spatial analysis, determined a significant positive change in all of the indices except taxonomic distinctness and Pielou's index in the upper and central estuary. In these zones taxonomic distinctness fell slightly, while Pielou's Index remained fairly consistent across all the estuarine zones. In the central estuary significant changes in ecosystem structure were expressed by the Margalef, Shannon-Wiener, Simpson and Total taxonomic distinctness indices. No significant differences could be detected from any of the seven indices in the lower zone, suggesting a stable environment.

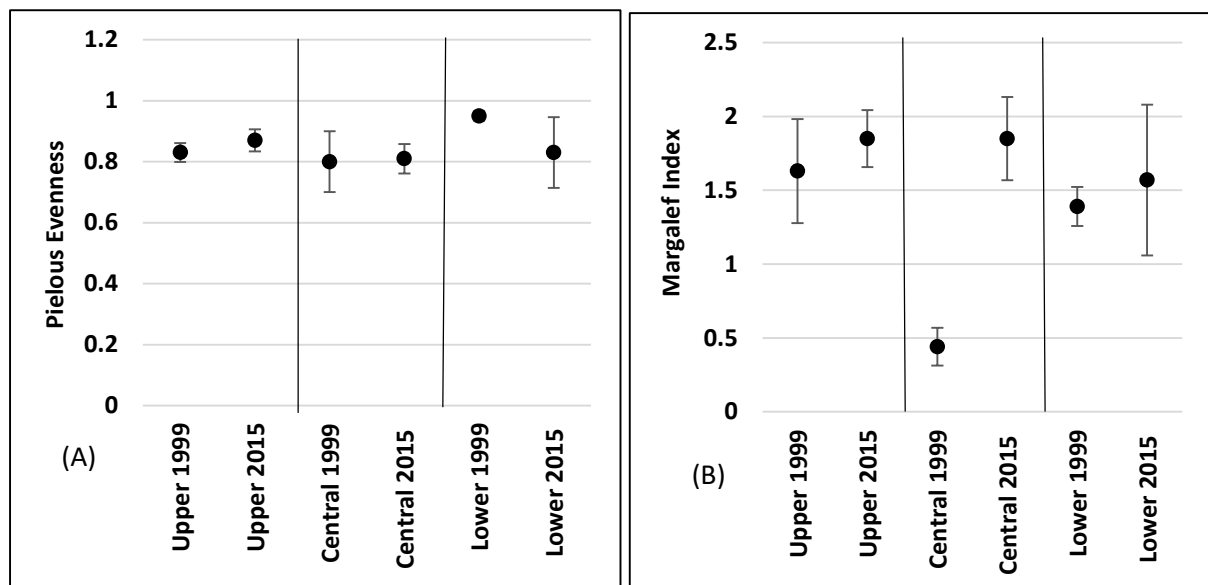


Figure 3.22. Temporal and spatial variation of the ecological indicators, based on inter-tidal macro-benthic communities for each zone (upper; central and lower) of the Eden estuary (1999-2015). (A) Pielou; (B) Margalef.

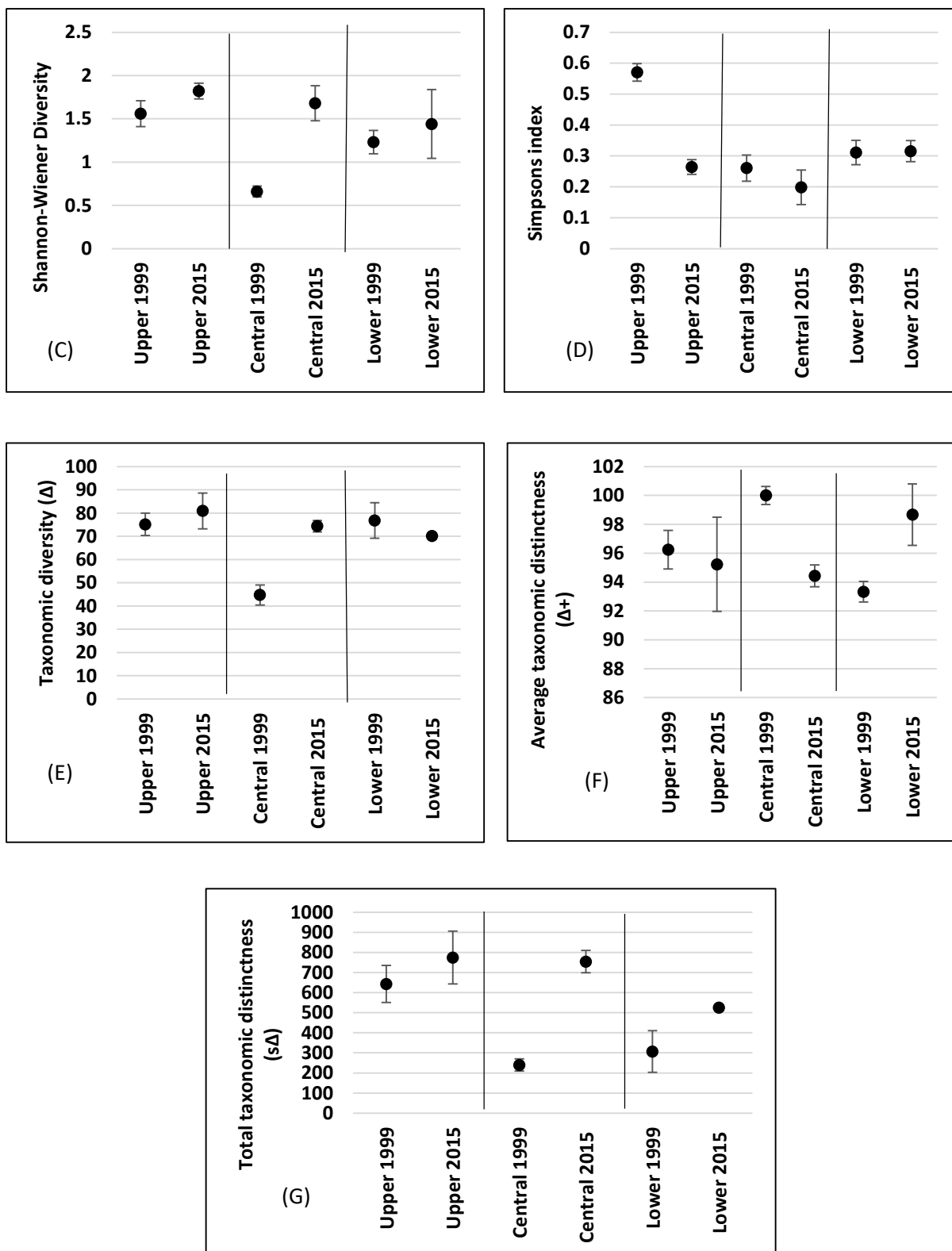


Figure 3.22 (continued). Temporal and spatial variation of the ecological indicators, based on intertidal macro-benthic communities for each zone (upper, central and lower) of the Eden Estuary (1999-2015). (C) Shannon–Wiener; (D) Simpson; (E) taxonomic diversity; (F) taxonomic distinctness; (G) total taxonomic distinctness.

Table 30 Synopsis of the ecological indicators trends obtained for the Eden estuary. Arrows in an upward (Green) and downward (Red) direction represent an increase and a decrease in the indicators mean values between each period, respectively. Horizontal lines (Yellow) indicate similar indicators mean values between periods. No significant statistical differences (Orange) in indices values among years and thus, between periods, showed by ($p > 0.05$), considering a significance level of 0.05.

Estuarine zones	Ecological indicators						
	Pielou	Margalef	Shannon-Wiener	Simpsons	Taxonomic diversity	Taxonomic distinctness	Total taxonomic distinctness
Whole estuary 1999 vs 2015	$p > 0.05$	↑	↑	↓	↑	$p > 0.05$	$p > 0.05$
Upper estuary 1999 vs 2015	$p > 0.05$	↑	↑	↓	↑	↓	↑
Central estuary 1999 vs 2015	$p > 0.05$	↑	↑	↓	↑	↓	↑
Lower estuary 1999 vs 2015	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

Resulting from a combination of the diversity indices, Ecological Status of the Eden, was considered to be ‘high’ at the estuarine level across both periods, based on both M-AMBI and IQI permutations (Table 3.31). At the zone level, both indices recognised an improvement in habitat quality in the central estuary after catchment alterations. In contrast to M-AMBI, the IQI index could not detect a change in ecological status in the upper area of the estuary. As with the univariate indicators, neither index could distinguish any perturbations influencing the lower estuary.

Table 3.31 M-AMBI and Infaunal Quality Index (IQI) EQR scores from The Eden estuary 1999 -2015. Different colours represent environmental status; High (Blue), Good (Green), Moderate (Orange), Poor (Yellow).

	MAMBI		IQI	
	1999	2015	1999	2015
Whole	High	High	High	High
Upper	Good	High	Good	Good
Central	Poor	High	Moderate	Good
Lower	Good	Good	Good	Good

3.5.5 Biological traits of the Eden benthic community.

When considering the biological traits composition data from all of the estuarine zones together throughout the study period (Table 3.32), a significant interaction for the factors ‘year’ and ‘zone’ was detected by the two-way PERMANOVA analysis (two-way PERMANOVA, all zones: $p < 0.05$) indicating the existence of spatial and temporal differences between the time periods.

Table 3.32 Pseudo-F (pF) values and significance levels (P) for two-way PERMANOVA tests, employing separate Euclidean distance resemblance matrices constructed from the ‘traits by station’ matrix, across the 1999 and 2015 periods. df= degrees of freedom. Significant differences ($p = < 0.05$) are highlighted in bold.

Whole estuary	pF(df)	p
Year	2.9262 (4)	0.037
Zone	8.5167 (2)	0.001
Yearxzones	3.1987 (8)	0.003

Further, in the nMDS ordination coded for both the temporal factor 'year' and spatial factor 'zone', clear patterns in inter-tidal benthic community functioning (Figure 3.23) were evident, with samples representative of the different years and zones showing low superimposition. It should be noted however that high stress values were observed (0.09) which accounts for some caution in results interpretation from a two-dimensional plot.

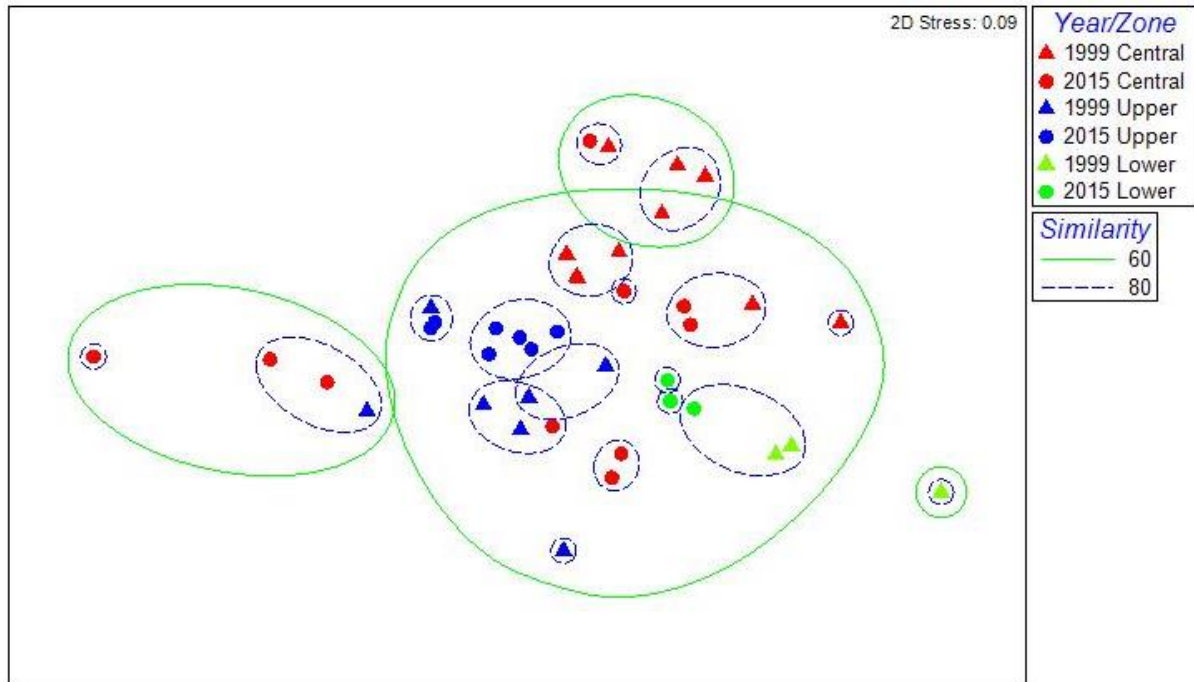


Figure 3.23 nMDS ordination plots of biological traits composition data considering data from all estuarine zones together over the time periods defined by the intervention under study: Pre-management 1999 (Triangles), and Post-management 2015 (Circles).

With regard to the main trait categories characterising the Eden estuary during the time periods (Figure 3.24):

Body Size: Spatial distributions of different body size categories changed between the pre- and post-management periods, with a graduation towards a more evenly distributed size structure across the estuary. In 2015 very small (<1cm) and large (11-20cm) individuals increased in contribution to overall biomass, concurring with a fall in medium (3-10cm) sized individuals.

Life Span: Species with a medium (2-5 years) life span were only found in the 2015 period. There was also a simultaneous increase (15 %) in long lived individuals during this period.

Growth form: Tubicolous species only contributed to <2% of the total ecological functioning of the estuary across both periods. Between the periods there was a general increase in bivalve or turbinate species relative to a decline in articulate and vermiform segmented species, with the latter dominating the morphology of the estuary as a whole.

Reproductive method: Species with a hermaphroditic reproductive technique contributed most (~70 %) to the biomass of the system during the 1999 period, followed by a shift to a system where individual organisms were more often gonochorous (~60%).

Resource capture method: Deposit feeding individuals were the most representative feeding traits expressed in the Eden estuary (>60% in both scenarios). Following management interventions there was a decrease in deposit feeders and an increase in the three other resource capturing methods: filter/ suspension, opportunistic/scavenger and predators.

Mobility in the sediment: Overall slow free moving taxa dominated the biomass of both periods, while sedentary tube dwelling taxa were absent from the pre-management period. During the contemporary period, limited and free moving taxa increased in eminence.

Environmental position: Distributions of taxa across the sediment-water interface were almost equivalent between the two periods, with a slight increase (5%) in hyperbenthic species during the 2015 period.

Bioturbation functional type: Biodiffusing taxa were the most influential taxa in facilitating geochemical cycling processes, during both periods. Contributions to ecological functioning of surficial modifying taxa, almost doubled (from 20 to 40%) during the 2015 period.

Salinity preferences: Tolerance to differing salinity regimes at the estuarine level, was largely analogous between the two periods, suggesting no substantial changes in species taxa distributions due to the increasing influence of freshwater inputs.

Ecological group: The vast majority (>95%) of taxa across both periods, were classified as tolerant or very tolerant to disturbance. Following management measures (2015), there was an approximately 30% reduction in very tolerant species classified.

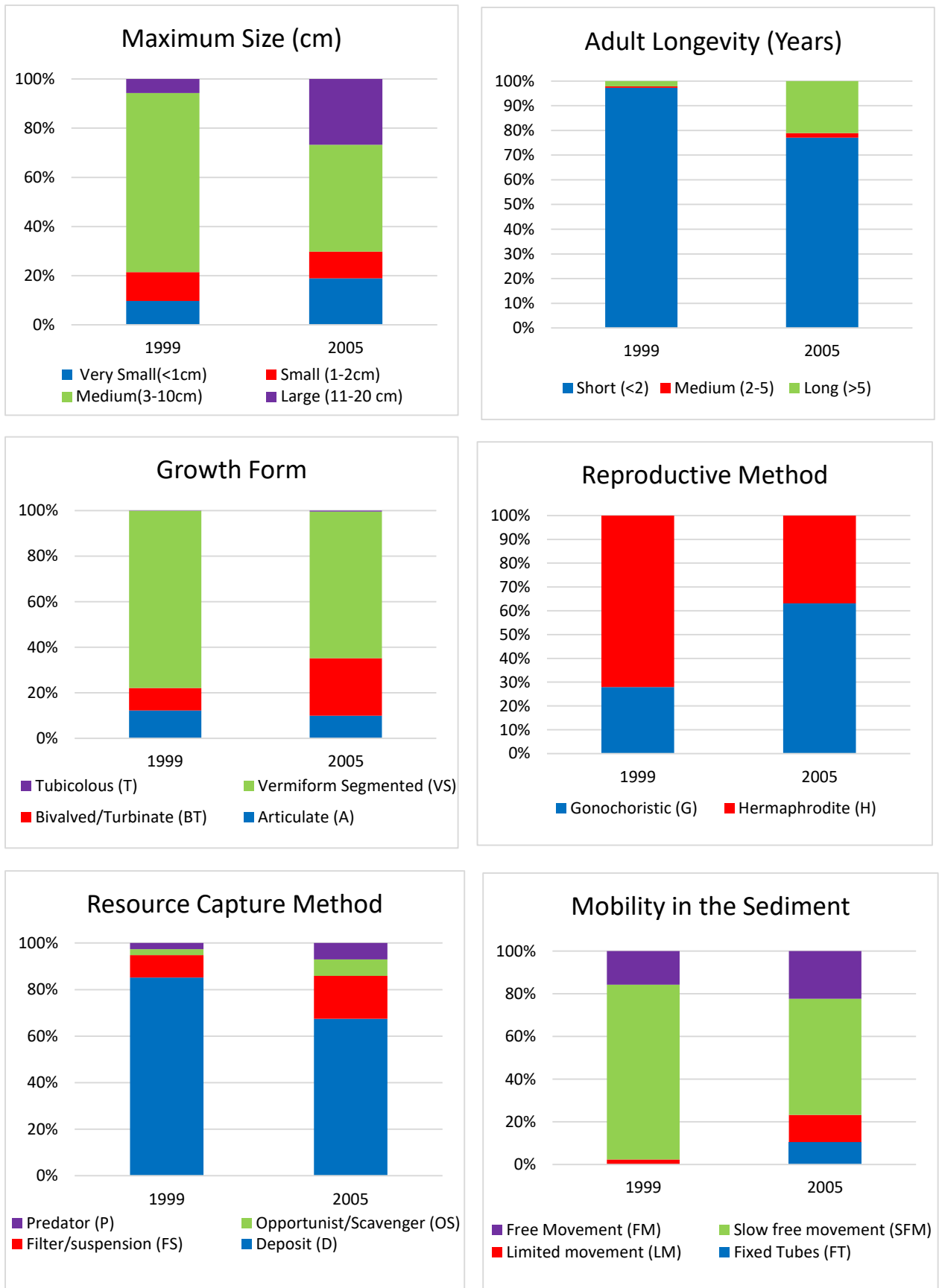


Figure 3.24: Biological traits patterns for whole estuary over the study period (1999–2015).

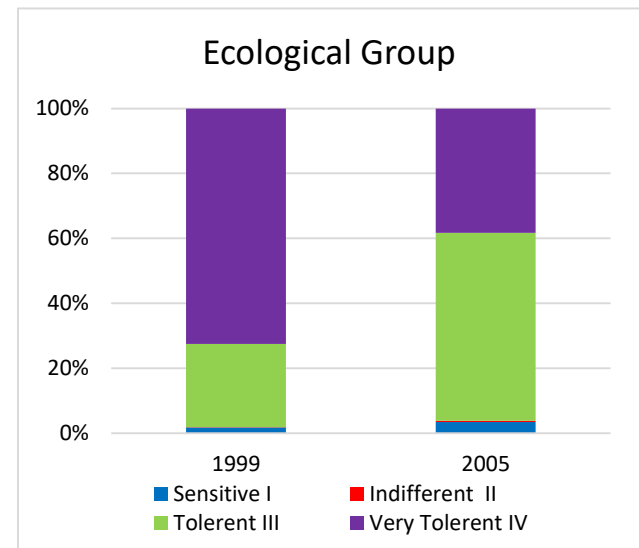
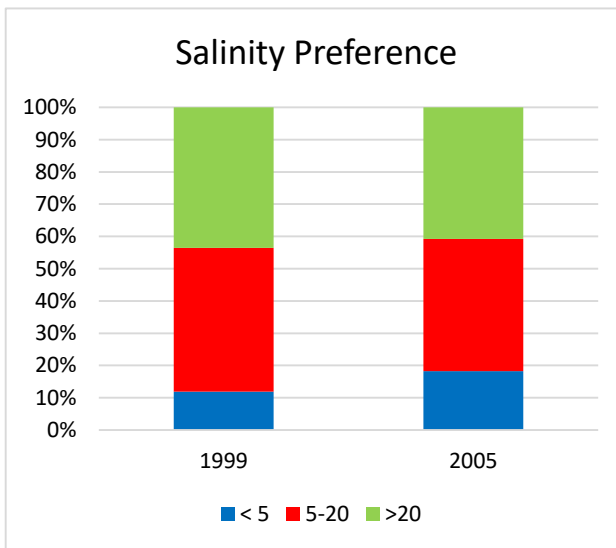
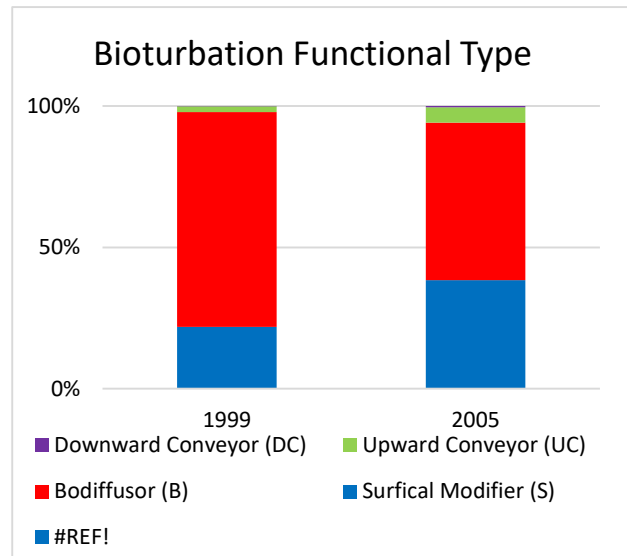
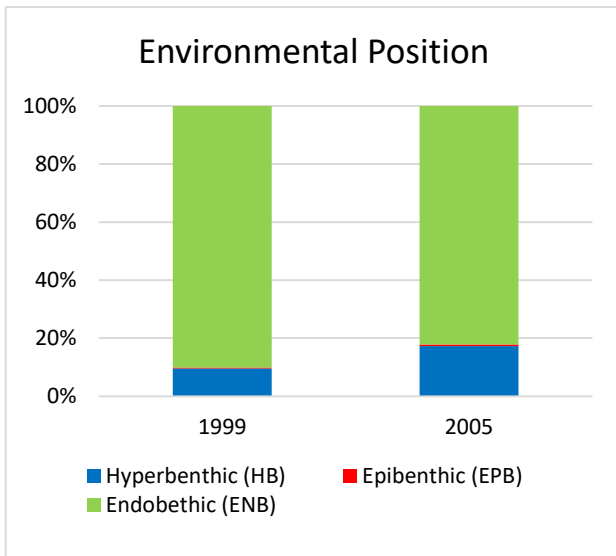


Figure 3.24 (continued): Biological traits patterns for whole estuary over the study period (1999–2015).

Moving to the assessments of each zone individually, clear temporal trends in traits composition were visible on the nMDs plots across all zones (Figure 3.25). However, significant changes in relative ecosystem functioning were only detected (one-way PERMANOVA, $p < 0.05$) in the upper and central estuarine zones (Table 3.33).

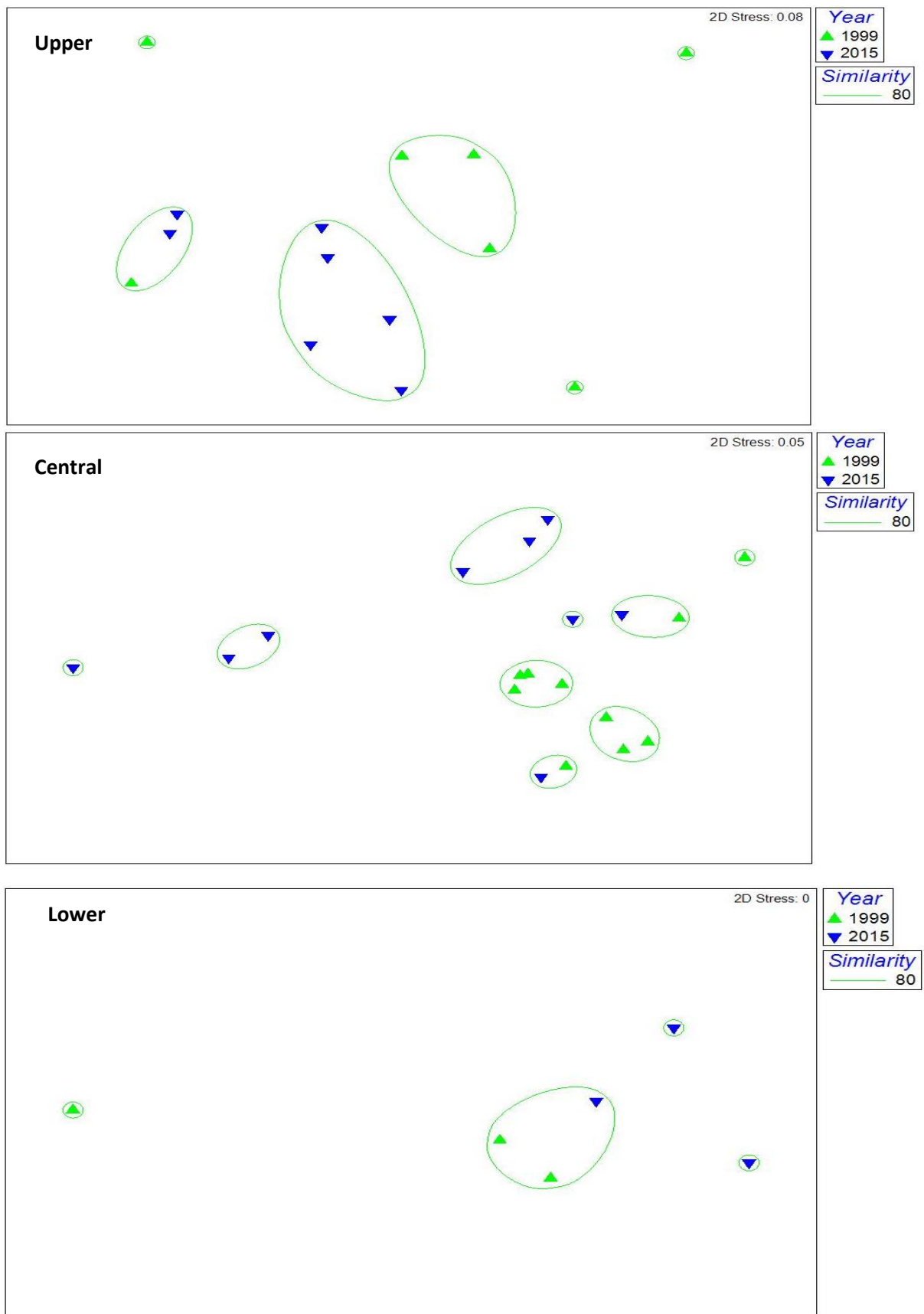


Figure 3.25: nMDS ordination plots based on macro-benthic biomass data for the three individual zones (Upper, Central and Lower), and coded for the temporal factor 'year'.

Table 3.33 One-way PERMANOVA pair-wise post hoc comparisons between years for each estuarine zone using the t-statistic. Values in bold were significant at ($p < 0.05$).

Year	Zones		
	Upper	Central	Lower
1999, 2015	1.7492	2.0706	2.0287

With regard to the biological trait changes observed at the level of individual zones (Figure 3.25), trait changes were largely consistent with the estuary as a whole but spatial differences were reflected particularly in the lower estuarine zone, due to the unbalanced two-way crossed (orthogonal) nature of the sampling design. When samples sizes were normalised, trait categories were expressed as follows:

Body Size: Was highly heterogeneous in nature between the zones. While the upper estuary was generally characterised by a diverse range of body sizes with a graduation towards medium (3-10cm) size individuals, the lower estuary was predominated by large (11-20cm) individuals such as the sandworm (*Arenicola marina*). In contrast, preceding an increase in their numbers, large (11-20cm) and also small (1-2cm) individuals were completely absent from the central estuary during the pre-management period.

Life Span: Similarly to the trends of the estuary as a whole, short lived species dominated the ecological functioning of the upper and central zones of the estuary. This was followed by a slight increase in long lived (>5 years) taxa following management measures. In the sandy lower estuary long lives species exhibited the greatest temporal biomass.

Growth form: Bivalved and turbinate species increased in biomass across all three zones between the time periods. Articulate taxa were particularly abundant in the upper estuary, but showed a relative >30% decline in biomass.

Reproductive method: Spatial analysis revealed that, taxa with a hermaphroditic reproductive method were largely only found in the upper and central zones of the estuary. A shift from a hermaphroditic to a gonochoristic life strategies was expressed in the central region, while the opposite pattern was depicted in the upper reaches.

Resource capture method: Minor changes to feeding strategies was observed during the study period in the upper and lower estuary, while the central estuary expressed a 30% increase in trait diversification from deposit feeding taxa.

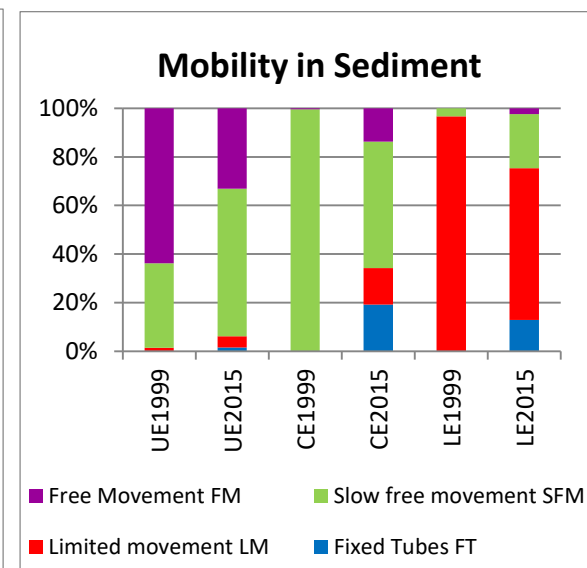
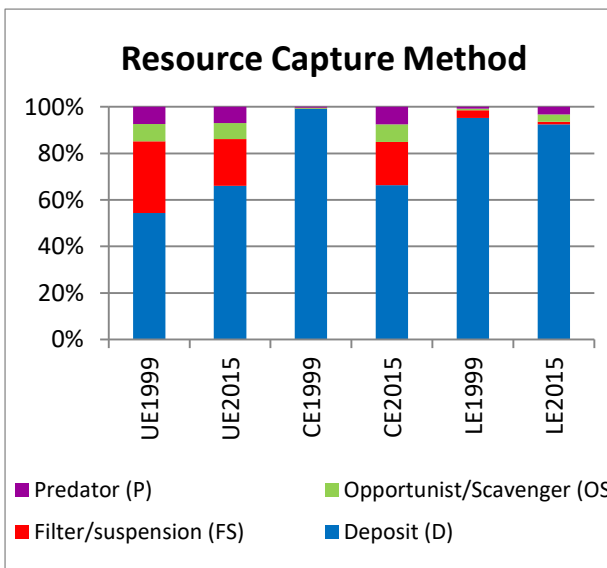
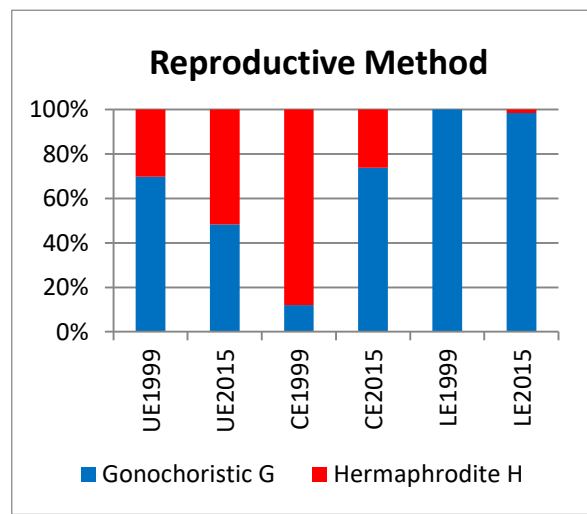
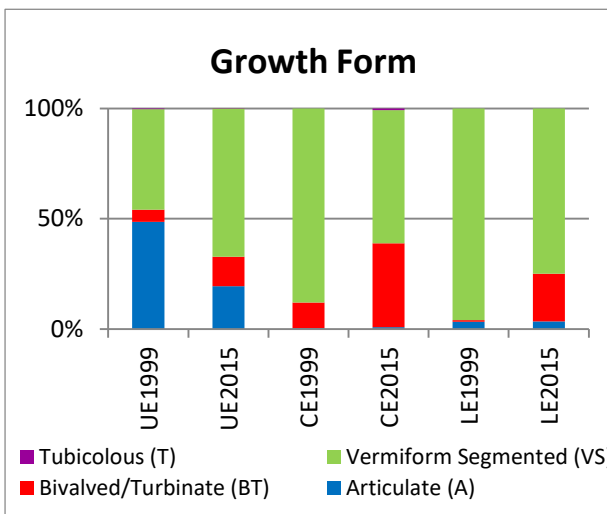
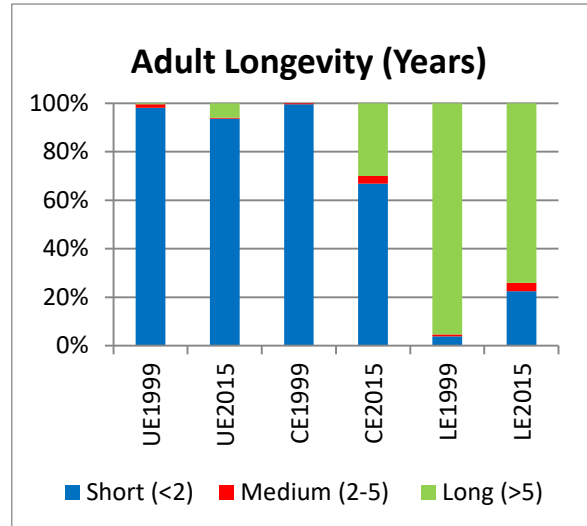
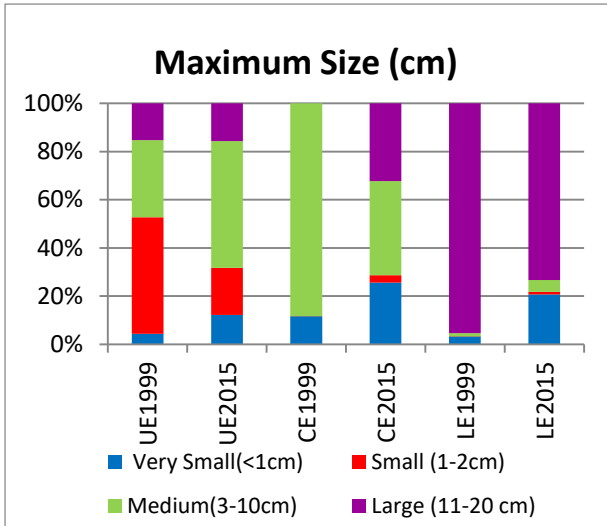
Mobility in the sediment: Free and slow moving taxa was the hallmark of the upper estuarine zone, with a valediction towards the latter. Complete supremacy of slow free moving species in the central estuary, was fragmented by an increased presence of free moving and more solitary species by the 2015 period. In a similar way, limited mobility species were replaced by free moving and tube dwelling species in the lower estuary.

Environmental position: Habitat preference followed the trends described for the estuary as a whole across all zones.

Bioturbation functional type: Sediment reworking modes showed very different trends to those at the estuarine level. Biodiffusor and upward conveying benthic species co-dominated the upper estuarine zone with a successive increase in the latter. Similar trait compositions were also expressed in the central estuary, prior to an insurgence of surficial modifying and biodifusive taxa. Sharply contrasting the mudflat zones the lower sandy zones geochemical processes were mediated by a prevalence of downward conveying species.

Salinity preferences: Tolerance to salinity remained relatively constant and was comparable to the patterns of the estuary as a whole, but the finer resolution, suggested a greater proportion of species with high tolerances to low salinity (<5psu) to be present in the upper zone (at the river-estuarine interface) and the converse of a high proportion species biomass with a preference for high salinity (>20psu) found at the mouth of the estuary.

Ecological group: Tolerant and very tolerant taxa were the mainstay of the upper and central zones, with the former recording an increase in the proportion of very tolerant individuals, parallel to the opposite trend in the central estuary. Contrastingly, sensitive species were the largest group in the lower estuary with >99% representation in the 1999 period. This was followed by an influx (~40%) of more tolerant individuals.



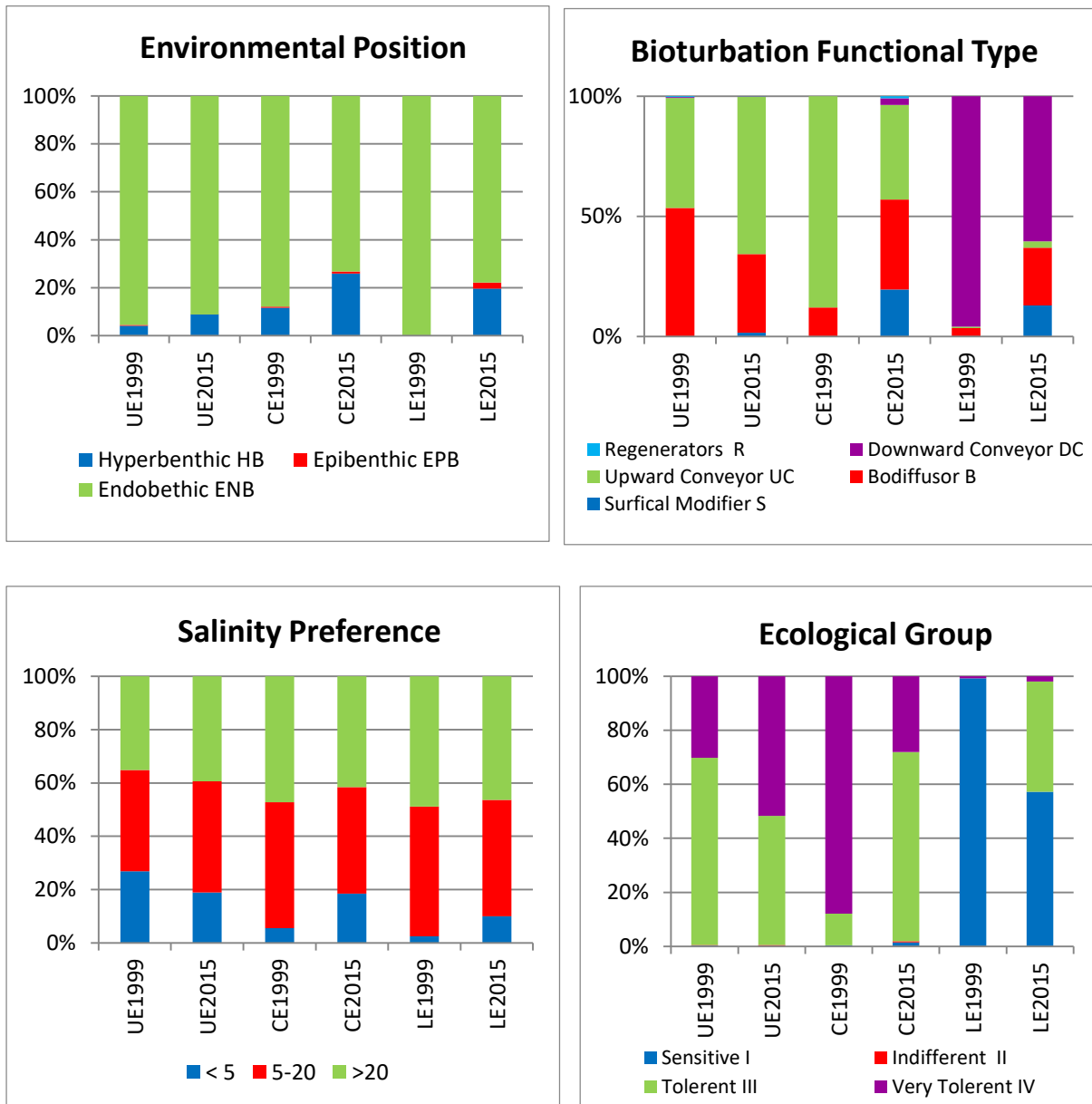


Figure 3.25 (continued): Biological traits patterns for each zone of the Eden estuary over the study period (1999–2015).

3.5.6 Bioturbation potential (Bpc) results

Bpc calculations for the estuary as a whole, illustrated a general increase in biogenic functioning between the periods (Figure 3.26), from 318 to 438.

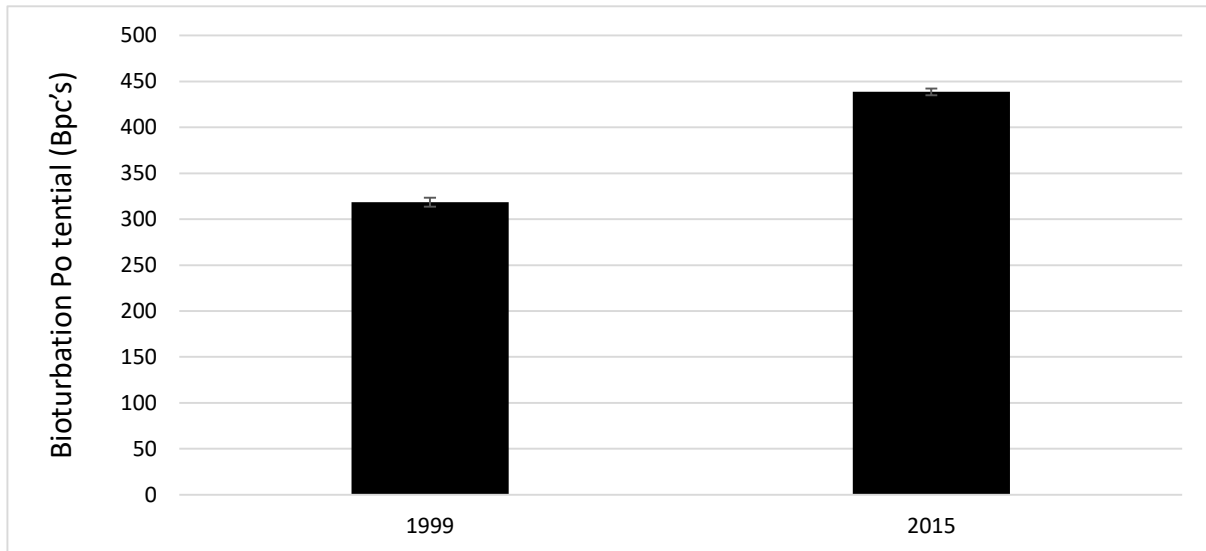


Figure 3.26 Bioturbation potential (Bpc) values for the Eden Estuary (1999-2015) with 95% confidence intervals.

When the resolution was increased to the level of individual zones, Bpc values ranged from 23-230 (Figure 3.27). Relative benthic functioning, increased across all zones under the post-management initiatives. The lowest Bpc values were registered in the sandy lower region of the estuary and the highest in the transitional upper zone.

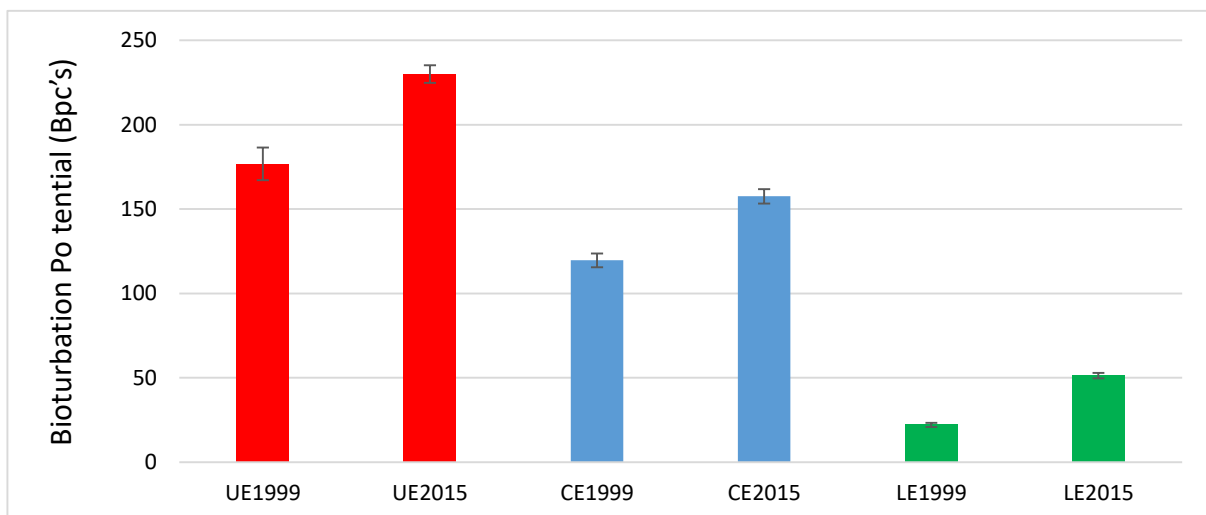


Figure 3.37 Bioturbation potential (Bpc) values for the Eden Estuary by year (1999-2015) and zone based on equal sample sizes; upper (red), central (blue) and lower (green) with 95% confidence intervals.

3.6 Discussion

3.6.1 Environmental variables- Assessing the evidence of anthropogenic and climatic change on the Tamar Estuary

Concerning the environmental variables analysed, the Tamar data showed a clear decrease in estuarine water quality during the eutrophic event in 1990, with highly saline, low oxygen and high nutrient conditions attributed to lengthy low river-flow conditions, caused by drought and relatively high summer water temperatures, (Darbyshire, 1996; Harris, 1988; 1992) which subsequently promoted increased algal growth and microbiological activity. High levels of nutrients persisted during the following two recorded years consistent with known long recovery times often associated with eutrophication events (Lotze *et al.*, 2006), often due to internal recycling from a large pool of nutrients in sediments and the complex feedback mechanisms of environmental hysteresis (Carpenter, 2005).

In the following decade after intervention of management measures (2005), results of PCA indicate a general increase in the quality of water entering the catchment including ammonium, nitrite and reactive phosphates. These results are consistent with more contemporary accounts of temporal variability in nutrient concentrations and loads in the River Tamar (e.g. Tappin *et al.*, 2013), with lower phosphate levels ascribed to either increased stripping from sewage treatment work effluents due to numerous infrastructural improvements across the catchment or reductions in phosphate fertiliser applications.

In contrast, it is noteworthy that nitrates showed no indication of a downward trend (if not a slight increase) between the pre- and post-management periods, suggesting that management action did not produce any visible variation on this physico-chemical parameter. These trends mirror a similar problem across many catchments both in the UK and worldwide, reflecting the ongoing difficulty in controlling diffuse inputs at such large scales, despite the reduction in (national) nitrogen fertiliser to farmlands. Although limited in scope and lacking contemporary data post 2005, these results support the notion that nitrogen mitigation within the catchment may be not sufficient and further additional management practices could be required.

3.6.2 Structural indicator performance Tamar Estuary - Eutrophic period

Changes in benthic ecological quality were detected by almost all of the structural indicators (abundance, biomass, species richness, Pielou, Margalef, Shannon, Simpson and taxonomic diversity) tested under the high nutrient periods (PERMANOVA) <0.05), with the exception of the taxonomic distinctness indicators. These results suggest a fall in the general richness and evenness of the communities found during the 1990-1992 period, coinciding with an increase in dominance of a few closely related, mainly polychaete individuals. In addition, results of the 'habitat quality' or sensitivity

indices (M-AMBI and IQI), both suggested a general decrease in benthic ecological condition of the estuary, during the eutrophic period (1990). This was followed by an increase in quality in the ensuing years (1991 onwards). These changes were registered at the level of individual zones and across the estuary as a whole, with the greatest change in benthic quality recorded in the upper estuary (High – Poor), illustrating the exponential increase of the errant polychaete *Hediste diversicolor* which is well known to thrive under pulse related disturbances.

Overall, these evident structural changes were noted to have had profound effects on the ecological functioning of the system, with a detailed investigation of the activity of *Hediste diversicolor* on nutrient fluxes over the same period (1990-1992) by Davey & Watson (1995) showing fluxes of soluble ammonium to be up to 100 times greater from burrow surfaces than those calculated from pore-water concentration gradients. During the same investigation cores with the most worms (up to 5000 per m²) had burrow surfaces areas equivalent to between 200 and 300% of the unburrowed interface and when calculated over the whole of the Tamar Estuary, *Hediste diversicolor* populations were thought to account for fluxes to the water column of between ten and twenty times the measured inputs of soluble nutrient derived from riverine and sewage sources. Indeed these changes were captured here with large increases in benthic function recorded by the Bpc index, particularly in the upper estuary where *Hediste* numbers were most prevalent.

3.6.3 Species composition and structural indicator performance Tamar Estuary: Following restoration

Results of the nMDs and multivariate analysis indicate there was significant temporal differences (PERMANOVA <0.05) between the pre- (1992) and post-management (2005) period in terms of community composition (density or biomass) at either the estuarine level or at the level of individual zones. Significant changes were encapsulated by a large reduction in the numbers of individuals (and also biomass in the upper and lower estuary) during the 1992-2005 period, culminating in levels far more consistent with the community structure observed during the historic 1937 period. These declines were largely attributed to major drops in numbers of the disturbance tolerant polychaete *Hediste diversicolor* across all zones, but particularly in the upper estuary which showed a decline of (9457) individuals. Other notable changes in community composition between the periods was the re-emergence in numbers of the taxa mollusca, mostly represented by the species *Peringia ulvae*, an important sentinel species that has been shown in other estuarine studies (e.g. Cardoso *et al.*, 2005) to respond favourably under the impact of nutrient remediation measures. Based these changes in dominant taxa alone, it could be suggested that there has been at least some improvement in water quality. However other observations, such as the emergence of the oligochaete *Tubificoides benedii*

in the 2005 samples, which normally points to anthropogenic enrichment impact, make it hard to discern how much of an improvement has been made.

Evidence from the structural indicators (species richness, Pielou, Margalef, Shannon, Simpson and taxonomic diversity) was far more concise, indicating unanimously with the exception of the taxonomic distinctness indicators, an increase in ecological quality in the post-management period at least at the estuarine level, and at the level of individual zones. Results of M-AMBI and IQI were also effective in highlighting changes during the eutrophic period in 1990, and as such suggest that structural changes in benthic fauna did translate into changes in overall ecological quality. However, after management measures had taken place both indicators could detect little change in the overall ecological quality of the Tamar system suggesting the benthic environment to be in a worse ecological state (“moderate” =moderate change in composition, biomass) than it was in 1937 (generally “high (= nearly undisturbed conditions) or good (=slight change in composition, biomass) depending on the zone). Overall, most of the structural indicators tested responded in accordance to the temporal changes observed at the macro-benthic community structure and composition, despite not always consistent with an improvement in environmental quality.

3.6.4 Relationships between macro-invertebrate biological traits and sea bed functioning in the Tamar Estuary

In concert with the changes in ecological structure observed above, benthic ecosystem functioning between the high nutrient (1990-1992) and post-management period (2005) differed markedly.

Considering both the estuary as a whole and individual zones, effect traits pertaining to the “mobility”, “adult longevity” and “growth form” of individuals during the high nutrient periods, were consistent with increased ecological stress on the system (Warwick *et al.*, 1994) with communities existing almost entirely of “free moving”, short lived, vermiform segmented individuals. During the same period there was also an elimination of ‘sensitive’ hyperbenthic or sessile/fixed tubed individuals, indicating the possibility of sub-benthic stress (Diaz & Rosenberg, 1995; Sagasti *et al.*, 2001). This is consistent with evidence of suboxic conditions found in the upper estuary during the 1990 period (Darbyshire, 1996; Harris, 1988, 1992). While many of the zones displayed slightly different trait compositions during the high nutrient periods, trait distributions were exclusively more homogenous than the respective historic or post- management period suggesting a lesser degree of trait overlap and reduced ability of the system to respond to environmental pressures.

Evidence of an increased cycling capacity of the system was also expressed by the Bpc index during the high nutrient periods with, the greatest benthic activity recorded in the upper estuary almost certainly attributed to the increased activity of the polychaete *Hediste diversicolor*. Taken together,

the trends of declining diversity, through attrition of intolerant species and elevated dominance, as well as increased body size yielded during the high nutrient periods, almost certainly had repercussions for altered trophic structure, energy flow pathways, and corresponding ecosystem services such as production, organic matter cycling and organic carbon burial.

Following remedial actions, the functional complexity of traits expressed (both response and effect) almost universally increased across all spatial zones, suggesting an improvement in general functioning of the system compared to the high nutrient periods. As all of the response traits tested here are fundamentally linked to effect traits (i.e. they are co-variable (Woodworth, 1987)) improved responses in these variables would indirectly propose a positive impact on ecosystem functioning.

In general, BTA and Bpc allowed highlighting broad patterns in trait–environment relationships. However easy to distinguish if traits responded to “natural” or to “human induced” stress, or a combination of both.

3.6.5 Environmental variables- Assessing the evidence of anthropogenic and climatic change on the Eden Estuary

The available historical data for comparative analysis, confirms there has been nitrate and phosphate pollution in the rivers entering the catchment since before the investigated 1999 period. However there is strong evidence for genuine water quality improvements within the catchment in terms of ammonia, nitrites, nitrates and phosphates since the implementation of the EU’s Nitrates Directive (91/676/EC) which became effective for the Eden Catchment in 2003. These changes, particularly with regard to nitrates can be attributed to the positive impact that the introduction of NVZ status has had on farmer’s attitudes to on-farm nutrient management (Macgregor & Warren, 2015). While phosphate is not a parameter of concern in this Directive, it must also be regarded as important if the WFD’s stated aim of returning this catchment to Good Ecological Status (MSFD, 2008) and as such these trends are encouraging. Also on a positive note, as with previous studies by the SEPA (2006) our results suggest the waters entering the estuary, have been consistently well oxygenated.

Although data regarding changes in salinity were too disparate in time to be statistically comparable, changes to salinity regimes between the study periods, were likely to be influenced by the increasing trends observed for river discharge (and by proxy precipitation) entering the estuary. A more detailed study of tidal asymmetry on the Eden Estuary by Chocholek (2013), suggests that historic and current regime shifts in river flow are likely to be a result of the temporal proximity of a persistent positive phase of the NAO.

Cumulative interactions between the NAO and increasing river flow within the catchment, are also likely to have had an influence on other physiochemical and morphological variables observed on the

estuary over the investigated period. For instance, increasing decreasing depth of the main river channel and evidence of an increase in finer sediments in the central estuary could be linked to evidence in shifts in the hydrodynamics of the system, with consequential feedbacks on the future stratification, water residence times and morphological development of the estuary. Likewise while although no clear trend or 'signal' could be determined from our temperature data, surface air temperature and SST across wide regions of the North Atlantic Ocean, are significantly correlated with NAO variability (Hurrell *et al.*, 1995).

Evidence of an increasing alkalinity of waters entering the catchment, is also of particular interest, because a lot of work over the last decade has been on the recognition of marine waters becoming increasingly acidic (Guttuso & Hansson, 2011a, b; Kroeker *et al.*, 2013) due to processes commonly referred to as ocean acidification (OA). In contrast , there has been far less emphasis placed on investigating waters becoming more alkaline, perhaps because this is a far more desirable state .As such the impact on marine organisms of adding comparatively large quantities of alkalinity to seawater is almost completely unknown (Cripps *et al.*, 2013).

Having investigated a broad number of hydrodynamic considerations and disturbance regimes, assumptions can also be made regarding the state and influence of the benthic primary producers of the system. While our results suggest a relatively stable microphytobenthic (MPB) community structure across the central and lower estuary, the greatest changes detected were in the upper estuary. This is important particularly with regard to ecosystem functioning, with benthic microalgae well known to be important in supporting a number of ecosystem services such as nutrient and carbon cycling (DeNicola *et al.*, 2006) and sediment stability (Paterson, 1997; Lubarsky *et al.*, 2010).

In context, while our study only compared two temporal reference periods, during this period evidence by Spears *et al.*, (2008) on the same system, observed a correlation between the increased presence of benthic microalgae and total phosphorous in the sediments. This evidence combined with, our contemporary analysis of nutrient trends suggest that benthic microalgae are likely to have played a key role in the recovery of this ecosystem from eutrophication. Therefore, while an overall increase in benthic algae biomass following a reduction in nutrients may seem counterintuitive, this is likely due to the localised source of nutrients for MPB, derived locally from the sediment–water interface rather than the water column itself (Dyson *et al.*, 2007). Further, while an increase in overall benthic microalgae biomass particularly in the upper estuary of the Eden may seem at present to be advantageous to the supply of various ecosystem services, future changes in river flow, salinity and the bioturbatory behaviour of organisms have been shown to disrupt the supply of key ecosystem functions carried out by benthic algae. For example, biostabilisation of sediments has been shown to

play a less important role in freshwater sediments compared with estuarine environments (Spears *et al.* 2007), while increases in species that vertically convey material from the sediment, may release previously stored nutrients back into the water column (Biles *et al.*, 2002; Gilbertson *et al.*, 2012) .

3.6.6 Species composition and structural indicator performance Eden Estuary: Following restoration 1999:2015

Under impact of the aforementioned stressors, macro-benthic community structure between the pre- and post-management periods differed markedly both temporally and spatially. Overall macro-benthic community response to the restoration measure implemented in 2003 was different in each of the three areas evaluated (upper, central and lower).

In the upper zone, all structural indicators were able to detect significant differences between years and thus, between the time periods. Therefore, most indicators with the exception of taxonomic distinctness reflected changes in the community structure and composition consistent with an indication of a better ecological condition in this estuarine zone. Taken in context, these indicators based upon measures of equitability and dominance were apparently, reflecting the large decrease in abundance of four of the five most numerous taxa and the increase in greater richness or potential of the community to respond to future perturbations. For instance, large negative changes in the indicator species *Tubificoides benedii*, in the upper and central estuary, point towards recovery from anthropogenic enrichment, while an increase in overall species richness/diversity has likely lead to an increase in the functional redundancy and therefore resilience of the system.

In the central estuary, while species density and biomass fell between the pre- and post -management periods, assemblages were deemed to be similar (PERMANOVA <0.05) in composition. In contrast, the structural indicators: Margalef, Shannon–Wiener and Simpson’s, successfully calculated significant temporal changes in the evenness and dominance of the community. As with the upper estuary, Pielou’s Evenness was unable to detect temporal differences between the time periods. Taxonomic diversity, which measures the average path length between individuals including those from the same species, showed similar values before and after the restoration measures; while total taxonomic distinctness accounting for the total taxonomic breadth of an assemblage, exhibited higher values in the post-management indicating higher biodiversity and that species were on average closely related.

A final assessment of the geomorphologically different lower estuary showed this zone to be a highly stable environment, with no significant variations detected by any of the compositional or structural indicators (PERMANOVA). Generally, the number of species abundance and species richness present in this zone was found to be low and spatially uniform, characteristic of un-impacted sand dominated transitional environments (e.g. McLachlan & Brown, 2006).

3.6.7 Relationships between macro-invertebrate biological traits and sea bed functioning in the Eden Estuary

Considered at the estuarine level, the results of the BTA showed quite similar effect trait distributions between the pre-and post-management periods, suggesting at least when considered as a whole, the estuary is continuing to function in a similar manner under the influence of abiotic change. Response trait diversification, however, increased between the periods suggesting an increased overlap in traits and therefore the functional redundancy of the system to buffer against future changes (Hooper *et al.*, 2005).

At the level of individual zones, the results of the BTA showed quite similar trait distributions (both effect and response) within the lower estuary, whereas, the trait distributions at the central and upper most part of the estuary were considered to be significantly different (PERMANOVA <0.05), suggesting the observed structural changes in community composition had influenced ecosystem functioning within these zones. Changes of traits in relation to patterns of environmental disturbance were reflected by several response traits in the post management period, with the percentage of individuals being 'larger', 'longer lived' and 'hyper-benthic' all increasing. Generally these traits are generally cited as being indicative of a less stressed environment (Philippart, 1998; Basset *et al.*, 2004)

Additional impacts on response traits, pertaining to the assimilation and cycling of matter, were most prominent within the central region of the estuary, with a shift from slow free moving deposit-feeding benthos to a more heterogeneous community composed of more sedentary filter-feeding and mobile scavenger/predator species. These changes echo the fall in dominance of the deposit feeding oligochaete, *Tubificoides benedii*, and rise in numbers of the filter-feeding bivalve, *Cerastoderma edule*. As these species represent a significant proportion of the organic carbon within the estuary, such significant changes in numbers and by proxy traits is likely to have important consequences on many ecosystem processes. For example, following nutrient disturbances *Cerastoderma edule* has been shown (e.g. Kang *et al.*, 1994; Cesar & Frid, 2012) to revert from a diet consisting of material from the benthos to more material consisting from the water column. Therefore, in comparison to the high nutrient periods of 1999, trait distributions of the central estuary imply there is a greater degree of benthic-pelagic coupling taking place, which has implications for the transfer and processing of nutrients and carbon within the sediments (Loo & Rosenberg, 1996).

One hypothesis that could account for these changes is: the observed increase in flow conditions, meaning suspension feeding is more efficient, to allow removal of particulate matter from the water column (Riisgård & Kamermans, 2001) in contrast to static conditions, where deposit feeding may provide a better source of food as particulate matter settles to the sediment bed.

Considering the movement of material once it enters the benthos, Bpc results for the entire estuary indicate an increase in the potential biogenic functioning of the sediments relative to the pre-management period, with the greatest capacity for sediment turn over estimated in the upper estuary. Based on the classification of marine invertebrate infauna into bioturbation groups *sensu* (Queiros *et al.*, 2013) it was also apparent different zones displayed different traits underlying the ecosystem processes of bioturbation and bioirrigation. In the muddy upper and lower zones, community traits trended towards biodiffusers (whose activities result in a constant and random diffusive transport of particles over short distances) and upward conveying (that actively transport sediment from the sediment surface) reworking types, while the lower estuary was dominated by species with downward (that actively transport sediment to the sediment surface) conveying traits.

Finally with regards to the threat of increasing river flow and therefore osmotic stress to the system, the response trait *salinity preference* suggested no substantial changes in species tolerance across any of the zones between the sampling periods. This is a particularly important result regarding the upper estuary, where changes in flow dynamics and salinity are most likely to impact organisms. These results suggest that species have and may continue to cope under this particular stressor.

3.7 Conclusions

Temporal changes in water quality and benthic communities can be used to evaluate the success of management actions, even if tracking temporal differences against a background of natural variability in environmental conditions is difficult (de Jonge *et al.*, 2002; García-Barcina *et al.*, 2006). In the present study, temporal changes in water quality and inter-tidal macro-benthic communities over two geomorphically different estuaries were evaluated as case studies. As estuarine systems are at the prime interface between land and sea (Attrill & Rundle, 2002; McLusky, & Elliott, 2007) and are subject to multiple stressors, occurring over multiple temporal and spatial scales, successful management of such systems requires the proper identification of the pressures acting on them (Borja *et al.*, 2011). Principle components and trend analysis was used as a descriptor of the predominant effects resulting from climatic variability and the management measures carried out on each catchment.

The main pressure found to be acting upon the Tamar Estuary during this study was anthropogenic nutrient enrichment. Some parameters recorded such as ammonia, nitrites and phosphate, showed signs of water quality amelioration following management intervention but were countermanded by high levels of nitrates thought to still be prevalent with the waters of the catchment. A combination of improvement and degradation in water quality was therefore observed. These trends were also reflected by the structural and functional changes exhibited by the benthic in-fauna of the estuary, which displayed a general trend of improved structural and functional attributes thereby inferring

increased ecological function linked to the provision of ecosystem services, but these changes were not always consistent with an improvement in environmental quality.

Overall these results suggest that the Tamar has returned to its pre-eutrophic state, but there is still evidence of disturbance within the system and hence it is still unclear the effectiveness of the management intervention at the inter-tidal macro-benthic community level. As the Tamar is affected by a large number of stressors both anthropogenic and climatic (outlined in Chapter 2) clear cause-effect relationships and their ecological meaning are difficult to interoperate for the current and future threats to the Tamar, compliant with the “Estuarine Quality Paradox” outlined by Elliott & Quintino (2007). While our lack of knowledge on all the pressures acting upon the system might have introduced some degree of uncertainty thus limiting to some extent our ability to make predictions and assess environmental change, the influence of anthropogenic eutrophication has clearly had an impact in the ecological functioning and structure of the benthic inhabitants of the Tamar.

Evidence of climatic variability experienced in the estuary over the monitoring period might have played a significant role in masking the potential effects of full restoration (Widdows *et al.*, 2007). Further, the effects of the management efforts were monitored for only one year after the implementation of mitigation measures, which may be too short of a period of time to assess benthic response. Particularly as species composition has altered during the study period, continued post-management monitoring is, thus, recommended for adequately demonstrating functional effects (or stability) over the long-term.

In contrast to the Tamar, quantifying the main pressures presently acting upon the Eden estuary was considerably easier due to the smaller spatial scale and limited influence of human activities (endogenic pressures) and management measures confounding signals of natural climate variability (exogenic pressures). The main pressures identified were (a) the high spatial and temporal variability in salinity/water flow (natural); (b) anthropogenic reduction in nutrients following management measures and (c) fluctuations in pH of waters entering the estuary, recently towards alkaline conditions. Taken overall, environmental results for the Eden indicate, definitive positive changes in anthropogenic inputs to the estuary over the investigated period, alongside evidence for climatic signals emerging from the ‘noise’ of natural climate variability. In particular both river flow and the NAO proved to be good indicators of climate driven change in this system.

Coinciding with the reduction of nutrients entering the estuary, structural and functional indices revealed an increase in benthic ecological quality in both the upper and central regions of the estuary, suggesting that the benthic biodiversity of the estuary as a whole has been positively affected with regards to ecosystem health and the ability to provide ecosystem services associated with the benthic

environment such as carbon and organic matter cycling. Although water quality and ecological functioning of the estuary has generally improved, our results also highlight that only in the upper estuary has there been significant compositional changes in ecological structure. This is an important consideration, as previous assessments of the macro-benthic structure of the estuary have mainly focused on the central region (e.g. Chocholek, 2013). This specificity seems important from a management perspective, namely when implementing the WFD, with the need to account for different zones inherent natural variability to environmental conditions (Teixeira *et al.*, 2008) all the while exemplifying the need for an ecosystem-based approach to management that considers the entire ecosystem.

One explanation for the observed structural changes in the upper estuary could be due to the increased levels of river flow recorded in this study, causing localised hydrodynamic and osmotic stress to individuals altering community compositions. However salinity data were largely unavailable in this study and clearly longer-term studies are needed to elucidate the responses of organisms to predicted flow changes, but unfortunately for the Eden estuary few such data sets exist. Therefore based on the current evidence provided by this study, it could be advocated, that future research, monitoring and management measures should include representative consideration of the upper estuarine zone as the influence of multiple stressors is likely to be greatest here.

Continued monitoring, and research of the Eden estuary as a whole is also of paramount importance with highlighted anthropogenic (nutrients, human influence) and climatic (river, NAO) sources of activity likely to be a key to feature for management within the foreseeable future. For instance, increased infrastructural development underway in the upper reaches of the estuary at the Guardbridge paper mill site, including a new 'state-of-the-art' biomass facility and micro-brewery, which could have unforeseen impacts on the bio-physical properties of the estuary (Prophet, 2015). As such, the comprehensive large scale monitoring information provided in this study is extremely valuable as a baseline with which future studies can be compared against in order to prevent future degradation and to maintain the prevailing ecological conditions of the estuary.

Comparing the performance of the structural indices from both the Tamar and Eden estuaries, almost all of the structural indicators selected were effective in detecting the prevailing ecosystem conditions and behaved consistently with the inter-tidal ecological community. Most of the indicators tested (Margalef, Shannon–Wiener, Pielou, Simpson) were able to capture useful information about the state of the inter-tidal macro-benthic community with regards to increasing or decreasing nutrient regimes. Both the sensitivity indices M-AMBI and IQI were also able to successfully track the ecological trends in each time series, despite the EQRs showing different temporal and spatial patterns. Comparatively,

IQI was found to be a more conservative index than M-AMBI, concurring with recent studies (Kröncke & Reiss, 2010; Kennedy *et al.*, 2011) suggesting IQI to be less sensitive to climatic and natural variation than M-AMBI. This is an important consideration when analysing for significant change in ecological status, and the future purpose of devising EQRs. Contrastingly, taxonomic diversity measures seemed to have been the least efficient in reflecting the ecological conditions under this investigation.

With regards to benthic ecological functioning, both Biological Traits Analysis and community bioturbation potential (Bpc) seemed effective in highlighting the general picture regarding the functioning of the inter-tidal benthic communities, suggesting a substantial decrease in benthic functioning under increasing nutrient stress. In both systems under the influence of a reduction in nutrients (i.e. in the post management periods) there was almost in every case an increase (or stayed the same to a lesser extent) in the diversity of functional traits expressed by taxa suggesting communities were more resilient to future change under lower nutrient conditions. This could suggest that taxa in similar habitats but in different geographical locations might present the same reaction to this stressor/management intervention. This has important implications for management, as although the link between biodiversity and function is still controversial (Cardinale *et al.*, 2012; Hooper *et al.*, 2012), if the idea that the identity (functional characteristics) of species may matter most to functioning than the species richness (Raffaelli *et al.*, 2003; Veríssimo *et al.*, 2012) then instead of preserving each species individually (Bremner *et al.*, 2006a), managers could possibly rely on maintaining only particular traits within communities, instead of preserving each species individually (Bremner *et al.*, 2008).

However, while functional traits approaches may be useful in highlighting changes to ecological functioning, the ability to use these approaches to address the functional impacts of anthropogenic and/or climate change is currently hindered by a number of well cited (Linden *et al.*, 2012; Tyler *et al.*, 2012; Veríssimo *et al.*, 2012a; Bolam *et al.*, 2013; Queirós *et al.*, 2015) conceptual and methodological factors, the main ones being; 1) Lack of basic biological trait information regarding benthic invertebrate taxa. 2) How to select traits repeatedly within specific ecosystems 3) Understanding of the mechanisms underpinning each trait category, 4) A lack of appreciation of the distinction between 'response traits' (i.e. those which vary along an environment gradient and/or disturbance regime) and 'effects traits' (i.e. those which have an effect on an ecosystem process). Therefore, although the current approach, based on concomitant trait composition assessments may be limited in cause-and-effect inferences, we have shown that describing changes in trait composition offers a much better perspective of ecosystem functioning than that based on (multivariate) structural approaches which are based on taxonomic identity.

Furthermore, in this work, we started our process by accepting functional indicators, which are relevant to sediment carbon/nutrient cycling with an indicator of community bioturbation potential (Bpc), which can be considered a qualitative proxy for seabed function at large spatial scales (Birchenough *et al.*, 2012). Overall, Bpc proved effective in highlighting changes in community bioturbation as a consequence of the response of macro-fauna to environmental stimuli. Additionally when the functional traits of macro-fauna considered in the index (i.e. mobility and reworking mode) were combined with BTA, this allowed a greater visualisation of the influence of specific traits and how they were likely to affect ecological functions. Care should be taken in interpretation of the Bpc results however, as the empirical relationships reported do not provide information about which mechanistic attributes of bioturbation as a community process influence sedimentary systems, other than the functional traits of macro-fauna considered in the index (Queirós *et al.*, 2015). It could be acknowledged therefore that a focus on acquiring accompanying metrics of functioning (e.g. sediment biogeochemistry, secondary production) aligned with traits information would significantly improve this studies ability to determine both the identity and importance of effects traits for specific ecosystem processes relating to carbon and nutrient cycling.

In the interim, these types of complementary approaches are valuable tools for understanding the biodiversity of these systems including: in-faunal processes in the sediments and characteristics of *in situ* sediment redox state (Rosenberg *et al.*, 2003) and may remain one of the best options to predict large scale patterns of biogenic cycling in real ecosystems for the foreseeable future (Queirós *et al.*, 2013). The aim of course is to be able to predict with some confidence how functioning will change if traits change in situations where no functioning data are available. Therefore even if traits can be used to indicate directions of change in functioning (and associated services) in areas where functioning data is unavailable, this would be a useful management tool.

As mentioned at the beginning of this chapter, some directives (e.g. WFD and Habitats Directive) have focussed on the structure of the ecosystem and its components (such as species richness, abundance, biomass) rather than the functioning (such as rate processes, primary production, and population dynamics) (Hering *et al.*, 2010). Despite this, the maintenance of ecosystem functioning and its relationship with biodiversity is central to a healthy ecosystem (Danovaro *et al.*, 2008; Tett *et al.*, 2013). Furthermore, many of the ecosystem process mediated by benthic species have important contributions to human well-being, such as the regulation of climate through burial of carbon in marine sediments (Beaumont *et al.*, 2014). Thus, understanding large-scale patterns of biogenic functioning is of increasing relevance to policy-makers and other stake-holders of the marine environment.

It could be advocated therefore that, as long as the appropriate biological components are sampled, biodiversity data integrated with simultaneous measures of multiple functions can provide important information on the ecosystem health and vulnerability to biodiversity loss. A methodology using ecosystem functions coupled with biodiversity based estimates is likely to be cost effective and complementary to other forms of monitoring as biodiversity information is routinely collected for several purposes (Dauvin, & Ruellet, 2009). Overall the current work has incorporated a combination of these measures, which in combination can be considered as valuable information to support UK targets for the assessment of estuarine ecosystems.

Table 3.32 Verification of hypotheses set at the beginning of the chapter Accept ✓ or reject X

Hypotheses	Description	Tamar	Eden
H1	Faunal composition and/or structural indicators of each case study will differ significantly following nutrient remediation actions.	✓	✓
H2	Faunal composition and/or structural indicators of each case study will differ spatially (i.e. between upper, central and lower zones).	✓	✓
H3	Functional indicators of each case study will differ spatially (i.e. between upper, central and lower zones).	✓	✓
H4	The relative ecological functioning linked to the provisioning of the ecosystem services carbon sequestration and waste remediation will improve following nutrient remediation actions.	X	✓

Chapter 4: A mass-balance approach to biodiversity–ecosystem service relationships in two estuarine ecosystems under the influence of nutrient reductions.

Chapter Summary

The present chapter aimed to explore the potential of a mass-balance approach for understanding the relationship between biodiversity-ecological functioning and the provisioning of ecosystem services at seascape scales. Specifically, consideration was made as to how historical biodiversity loss caused by high nutrient inputs lead to changes in the functioning and management of two contrasting temperate UK estuaries, the well-documented Tamar Estuary, Devon, south-west England and the smaller less well studied Eden Estuary, Fife, north-east Scotland. Both systems have gone through extensive periods of ecological change over the last 30 years due to nutrient related issues, from changes in agricultural land use practices and regulation of discharge of sewage in the estuaries allowing the representation of eutrophic and post-eutrophic states.

Biodiversity of the study systems was quantified in terms of biomass and the mass-balance model (Ecopath v6.3) was constructed for the years 1990, 1992 and 2005 (Tamar) and 1999 and 2015 (Eden) representing eutrophic and post-eutrophic systems. The functions of interest are measures of information content related to the cycling of carbon, nutrients and the productivity of the systems, the subsequent implications for change in flows of natural capital stocks and flows from those stocks on ES provisioning. Other indices were also calculated to identify the prominence of keystone species within each system. This work was a first study of both estuarine systems using a mass-balance model of trophic interactions.

4.1: Introduction

There is an urgent need to understand how best to manage ecosystems sustainably so that they can continue to deliver the goods and services on which society depend (Beaumont *et al.*, 2007; Potschin & Haines-Young, 2013; Bennett *et al.*, 2015). Since the articulation of the Millennium Ecosystem Assessment in 2005, there has been a growing consensus that the majority of the Earth's ecosystems have become increasingly impacted by human activity and that the majority of services delivered by marine ecosystems is similarly on the decline or threatened (Carpenter *et al.*, 2009; Costanza. *et al.*, 2014). This is particularly the case for coastal marine systems where increasing population pressure, urbanisation of the coastal zone and nutrient run-off from agriculture and forestry has increased the number of large-scale and cumulative impacts affecting coastal and estuarine systems (Dolbeth *et al.*, 2011; Ellis *et al.*, 2015). As a consequence, there is a growing movement towards an integrated 'Ecosystem-based' approach to management, which focuses on how individual actions affect the

ecosystem services (ES) that flow from coupled social-ecological systems in an integrated fashion, rather than considering these impacts in a piecemeal manner (McLeod & Leslie, 2009).

The recognition that ecosystems require a systems-based approach for their analysis has a long pedigree in mainstream ecology but has traditionally been subsumed to more reductionist approaches (see Raffaelli & Frid, 2010; Moore & de Ruiter, 2012 for a review). For instance, despite the large literature presence that now exists on biodiversity and ecosystem functioning (BEF) research (Caliman *et al.*, 2010), much of the marine research in this area has focused largely on a single trophic level or taxonomic grouping (e.g. Chapter 3) set within a much larger food web (Raffaelli *et al.*, 2002). Whilst these studies have advanced our understanding of the mechanistic links between biodiversity and ecosystem function (Gamfeldt *et al.*, 2014), there are still substantial challenges in understanding how the cascading effects of biodiversity loss across several trophic levels will affect whole system functioning (Worm & Duffy, 2003; Thompson *et al.*, 2012) and by extension the provisioning of ESs. In part this is because many ESs are underpinned by many ecological functions and hence groupings of species that are generated at much larger landscape or seascape (e.g. a combination of adjacent land, coastline and sea within an area, defined by a mix of land-sea inter-visibility, with major headlands forming division points between one seascape area and the next) scales (Hooper *et al.*, 2005; Barnes *et al.*, 2014). For ESs, this issue is nontrivial, because their provision is likely to scale differently with the spatial extent and arrangement of biodiversity elements and with the trade-offs made between services (Raffaelli & Moller, 2000). Therefore, there is an acknowledged need to move beyond small-scale experiments and to explore the relationships between biodiversity and ecological functioning at seascape scales (e.g., Raffaelli, 2006), since it is at such scales that management operates and at which ESs are delivered to society.

4.1.1 Systems analysis, stocks and flows: A mass-balance approach to biodiversity–ecosystem service relationships

Systems ecology is the science of stocks (usually the biomasses of species or functional groups of species) and flows of energy or material within ecosystems, and seeks to provide a holistic view of the interactions and transactions within and between ecological systems (Raffaelli & White, 2013). Central to this approach is the idea that an ecosystem is a complex system exhibiting emergent properties (e.g., Odum, 1983), which can be influenced by human interventions (e.g. anthropogenic stressors). A core tenant of systems ecology is the general application of the principles of energetics to all systems at any scale. Perhaps the most notable proponent of this approach was Howard T. Odum who pioneered much of the early ecosystem principles and terminology that define the discipline (e.g. Odum, 1953;1996; Odum & Odum, 1959), including the thermodynamic notions of work, entropy and exergy. Since the inception of such theories, the application of a stocks and flow approach to large-

scale anthropogenic problems has been appropriated by the Natural Capital movement (<https://www.naturalcapitalcommittee.org>) and has found the broadest articulation with marine scientists concerned with ecosystem health (Ulanowicz, 1986;1997;2012) and the sustainable management of fish stocks and fisheries (Link, 2002; Heymans *et al.*, 2014). In contrast, there has been limited effort to apply this area of research to elements of the biodiversity-ecosystem processes-services research agenda. An exception to this, is work by Raffaelli (2006; 2011; 2015) working on the Ythan estuary in Aberdeenshire, Scotland, UK and in the growing field of ecological-economics by providing an alternative monetary valuation methodology (Odum, 1985; Turner *et al.*, 1988; Odum and Odum, 2000), whereby estimates are made of how much work an ecosystem has to do in order to produce ESs and then expressing this work in a quasi-financial currency (exergy-dollars).

This lack of a more general application of a systems approach is somewhat surprising given that a stocks and flows approach has a number of attractive characteristics for exploring relationships in the context of ESs and environmental management. Ecological Network Analysis (ENA) tools for instance, are available within a number of easily accessible software packages including NETWRK4 (Ulanowicz & Kay, 1991), WAND (Allesina & Bondavalli, 2004), Ecopath with Ecosim (Christensen & Walters, 2004) and R (Laua *et al.*, 2015) and could be used to map associated ecosystem characteristics and flow parameters onto elements of the biodiversity-ecosystem processes-services framework.

The most commonly used and emerging example of this type of modelling approach is the Ecopath with Ecosim (EwE) modelling software (Christensen *et al.*, 2005) which has over 400 models published to date (Colléter *et al.*, 2013), and is the most applied tool for modelling marine and aquatic ecosystems globally. While choice of modelling technique or framework should always depend on the policy or research question that is to be addressed, EwE has a number of laudable features that can be selected to: identify and quantify major energy flows in an ecosystem, interactions between species, identify keystone species, evaluate the effects of climate induced or anthropogenic variability on ecosystems, explore management policy options by incorporating economic, social and ecological considerations, evaluate the placement and impact of marine protected areas, or predict the bioaccumulation of persistent pollutants (reviewed by Coll *et al.*, 2015). EwE models have also been applied in testing ecosystem theories on resilience, stability and regime shifts (Pérez-España & Arreguín-Sánchez, 2001; Tomczak *et al.*, 2013; Arreguín-Sánchez & Ruiz-Barreiro, 2014; Heymans & Tomczak, 2015). The EwE approach is therefore well placed to be able to address many of the questions asked by managers on marine policy or conservation issues such as natural variability and monitoring, management measures, ESs, “Good Ecological and Chemical Status” targets for the EU Water Framework Directive (WFD) and environmental change and climate adaptation under multiple stressors (Steenbeek *et al.*, 2014; Hyder *et al.*, 2015).

4.1.2 Issues of validity, scale and trophic complexity

Applying a EwE-type system analysis to marine ecosystems is not without its challenges however. Because of its ease of construction and lack of automatic checks, beyond the ecological experience of the user, many published EwE models have been used for management purposes without proper verification and validation (Heymans *et al.*, 2014). This ease of use, combined with limited quality control has perhaps been one of the reasons of the limited utilization of EwE models for management applications. (Townsend *et al.*, 2008). Within the last few years however, a growing number of diagnostic checks have been developed to establish best practices in creating and using such models (Mackinson *et al.*, 2009; Darwall *et al.* 2010; Link, 2010; Heymans *et al.*, 2016). These guidelines take into consideration the underlying thermodynamic and ecological rules available to users, recommend approaches to balance an EwE model, the best tools to fit models to time series data, and how to evaluate uncertainty. In practice if these tenets are upheld, it would allow not only more rigorous and consistent models, but would also aid in the acceptance of EwE and other mass balance models within management.

A second problem in taking a seascape scale perspective, is describing and defining such open and complex environments such as estuaries, with difficulties about how best to delineate the area under question (Elliott & McLusky, 2002; McLusky & Elliott, 2007). Many of the regulatory processes that operate within estuaries are influenced by external drivers from the marine and terrestrial environment, the relative importance of which vary greatly from estuary to estuary (Elliott & Whitfield., 2011). This problem can be overcome however, by externalising these factors when developing a dynamic model, allowing the user to deal with the input and export of the biophysical elements of the system, for instance the transport of excess nutrients from the catchment hinterland to the open ocean (e.g. Raffaelli, 2011) . This is also sensible when dealing with highly migratory estuarine species such as shore birds, diadromous fish (all fishes that migrate between the sea and fresh water) and crustaceans, which may constitute a substantial proportion of the ecology of the system but are represented by a transitional life cycle, with the remainder of their time spend often tens to hundreds of kilometres distant from the estuary.

Moving to working at the large temporal and spatial scales associated with estuaries also brings with it the challenges of working across many trophic levels with the need to accommodate many of the hydro-geographical processes that operate at these scales (Bulling *et al.*, 2006; Raffaelli, 2006) Tractable research at these scales although inherently challenging can be achieved using modelling approaches that continually challenge the interpretation that multiple interactions of components other than those inferred are plausible using a series of alternative hypotheses (MacNeil, 2008). Using

this method a demonstration can convincingly be made that even a small a changes in biodiversity *per say* can result in a set outcome (e.g. reduction in functioning), out with the normal variation of the system (Marques & Jørgensen, 2002). The persuasiveness and scientific rigor of removing or weighting such confounding factors is particularly important when addressing management issues where the threat to maintaining ecosystem functioning may be large and no competing hypotheses can sensibly account for the observations.

4.2: Sampling methods and data collection

The sample sites and protocols for the collection of macrofauna species are described in Chapter 2 section 2.4.4 (Tamar) and 2.5.4 (Eden). All other sources of data used in the development of each of the five Ecopath models are described henceforth, along with the general modelling approach.

4.2.1 Tamar benthic primary producer data collection

Quantitative biomass data for the main benthic primary producers (microphytobenthos, macroalgae and other macrophytes) at the estuarine scale were initially unavailable for the periods chosen in the Tamar system. Therefore, all system level biomass estimates of primary producers were made using the Ecopath model based on case study specific estimates of their production, using data from small scale *in situ* measurements (e.g. Bale *et al.*, 2006) and knowledge of other trophic assemblages. Model estimates were examined and compared with the existing literature to ensure the predations were plausible. For instance, there have been a number of long-term biotope and aerial surveys of saltmarsh and macroalgal extent (Webster *et al.*, 1998; EA., 2000; Widdows *et al.*, 2007; Curtis *et al.*, 2010) on various regions of the Tamar complex (out-with the current sampling periods), which were used to compare our predicted biomass values. The macroalgal group here is likely to comprise of locally registered species such as *Enteromorpha* and *Ulvae sp.*, while the 'other' macrophyte grouping is likely to comprise a wide variety of seagrass and saltmarsh species such as by not limited to: common saltmarsh-grass (*Puccinellia maritime*), common cord-grass (*Spartina anglica*), common eelgrass (*Zostera marina*), red fescue (*Festuca rubra*) and sea couch (*Elymus pycanthus*).

4.2.2 Tamar macro-benthic invertebrate data collection

Invertebrate data were collected at the estuary scale through the extensive surveys carried out in 1990, 1992 and through identical surveys in 2005 (see chapter 2.4.2). Sample sites from each zone (upper, central and lower) were pooled to represent the biomass of the estuary as a whole. Invertebrate densities were converted to biomasses using Tamar-specific relationships (e.g. Dashfield & McNeill, 2014). Species that were not naturally present in one of the years or sites or whose roles in the trophic network were unimportant (biomass < 0.01 g AFDWm⁻²) were not taken into account.

4.2.3 Tamar demersal fish and epi-benthic crustacean data collection

Data on demersal fish species and epibenthic crustaceans could not be collected at the estuarine level for practical reasons. However, historical fisheries-independent trawl surveys mainly undertaken by the Marine Biological Association (MBA) reveal a relative temporal consistency in the overall numbers of flatfish and epibenthic crustaceans between historic and contemporary trawls. Resurveys of inshore sampling sites near Plymouth by McHugh *et al.* (2011) compared fishing records from Plymouth Sound and other inshore sites near Plymouth from 1913 to 1922 with those from 2008 to 2009 and found no significant differences between flatfish catches, including flounder (*Platichthys flesus*), in the 2 periods. Other observations by Russel., (1973) and Dando., (2011) from studies undertaken between 1976 and 1980 also agree with detailed studies undertaken by Wilson., (1939) and Hartley., (1940, 1947), suggesting there is no evidence of substantial changes in the Tamar flounder (*Platichthys flesus*) or demersal fish populations over the last 100 years. The numbers and sizes of fish caught in all these studies were known to be similar to those found in the 1970s, since Hartley gives details of the area swept by the tuck net used in the earlier studies (results not shown). Similar observations into the autecology of the brown shrimp (*Crangon crangon*) by Henderson *et al.* (1987; 1990) and later by Campos *et al.* (2008; 2009; 2012) across several British estuaries including the Tamar suggest a consistency in the population structure and phylogeography of this species over our study period. Therefore, given that the spatial structure of the demersal fish and caridean shrimp assemblage has remained relatively constant, similar biomass values for each of these taxa were used over the time periods.

4.2.4 Tamar waterbird data collection

Population numbers for waterbirds were obtained for the period 1990-2005 from the WeBS (Wetland Birds Survey) database (Frost *et al.*, 2016). Bird counts were based on monthly observations in 15 sectors covering the whole of the Tamar complex. Twenty-three waterbird species (representing >95% of the total bird numbers in the system, with those excluded largely representing seabird species) were selected from a list of over 183 known species to inhabit and feed on the estuary recurrently to increase the chance of interoperating temporal and spatial changes. The species selected are as follows: two Grebe species (great crested grebe (*Podiceps cristatus*) and little grebe (*Tachybaptus ruficollis*)), seven wildfowl species (canada goose (*Branta Canadensis*); mallard (*Anas platyrhynchos*); mute swan (*Cygnus olor*); red-breasted merganser (*Mergus serrators*); shelduck (*Tadorna tadorna*); teal (*Anas crecca*) and wigeon (*Anas Penelope*)), twelve wader species (avocet (*Recurvirostra avosetta*); bar-tailed godwit (*Limosa lapponica*); black-tailed godwit (*Limosa limosa*); curlew (*Numenius arquata*); dunlin (*Calidris alpine*); golden plover (*Pluvialis apricaria*); little egret (*Egretta*

garzetta); oystercatcher (*Haematopus ostralegus*); pintail (*Anas acuta*); redshank (*Tringa tetanus*); snipe (*Gallinago gallinago*) and turnstone (*Arenaria interpres*); whimbrel (*Numenius phaeopus*) and one seabird species (cormorant (*Phalacrocorax carbo* although)). Prior to analysis counts were converted to biomasses using species specific body weights outlined by Snow & Perrins (1998).

4.2.5 Eden benthic primary producer data collection

To obtain an approximate value for microphytobenthic biomass and production in the system, contact cores were taken across identical transects of each of the three main zones of the estuary in 1999 and 2015 by sampling the top 2 cm of the surface sediment (see Chapter 2.5.2 for protocols). The presence of macroalgae (biomass $t\ km^2$) was initially unavailable for the 1999 time period and therefore was estimated by Ecopath. Estimates for the 1999 period were compared for validity to a visual survey of macroalgae determined during the BIOPTIS campaign (see chapter 2.5) within 5m radius of each sampling point (Ford & Honeywill, 2002). For the 2015 period, macroalage cover was estimated using pictorial analysis of aerial photographs using Google Earth Pro[®] (Figure 4.1). Both biomass and area cover data were subsequently combined to provide an estimation of macroalgal biomass per unit area ($t\ km^2$), as outlined by the Water Framework Directive (Scanlan *et al.*, 2007). Macroalgae were mostly identified to be *Enteromorpha* and *Ulvae Sp.*

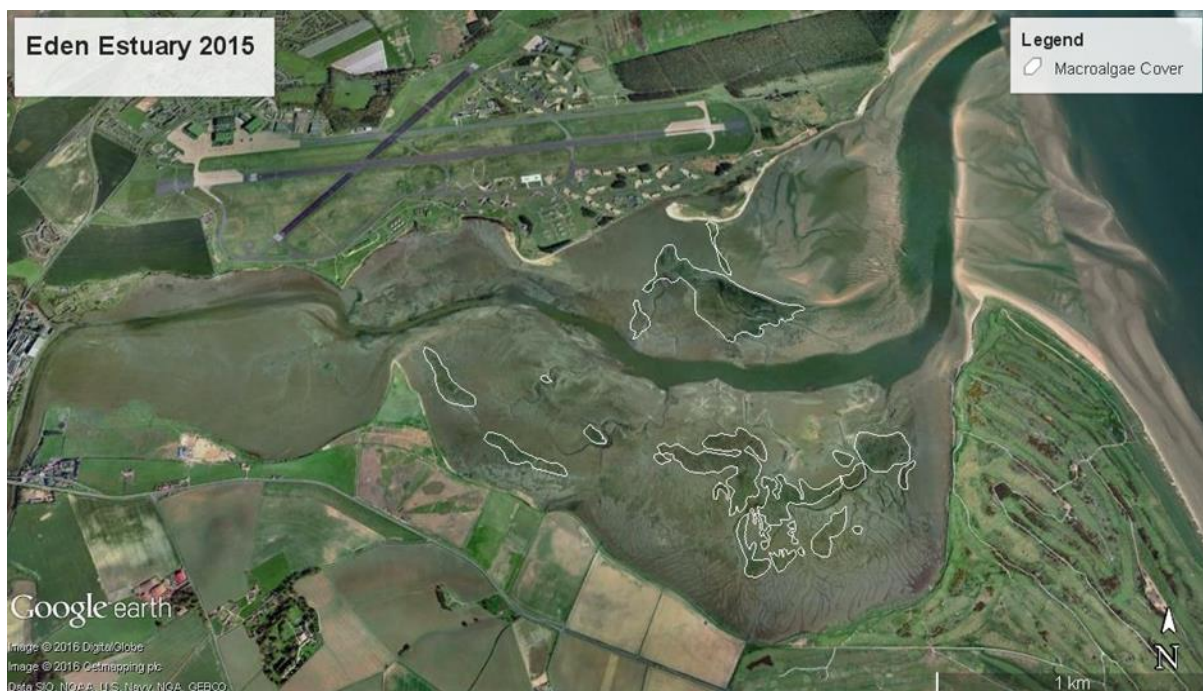


Figure 4.1 Macroalgal cover of the Eden Estuary for the 2015 period. White polygons represent macroalgal mats of $> 1\ kgm^{-2}$.

Estimates of 'other' macrophytes in the system were calculated by Ecopath, based on known *in situ* estimates of saltmarsh extent and production (Fife Council, 2008; Maynard, 2003; 2014; Maynard *et al.*, 2011). Common species represented by this grouping were likely to include common saltmarsh-

grass (*Puccinellia maritime*), sea clubrush (*Bolboschoenus maritimus*) and the eelgrasses (*Zostera augustifolia*), (*Z. noltii*), and (*Z. marina*).

4.2.6 Eden macro-benthic invertebrate data collection

Invertebrate data were collected at the estuary scale through the extensive surveys carried out in 1999 and through identical surveys in 2015 (see chapter 2.5.3). Sample sites from each zone (upper, middle and lower) were pooled to represent the biomass of the estuary as a whole. Invertebrate densities were converted to biomasses using Eden-specific relationships (e.g. Biles *et al.*, 2002). Species that were not naturally present in one of the years or sites or whose roles in the trophic network were unimportant (biomass < 0.01 g AFDWm⁻²) were not taken into account.

4.2.7 Eden demersal fish and epi-benthic crustacean data collection

As with the Tamar, data on benthic fish could not be collected at the estuary scale for the 1999 or 2015 periods in the Eden for practical reasons. Data on fish populations were also unattainable from the literature due to a paucity of fish monitoring surveys within the estuarine complex. Demersal fish biomass estimates were therefore estimated by Ecopath, based on knowledge of other trophic assemblages in the system. Data on epibenthic crustacean numbers, most specifically the brown shrimp (*Crangon crangon*) were obtained as part of the aforementioned macrobenthic invertebrate data collection.

4.2.8 Eden waterbird data collection

Population numbers for waterbirds were obtained for the period 1990-2015 from the WeBS (Wetland Birds Survey) database (Frost *et al.*, 2016). Bird counts were based on monthly observations in 5 sectors covering the whole of the Eden complex. Eighteen waterbird species (representing >95% of the total bird numbers in the system, with those excluded largely representing seabird species) were selected from a list of over 85 known species to inhabit and feed on the estuary recurrently, to increase the chance of interoperating temporal and spatial changes. The species selected are as follows: eight wildfowl species (eider (*Somateria mollissima*); greylag goose (*Anser anser*); mallard (*Anas platyrhynchos*); mute swan (*Cygnus olor*); red-breasted merganser (*Mergus serrators*); shelduck (*Tadorna tadorna*); teal (*Anas crecca*) and wigeon (*Anas Penelope*)), nine wader species (bar-tailed godwit (*Limosa lapponica*); black-tailed godwit (*Limosa limosa*); curlew (*Numenius arquata*); dunlin (*Calidris alpina*); golden plover (*Pluvialis apricaria*); grey plover (*Pluvialis squatarola*); knot (*Calidris canutus*); oystercatcher (*Haematopus ostralegus*) and redshank (*Tringa tetanus*)) and one seabird species (cormorant (*Phalacrocorax carbo* although)). Prior to analysis counts were converted to biomasses using species specific body weights outlined by Snow & Perrins (1998).

4.3 Modelling approach

4.3.1 Ecopath food webs and trophic structure

The final version of the Tamar food web (Figure 4.2), comprised 42 taxa distributed over four trophic levels including: waterbirds (avocet, bar-tailed godwit, black-tailed godwit, Canada goose, cormorant, curlew, dunlin, golden plover, great crested grebe, little egret, little grebe, mallard, mute swan, and wigeon); fish (flounder); other demersal fish; benthic invertebrates (*Ampharete spp.*, *Cerastoderma edule*, *Corophium volutator*, *Crangon crangon*, *Melina palmata*, *Mya arenaria*, *Mytilus edulis*, *Nephtys hombergii*, *Hediste diversicolor*, *Peringia ulvae*, *Scrobicularia plana*, *Retusa obtusa*, and *Tubificoides benedii*); benthic primary producers (macroalgae); other macrophytes; benthic microphytes and detritus, oystercatcher, pintail, red-breasted merganser, redshank,, shelduck, snipe, teal, turnstone, whimbrel.

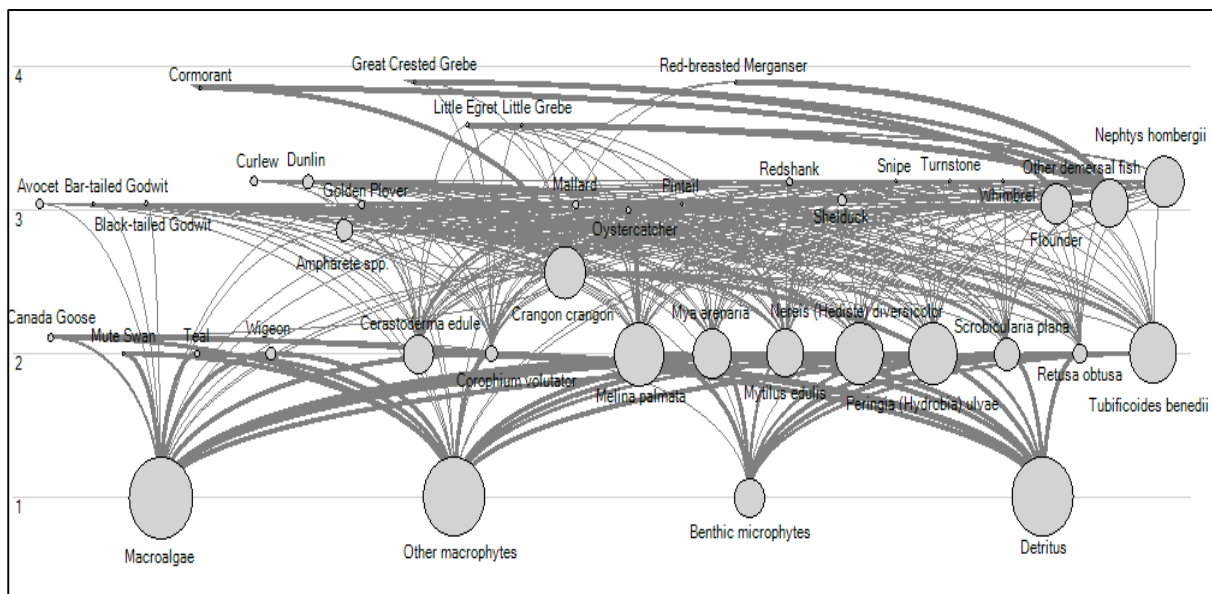


Figure 4.2 2D representation of the food web from the Tamar Estuary.

In comparison with the Tamar, the food web of the Eden was more finely resolved (Figure 4.3) composing 40 taxa also across 4 trophic levels including: waterbirds (bar-tailed godwit, black-tailed godwit, cormorant, curlew, dunlin, eider, golden plover, grey plover, greylag goose, knot, mallard, mute swan, oystercatcher, red-breasted merganser, redshank, shelduck, teal, wigeon); demersal fish; benthic invertebrates (*Ampharete spp.*, *Arenicola marina*, *Capitella capitata*, *Cerastoderma edule*, *Corophium volutator*, *Crangon crangon*, *Eteone longa*, *Eteone picta*, *Macoma balthica*, *Mya arenaria*, *Mytilus edulis*, *Nephtys hombergii*, *Hediste diversicolor*, *Peringia ulvae*, *Scrobicularia plana*, *Spio filicornis*, and *Tubificoides benedii*); benthic primary producers (macroalgae); other macrophytes; benthic microphytes and detritus.

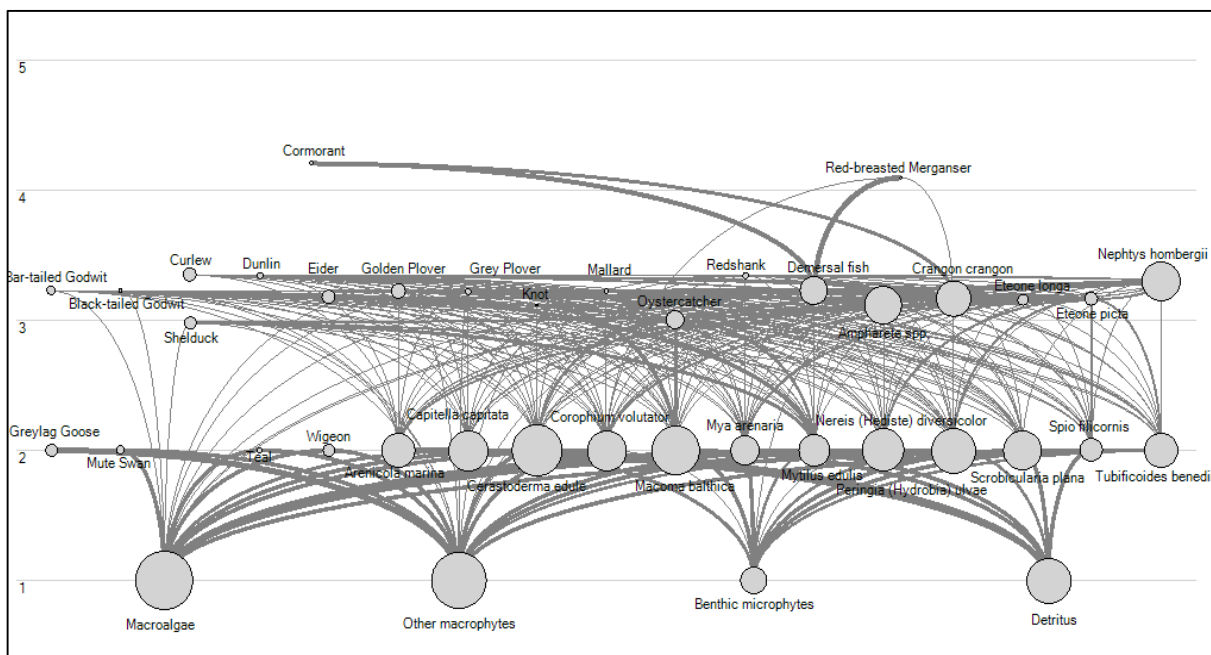


Figure 4.3 2D representation of the food web from the Eden Estuary.

Whilst benthic-microalgae are included due to their known importance in structuring benthic ecosystems, other water column elements (phytoplankton, zooplankton, planktivorous fish (e.g. shad, sand eel) and their consumers (species in the family *Salmonidae*)) were not included in this model and are considered to follow a separate non-overlapping trophic pathway (Hall & Raffaelli, 1991). This is due to both to both planktonic and benthic constellations of cycling representing independent domains of control (Baird & Ulanowicz, 1989), with flushing times in both tidal estuaries being rapid and therefore phytoplankton production and their derivatives are not constituting a significant proportion of benthic estuarine ecosystem functioning. This model instead centres on a detritus based pathway with particulate organic matter passing through micro-phytobenthos to macro-invertebrates to fish or birds (e.g. Raffaelli, 2011) and a second pathway is also used from macroalgae to macro-invertebrates or herbivorous wildfowl (Baird & Milne, 1981). By considering the trophic hierarchy in this way, it is possible to investigate some of the mechanisms responsible for the benthic

provisioning of ecosystem processes relating to the interaction with particulate organic matter such as the services of carbon sequestration and nutrient remediation.

In addition, although the harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) are known to roam freely through the Eden Estuary (and to a lesser extent the lower Tamar Estuary), they were not included in either modelling framework due to their diets mainly consisting of planktivorous fish (e.g. sandeels, whiting and species of the family *Salmonidae*) foraged outwith the estuarine area in question. For instance Sharples *et al.* (2009), noted in a study of the diet of harbour seals in the Eden and adjacent St. Andrews Bay to consist of 81 to 94% sandeels in winter and 63% in summer and autumn, with salmonids making up the remaining prey captured.

4.3.2 Compartments

Some groups of species were grouped into compartments based on identical ecological niches or similar functional traits. The benthic-microalgae group here is primarily composed of freshwater and marine diatoms with no single species dominating the community throughout the year. In the case of the Tamar, demersal fish species were amalgamated into one compartment comprising sole (*Microstomus kitt*), turbot (*Phrynorhombus norvegicus*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). In the Tamar Estuary, the flounder *Platichthys flesus* was considered as a separate compartment being the only ray-finned demersal fish to migrate and colonize the upper reaches of the estuary due to its considerable powers of osmoregulation (Hartley, 1940; 1947). In the Eden Estuary, the demersal fish biomass compartment was estimated by the model, with fish identity assumed to be a combination of all benthic fish species known to occur within the estuary (see Chapter 2.2.2).

In all models, invertebrate species belonging to family *Ampharetidae* were grouped together, with many of these species sharing a functional role. As a prerequisite to any Ecopath model, the detritus compartment reflects the standing stock of non-living organic matter in the sediments (including different types of plant tissue, microbes, and faeces); the suspended organic matter; inputs from the river basin and from the ocean and flows from living organisms. With regards to microorganisms, few to no data were available for bacteria, therefore the benthic bacterial biomass was considered as being part of the detritus compartment, as recommended by Christensen and Pauly (1992a, b).

4.3.3 Ecopath: mass balance model

Ecopath trophic models are mass balance models that create a static snapshot of energy flows and their interactions in an ecosystem represented by trophically linked biomass 'pools' or ecological guilds of species (Pauly *et al.*, 2000). In a model, the energy input and output of all living groups must be balanced. Ecopath parameterizes models based on two master equations one to describe the

production term and one for the energy balance of each group (Christensen *et al.*, 2005). The first equation divides the production of each compartment into individual components. This is implemented with the equation:

Production = catches + predation mortality + biomass accumulation + net migration + other mortality

Or, more formally,

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i - \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij} \right) - Y_i - BA_i - E_i = 0 \quad \text{Equation 4.1}$$

Where B_i and B_j are the biomasses of prey (i) and predators (j) respectively; P/B_i the production/biomass ratio; EE_i the ecotrophic efficiency which describes the proportion of the production that is utilized in the system; Y_i the fisheries catch per unit area and time; Q/B_j the food consumption per unit biomass of j; DC_{ij} the fraction of prey i in the average diet of predator j; BA_i the biomass accumulation rate for i (the default value of zero was used to indicate no biomass accumulation); and E_i is the net migration of i, calculated as immigration (migration into the area covered by the model) minus emigration (migration out of the area, the default value of zero was used). Within the model, biomass is expressed as tonnes km^{-2} and production and consumption is expressed as tonnes $\text{km}^{-2} \text{yr}^{-1}$.

Equation two expresses how the energy balance within each compartment is ensured when consumption by prey biomass = production + respiration + unassimilated food

Or, more formally,

$$B_i \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \quad \text{Equation 4.2}$$

where R_i is the respiration rate, and U_i the unassimilated food rate. Respiration is used in Ecopath, only for balancing the flows between groups and refers to the assimilated fraction of matter that is not used in production. The units of the model are typically expressed in terms of nutrient or energy-related currencies. Following other estuarine Ecopath models (e.g. Baeta *et al* 2011), it is assumed that autotrophs and detritus based organisms have zero respiration with all nutrients that leave the compartment being re-utilized. For each compartment unassimilated food (U_i) consists of food which is egested and flows to the detritus. In our energy model U_i comprised the default value of 0.20 for all groups (i.e. 20% of the consumption for all groups).

4.3.4 The estimation procedure

For parameterization Ecopath sets up a system with (at least in principle) as many linear equations as there are groups in a system, and it solves the set for one of the following parameters for each group:

- Biomass ($B \text{ t km}^{-2}$) for the year under consideration
- Production/biomass ratio ($P/Q \text{ yr}^{-1}$)
- Consumption/biomass ratio ($Q/B \text{ yr}^{-1}$); or
- Ecotrophic efficiency (EE proportion)

The loop above serves to minimize the computations associated with establishing mass-balance in Ecopath. While not all parameters used to construct a model need to be entered, the desired situation is that the biomasses, production/biomass and/or consumption/biomass ratios are entered for all groups and that only the ecotrophic efficiency is estimated, given that no procedure exists for its field estimation. To obtain an estimation of unknown flow values, ecosystem-level linear inverse modelling (LIM) methods can be used within Ecopath, to obtain values of unknown flows starting from a reduced number of known system parameters (Vézina & Platt, 1988; Niquil *et al.*, 2011). Having established biomass values per unit area (t/km^2), the remaining three parameters were estimated using this procedure for each compartment.

Production (P) refers to the elaboration of tissue (whether it survives or not) by a compartment over the period considered entered as the ratio of production over biomass (P/B). The P/B ratio is equivalent to the instantaneous rate of biomass turnover in relation to the time taken to replace the biomass by the population (e.g. Cusson & Bourget, 2005). P/B ratios required for Ecopath were collected from a number of web-based databases (e.g., Fishbase, Chesapeake Bay database and WeBS). For all vertebrate groups this information was readily available from these databases. For avian species, production was calculated as recruitment (R) of young into the adult population in units per individual (tonnes per year). As birds were assumed to fledge at adult weight, there was no need to incorporate a survival term (Stenseth, 2002) therefore ($R \leq P/B$). For the primary producer and invertebrate groups, Brey's (2001) Virtual Handbook on Population Dynamics, version 4 (Brey, 2012, www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.htm) was used to calculate the P/B for all species. The weight-to-energy ratios needed in order to apply the empirical method were also provided by Brey (2001). In the case of combined groups the means of each component parameters, were weighted by the relative biomass of the components.

Consumption (Q) is the intake of food by a compartment over the time period considered entered as the ratio of consumption over biomass (Q/B). For all heterotrophic compartments, the P/Q ratios were

entered into the program in order to estimate the Q/B ratio indirectly. The only exception was in the case of demersal fish species where a holistic predictive model for Q/B using asymptotic weight, habitat temperature, a morphological variable and food type as independent variables were calculated using Fishbase.

Other mortality (i.e. starvation, disease) in form of the ecotrophic efficiency (EE), is the proportion of the production that is utilized within the system. Independently it is both difficult to measure and calculate direct estimates of this metric from natural systems. To obviate such problems EE was estimated for most groups and model quality evaluated by checking if the EE values were intuitive (between 0-1). EE values were initially set at 0.1 for waterbirds (mostly top predators) and 0.95 (prey) for invertebrates, but the majority were re-estimated by Ecopath as slightly different values (mostly less than supposition) in order to balance the model. The EE of the detritus group is defined as the ratio between the flow out of the detritus, and the flow into the same compartment. EE for detritus cannot be entered, and therefore was calculated by Ecopath. Once the software has estimated each of the four parameters, the system balances the input and output of each group, using respiration R_i and unassimilated food U_i for adjustments.

4.3.5 Pre-balancing analysis (PREBAL)

To add rigor and validity to the models a set of pre-balance diagnostics (PREBAL) outlined by Link (2010) as recommended by Heymans *et al.* (2016) were made to assess any issues with the models structure or quality of the primary input data. These assessments were made in simple spreadsheets before any balancing or tuning of the models were executed. In the first instance, the logarithmic

ratios of biomass among various taxa groups were plotted (Figure 4.4) as they have been repeatedly identified as a major indicator of marine ecosystem functioning (Link, 2005; Mokany *et al.*, 2016). Biomass decomposition generally followed a sequential decrease moving across trophic levels, within all acceptable standards of highly dynamic estuarine systems. While detrital groups were not used (as recommended in calculating these slopes), it is noted for context that detrital standing stocks were on the same order of magnitude as primary producer biomass, consistent with systems such as estuaries and benthic orientated food webs that are particularly dependent upon detrital energy.

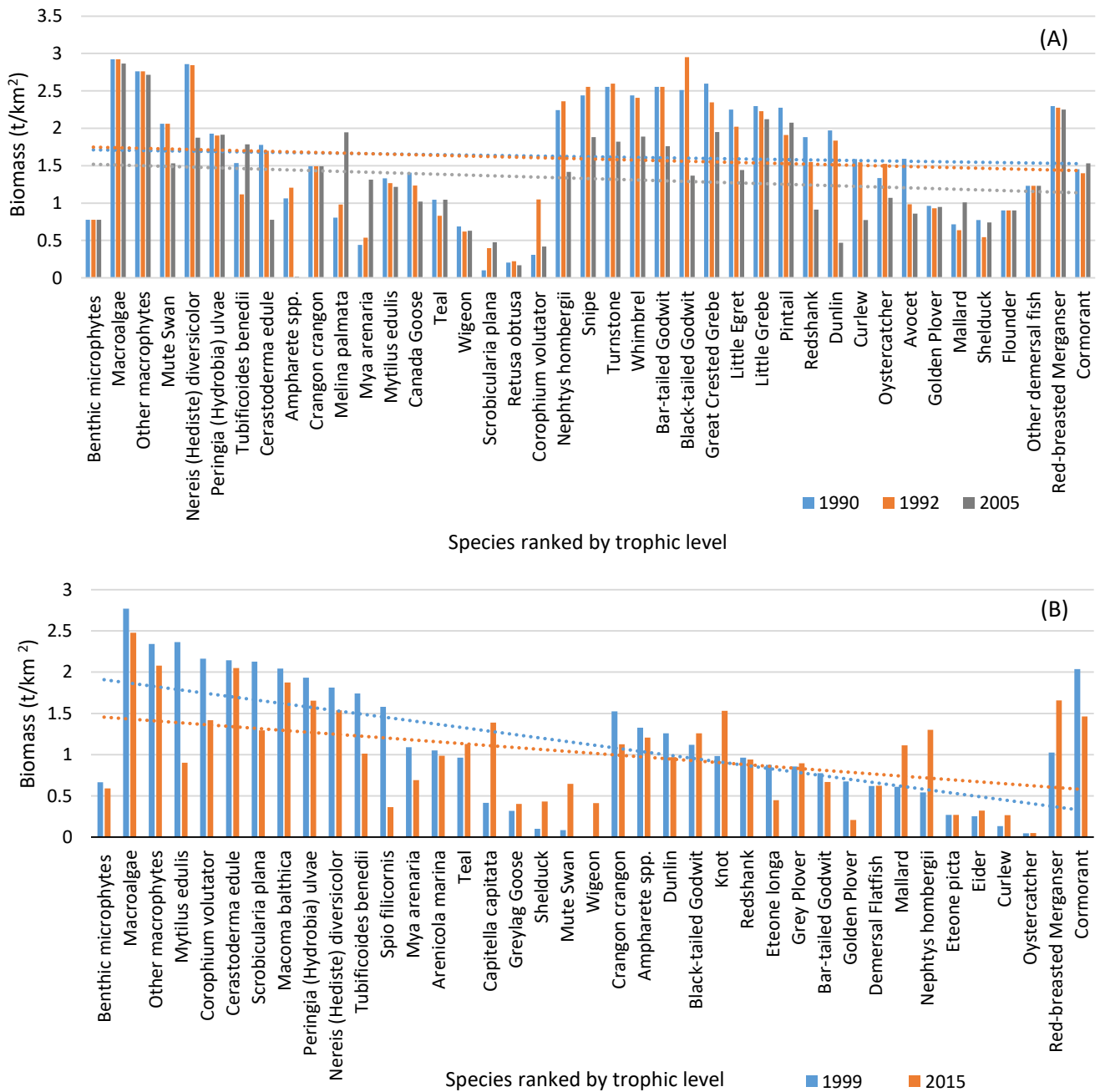


Figure 4.4. PREBAL Biomass estimates of the Tamar (A) and Eden (B) estuary models (t/km²), on a log scale vs species ranked by trophic level, from lowest to highest trophic level. Trophic decomposition (trend line), showing variously declining levels of biomass with increasing trophic level.

In a second step, the vital rates of all taxa, in the form of Production/Biomass ratio and Consumption/Biomass ratio were plotted (Figure 4.5 & 4.6) for comparison, as these ratios are reflective of an amalgamation of an entire suite of physiological processes. As with the biomass estimates, there was an acceptable decline in vital rates with increasing trophic level. Miss-parameterized discrepancies were identified at this point and addressed to avoid potential imbalances in system structure.

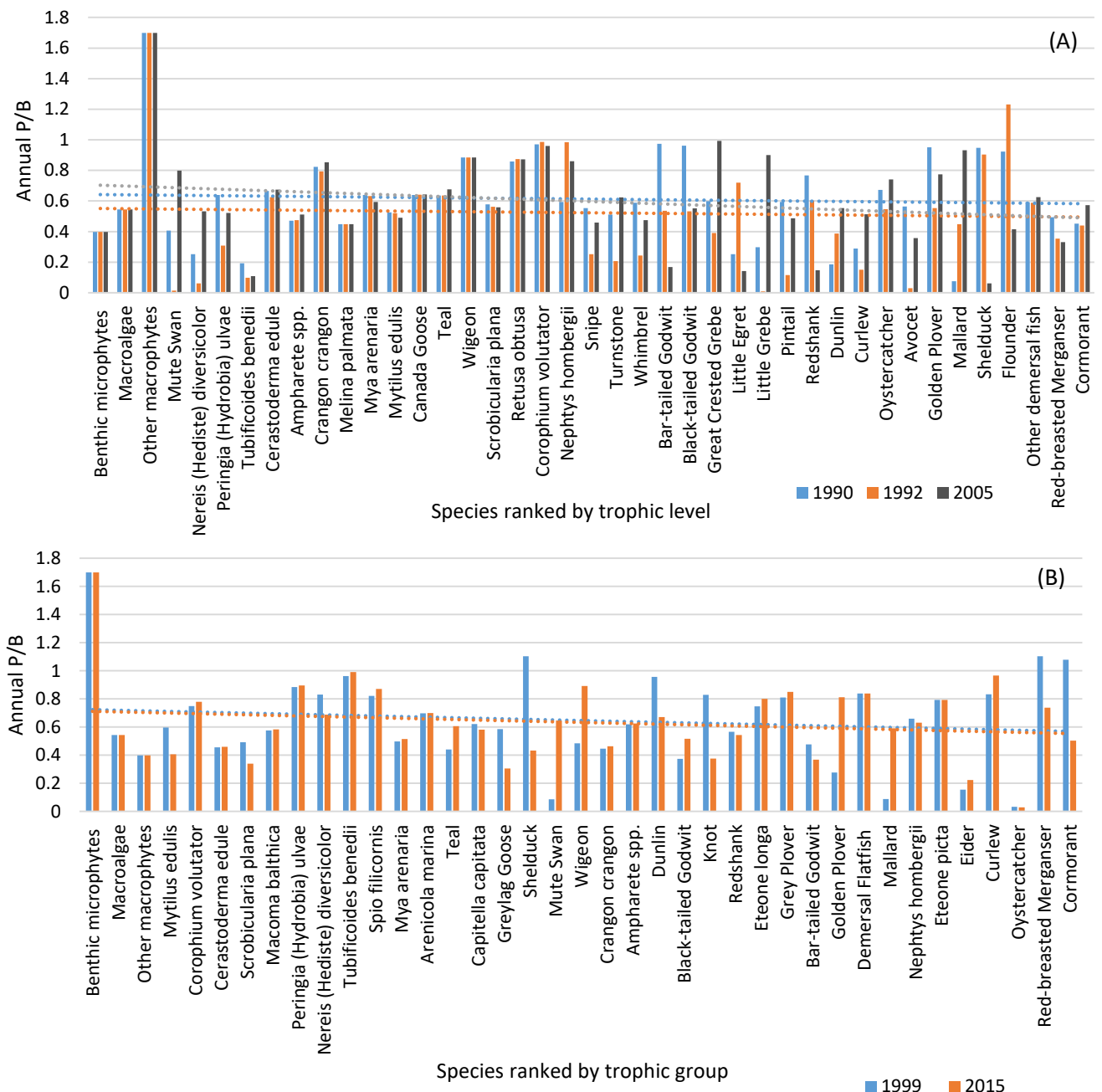


Figure 4.5. PREBAL Production/Biomass estimates of the Tamar (A) and Eden (B) estuary models (t/km²), on a log scale vs species ranked by trophic level, from lowest to highest trophic level. Trophic decomposition (trend line), showing variously declining levels of P/B with increasing trophic level

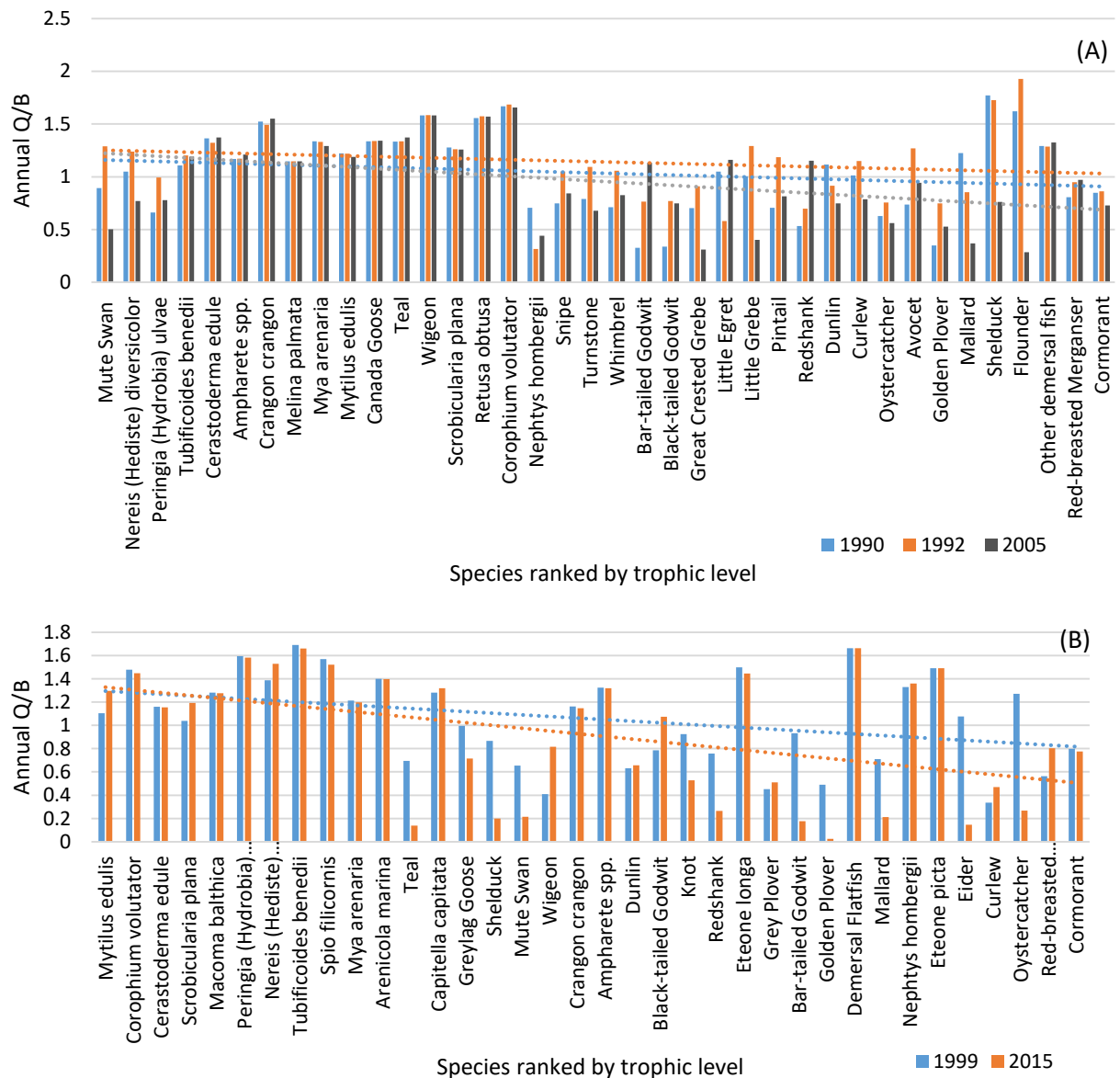


Figure 4.6. PREBAL Production/Biomass estimates of the Tamar (A) and Eden (B) estuary models (t/km^2), on a log scale vs species ranked by trophic level, from lowest to highest trophic level. Trophic decomposition (trend line), showing variously declining levels of Q/B with increasing trophic level.

4.3.6 Diet comparison

In a trophic model such as Ecopath it is predation that links together the different groups into a system with consumption for one group effectively becoming mortality for another. As such, diet composition must be entered for all groups. Diet matrices were built for each taxa using information from a wide variety of literary sources and summed to unity. Resident invertebrate diet compositions was compiled largely from MBA data holdings including MARLIN and BIOTIC database (www.marlin.ac.uk/biotic), while shorebird and flatfish data referenced from the WeBS and Fishbase databases respectively. Complimentary diet information was also gathered from the literature

(Appendix 4A). Initially all species were listed from each taxa along with their percentage contribution to the compartment. Each observed dietary item was then assigned to each individual group of species, with the final percentage of the diet assumed to be proportional to the fraction that its biomass comprised of the total biomass of the functional group.

4.3.7 Anthropogenic exports (Y_i)

A complete mass balanced model needs estimates of the export rates from the system, including the harvesting of economically important species. Commercial flat fishing mortality by means of landings from the Tamar was considered sufficiently small enough to be negligible, based on records of numbers of fish caught of species of 130 mm and upwards (Clark, 2012). Commercial fishing effort on the Eden Estuary was also considered to be minor, with the estuary and surrounding St. Andrews Bay protected by an Scottish Inshore Fishing Order (1989) which forbids the use of all mobile fishing gears, including trawling and dredging practices within the area. Similarly the harvesting of commercial invertebrate species such as *Cerastoderma edule*, *Mytilus edulis*, *Hediste diversicolor*, *Nephtys hombergii* and *Crangon crangon* for bait fisheries or human consumption was considered insignificant in terms of overall biomass export from the system Tamar (Curtis, 2010) and Eden where bait collection is strictly controlled.

4.3.8 Balancing the model

Once the basic input parameters were entered, the software then calculated unknown parameters across each of the models. Initially none of the models were mass-balanced (e.g. EE higher than 1, negative respiration values or irrational Q/B estimates). Using the ecological and thermodynamic rules for balancing Ecopath models outlined by Darwall *et al.* (2010) elements of the diet matrix or the values of the three inputted parameters were adjusted iteratively until all logical constraints were met. This was done starting with the lowest quality data first, preserving the most reliable data. Changes were made sequentially and the basic estimates routine re-run and examined.

In both the Tamar and Eden case studies, the most reliable data were the biomass and production values, and consequently these values were left largely unchanged. Diet matrices were principally unaltered but differed slightly to reflect the known trophic responses of species to different pressures. In all incidences the balancing parameter changes fell within the ranges of uncertainty associated the development of the 'pedigree' — a routine in Ecopath modelling that quantifies the quality of the input data by assigning confidence intervals based on the origin of the information. The index value ranges from 0-1 with an index value of 1 assigned to a model built primarily on *in situ* collected data and combined with qualitative supplementary information. Models that have relied on parameters from other models or used Ecopath to estimate the majority of its key parameters (i.e. biomass) would be

assigned a pedigree closer to 0 (Christensen & Walters, 2004). The pedigree index P calculated for all the Tamar models was 0.481 and 0.593 for the Eden, with the higher latter value reflecting the use of locally collected data and trophic information used to parameterise the models. In comparison with other Ecopath models (see review of over 393 models by Morissette, 2007) these can be considered as relatively good pedigree values and highlights the high level of work and knowledge that has been done on these systems over the past 30+ years.

4.3.9 Summary of system statistics and indices

Once a balanced Ecopath model is obtained, the flows of biomass among the groups and higher-order indices of ecosystem functioning can be interpreted using Ecological network analysis (ENA). To do this a suite of algorithms incorporated into Ecopath (Christensen *et al*, 2005) allow several system and network analysis indices to be produced which can be used for determining an ecosystems functioning, subsequent flows to ESs, structure, maturity, stability and resilience. These indices are categorised here into three groups 1) Measures of total ecological functioning (Table 4.1), 2) Measures of relative ecological functioning (Table 4.2) and 3) Network characteristics of mass balanced models (Table 4.3).

Table 4.1 Measures of total ecological functioning from mass balance models

System Indices	Description	Units
Sum of all consumption ($\sum C$),	$\sum C$ is the sum of all consumption in a system.	t km ⁻² yr ⁻¹
Respiratory flows ($\sum R$)	$\sum R$ is the sum of all respiratory flows in a system.	t km ⁻² yr ⁻¹
Flows to detritus ($\sum FtD$)	$\sum FtD$ consists of what is egested (the non-assimilated food) and those elements of the groups, which die of old age, diseases, etc.	t km ⁻² yr ⁻¹
Production ($\sum P$)	$\sum P$ is the sum of all production flows in a system.	t km ⁻² yr ⁻¹
Net primary Production (NPP)	NPP is calculated as the summed primary production from all producers.	t km ⁻² yr ⁻¹
Total biomass (excluding detritus) ($\sum B$)	Total natural capital in the system in the form of ($\sum B$) is related to system exergy (Christensen, 1995) which may be a useful measure of the overall ability of the system's capital stocks to provide a broad range of (undefined) services.	t km ⁻² .

Table 4.2 Relative measures of ecological functioning from mass balance models.

System Indices	Description	Units
Total primary production/total biomass (PP/B),	PP/B, is expected to be a function of the system's maturity. In immature systems, production exceeds respiration for most groups, and therefore the biomass can be expected to accumulate over time, which in turn will lead to a decline in the ratio (Odum., 1969). The system ratio behaves like that of individual groups; its dimension is time ⁻¹ and it can take any positive value. The metric of PP/B is also an expression of the flow of the ecosystem-provisioning service (plant production) from a stock of natural capital (total system biomass).	The PP/B ratio can take any positive value and is dimensionless.
Primary production/respiration (PP/R)	PP/R, is the difference between total primary production and total respiration. It is considered by Odum (1971) to be an important ratio for description of the maturity of an ecosystem.	The PP/R ratio can take any positive value and is dimensionless.
Total throughput cycled (T cycled)	T cycled is the fraction of, an ecosystem's throughput that is recycled.	t km ⁻² yr ⁻¹
Finn's index (FCI)	FCI captures the functions of carbon and nutrient cycling in the system using a proxy of (% of total throughput) and quantifies as one of Odum's (1969) 24 properties of system maturity and stress (Christensen 1995). In the context of ESs, the capacity of a system to provide the regulatory ESs of nutrient and carbon cycling is expressed by this index.	% of total throughput
Predatory cycling index (PI)	PI is a slightly modified form of the FCI index, computed after cycles involving detritus groups have been removed.	% of throughput w/o detritus
Average path length (APL)	APL measures the average number of transfers a unit of medium (e.g. carbon) will experience from its entry into the system until it leaves the system (Baird et al., 1991). Short cycles are usually indicative of fast cycling rates and longer path lengths of slower rates (Baird & Ulanowicz., 1989).	The APL is a positive value and is dimensionless.
The system omnivory index (SOI)	SOI specifies how consumer feeding interactions are distributed across trophic levels. A value close to 0 indicates the consumer is specialised (i.e. it feeds on one trophic level) while a higher value indicates a diet composed of prey across many trophic levels. The index is therefore, a measure of inter-compartmental connectance and the extent to which a system displays web-like features (Christensen et al., 2000).	The SOI is a positive value and is dimensionless.

Table 4.3 Network characteristics of mass balanced models

Network characteristic	Description	Units
Total system throughput (TST)	TST represents the entire amount of biomass flow within the system (consumption + export + flows to detritus + respiration) and represents the size of the system (Ulanowicz, 1986). As such, it is an important parameter for comparisons of trophic flow networks	t km ⁻² yr ⁻¹
Ascendency (A)	A represents both the size and organisation of a system. Size is estimated as TST and organisation by the average mutual information (AMI, how the flows are arranged); the product of these two properties is Ascendency (Ulanowicz, 1986, 1997). Ascendency is a measure of a systems stability and a proxy for a systems resilience. For example, ecosystems safely operate within a 'window of vitality' with respect to ascendency (Ulanowicz, 2002, 2005), too low a value and the system tends to disorder, having insufficient cohesiveness; too high a value and the system becomes very vulnerable to stressors.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.
Development capacity (C)	C represents the upper limit for the size of the Ascendency. Both ascendency and capacity are measures of a systems stability and resilience.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.
System Overhead (O)	O is the difference between capacity and ascendency and is also a measure of system resilience. Higher system overheads indicate that a system has a larger amount of energy in reserve (in flowbits) with which it can use to resist stressor impacts (Ulanowicz, 1986). In the present context, system Overhead could be viewed as the degree to which capital stocks are able to continue to provide flows of services.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision

4.3.10 Keystone species

In addition to the previously calculated indices, keystone-ness and relative overall effect were estimated for each compartment in order to identify keystone species. These two indices derive from mixed trophic impacts analysis (Libralato *et al.*, 2006; Coll *et al.*, 2007). The relative overall effect of a compartment (ϵ_i) is the square root of the sum of square of all trophic impacts of one compartment on each other. It allows the quantification of direct and indirect effects that one compartment would have on the others. The keystone-ness metric takes into account the biomass of the compartment, a keystone species being one showing a structuring role in the ecosystem. For compartment i :

$$KS_i = \log[\epsilon_i (1 - p_i)] \quad \text{Equation 4.3}$$

where p_i is the contribution of the compartment i to the total biomass of the food web.

4.4 Ecopath results

4.4.1 Biodiversity changes between the periods 1990; 1992 & 2005 (Tamar)

The biomass estimated for the three different years (1990, 1992 and 2005) and differences with respect to the 1992 pre-management period values are shown in Table 4. 4. At the base of the food web, benthic macrophyte biomass was estimated by Ecopath to be the same across all three of the periods. This relative stability is important because, this compartment plays an important role in maintaining secondary production in estuarine systems, by acting as a food source for the vast majority of the deposit feeding macro-benthos (Miller *et al.*, 1996, Page, 1997).

Macrophyte and macroalgal biomass estimates were similar for the 1990 and 1992 periods but decreased slightly between the 1992-2005 period, by around -99.80 and -60 t km⁻² respectively. The driver of this plant biomass change is most likely consistent with the reduction in loadings of nitrite and phosphate compounds entering the system (Chapter 3 section 3.3.1).

Biomass of the key prey species *Ampharete* and *Corophium* increased by 4.47 and 9.12 t km⁻² in 1992 following eutrophic symptoms, followed by large declines of -15.11 and -10.77 t km⁻² respectively following the implementation of nutrient mitigation measures in 2005. In the case of *Corophium* the former increase is likely attributed to its known intolerance to eutrophic conditions (Raffaelli., 1999), disrupting its feeding behaviour. The latter and much larger decrease in not just *Ampharete* and *Corophium* but also other major prey invertebrate species such as *Hediste* (-626 t km⁻²) and *Cerastoderma* (-43.90 t km⁻²) likely reflect the improving sediment physico-chemical environment, promoting increased interspecific competition and predation effects from higher trophic levels.

Table 4.4 Biomasses of groups used in Tamar mass-balance model.

Group Name	1990 Biomass (t km ⁻²)	1992 Biomass (t km ⁻²)	2005 Biomass (t km ⁻²)	Difference t km ⁻² (1992 relative to 1990)	Difference t km ⁻² (2005 relative to 1992)
Avocet	0.0255	0.1036	0.1383	0.08	0.03
Bar-tailed godwit	0.0028	0.0028	0.0174	0.00	0.01
Black-tailed godwit	0.0031	0.0011	0.0428	0.00	0.04
Canada goose	0.0392	0.0582	0.0955	0.02	0.04
Cormorant	0.0353	0.0400	0.0294	0.00	-0.01
Curlew	0.0258	0.0286	0.1680	0.00	0.14
Dunlin	0.0106	0.0146	0.3391	0.00	0.32
Golden plover	0.1092	0.1176	0.1123	0.01	-0.01
Great crested grebe	0.0025	0.0045	0.0112	0.00	0.01
Little egret	0.0056	0.0095	0.0361	0.00	0.03
Little grebe	0.0050	0.0059	0.0076	0.00	0.00
Mallard	0.1924	0.2299	0.0980	0.04	-0.13
Mute swan	0.0087	0.0087	0.0294	0.00	0.02
Oystercatcher	0.0462	0.0300	0.0854	-0.02	0.06
Pintail	0.0053	0.0123	0.0084	0.01	0.00
Red-breasted merganser	0.0050	0.0053	0.0056	0.00	0.00
Redshank	0.0132	0.0283	0.1226	0.02	0.09
Shelduck	0.1688	0.2845	0.1820	0.12	-0.10
Snipe	0.0036	0.0028	0.0132	0.00	0.01
Teal	0.0899	0.1476	0.0902	0.06	-0.06
Turnstone	0.0028	0.0025	0.0151	0.00	0.01
Whimbrel	0.0036	0.0039	0.0129	0.00	0.01
Wigeon	0.2055	0.2400	0.2335	0.03	-0.01
Flounder	8.70	8.70	8.70	0.00	0.00
Other demersal fish	17.06	17.06	17.06	0.00	0.00
Ampharete sp.	11.6074	16.0736	0.9644	4.47	-15.11
Cerastoderma edule	61.0000	50.0000	6.1000	-11.00	-43.90
Corophium volutator	2.0267	11.1467	0.3800	9.12	-10.77
Crangon crangon	31.0200	31.0200	31.0200	0.00	0.00
Melina palmate	6.4000	9.6000	88.6400	3.20	79.04
Mya arenaria	2.7520	3.4400	20.6400	0.69	17.20
Mytilus edulis	21.4500	18.4500	16.5000	-3.00	-1.95
Nephtys hombergii	174.8913	229.4573	26.0238	54.57	-203.43
Hediste diversicolor	719.3550	700.7910	74.7864	-18.56	-626.00
Peringia ulvae	85.0484	79.7582	82.2930	-5.29	2.53
Scrobicularia plana	1.3200	2.5000	3.4300	1.18	0.93
Retusa obtusa	1.6000	0.6000	0.6800	-1.00	0.08
Tubificoides benedii	34.4100	13.0680	61.1670	-21.34	48.10
Macroalgae	834.60	834.60	734.80	0.00	-99.80
Other macrophytes	580.00	580.00	520.00	0.00	-60.00
Benthic microphytes	6.00	6.00	6.00	0.00	0.00

Other major invertebrate species such as *Melina*, *Scrobicularia* and *Mya* increased in biomass across the periods highlighting their different feeding behaviours and sensitivities to the sediment environment.

The relative stability of *Peringia* biomass across the periods (-5.29 & 2.53 t km⁻² respectively), is almost certainly because it is a consumer of macroalgae as well as living at the sediment surface where it is less affected by a low redox environment (Anderson, 1971).

The responses of waterbirds following the 1990 period, was generally favourable with seventeen of the twenty-three species recorded increasing in biomass by the year 1992. Two species showed no changes in biomass over the 1990-1992 period, namely the bar-tailed godwit (*Limosa lapponica*) and mute swan (*Cygnus olor*), while the Snipe (*Gallinago gallinago*) and Turnstone (*Arenaria interpres*) showed small declines in biomass of -0.01 t km⁻², respectively. The most significant numerical changes in biomass following the 1990 period were exhibited by the oystercatcher (*Haematopus ostralegus*) with a -0.02 t km⁻² decline. Despite the large percentage decline in the black-tailed godwit, the relative change in abundance was small (6 individuals), and is likely to a factor of natural population fluctuations of this species, with godwits often using a mixture of estuarine and nearby wet grassland feeding areas, as estuarine prey is depleted. In the case of the oystercatcher, relative biomass decline could be tantamount to the reciprocal reduced biomass of its preferred prey species *Cerastoderma edule* (Norris & Johnstone, 1998).

In the 2005 period following nutrient reduction measures, most of waterbird species (sixteen out of twenty-three species) continued to increase in biomass. Coinciding with the decline in algal mats, the two main herbivorous species in the system, wigeon (*Anas Penelope*) and mute swan (*Cygnus olor*), displayed very little negative response (-0.01 t km⁻² wigeon) and (0.02 t km⁻²), probably because they also graze off-estuary. These changes agree with longer term observations of these species (see Appendix 4B) beyond the final year of this study (2005) suggesting there is still sufficient food resources to support these herbivorous species with the Tamar system. In contrast, the

largest declines in waterbird species were mostly attributed to the omnivorous wildfowl family Anatidae (Swans, ducks and geese) by the mallard (*Anas platyrhynchos*) -0.13 t km⁻²; shelduck (*Tadorna tadorna*) -0.10 t km⁻² teal (*Anas crecca*) -0.06 t km⁻² and also the piscivorous cormorant (*Phalacrocorax carbo*) -0.01 t km⁻². These trends are a reflection of a general negative year on year decline of these species on the system from the early 1990's to most recent 2015 period (Appendix 4B). In summary, it is clear that there have been substantial changes to the biodiversity

composition of the Tamar Estuary food web between 1990 and 2005 periods. Two years after the major eutrophic event, the system was still characterized by dense macroalgal mats and large populations of the opportunistic species *Hediste*, despite showing signs of recovery *via* large-scale increases in the amphipod *C. volutator*, one of the main prey for many consumers at various trophic levels. Indeed the persistent nature of the impacts were ecologically and politically significant enough to declare a range of nutrient remediation strategies in the focal 1992 year (Chapter 2 section 2.4). These changes heralded changes to the foundation primary producing species of the estuary, with the bottom-up effects of nutrient reduction reducing macroalgae biomass, which likely had cascading changes on invertebrate and waterbird biomass up through the food web. As a result the biomass of these species is largely different between the 1992 and 2005 periods. Overall it is not clear how much of the positive changes in bird biomass are due to the increased availability of prey (*Ampharete*, *Cerastoderma*, *Peringia*, and *Hediste* especially) under improved sedimentary conditions or due to the improved survival of birds on breeding grounds elsewhere, leading to higher numbers of birds arriving on the estuary. What is clear is, a number of species show long term trends of increasing biomass on the estuary and that their demand on the prey base of the Tamar has noticeably increased.

4.4.2 Keystone species (Tamar)

Figure 4.7 represents the estimated keystone index for the functional groups of the three selected models, representing the Tamar system. Across all periods different groups of benthic primary producers (macroalgae, other macrophytes and benthic microphytes) showed high keystone index, suggesting that the lower part of the trophic web is very important in this system. Other benthic species such as *Nephtys hombergii* and *Hediste diversicolor* also ranked within the top five key species during the 1990 and 1992 periods (Table 4.5), but were subsumed in importance by the mudsnail *Peringia ulvae* and the waterbirds, great crested grebe and little egret, by the 2005 period. Demersal fish also, ranked highly across all periods, becoming the most important species group during the 2005 period. Generally, most species of waterbird species expressed low keystone index values, relative to low total impact scores, suggesting pressure from higher trophic levels was less important for the structuring of this system.

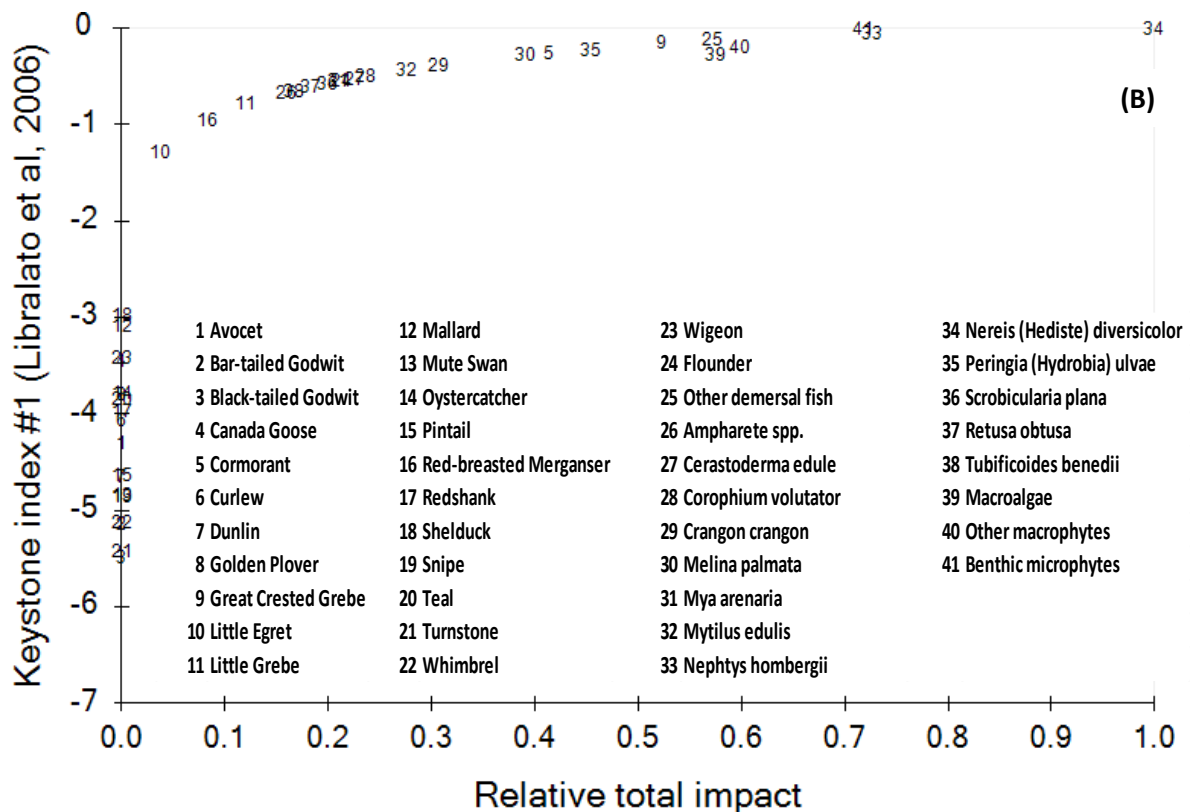
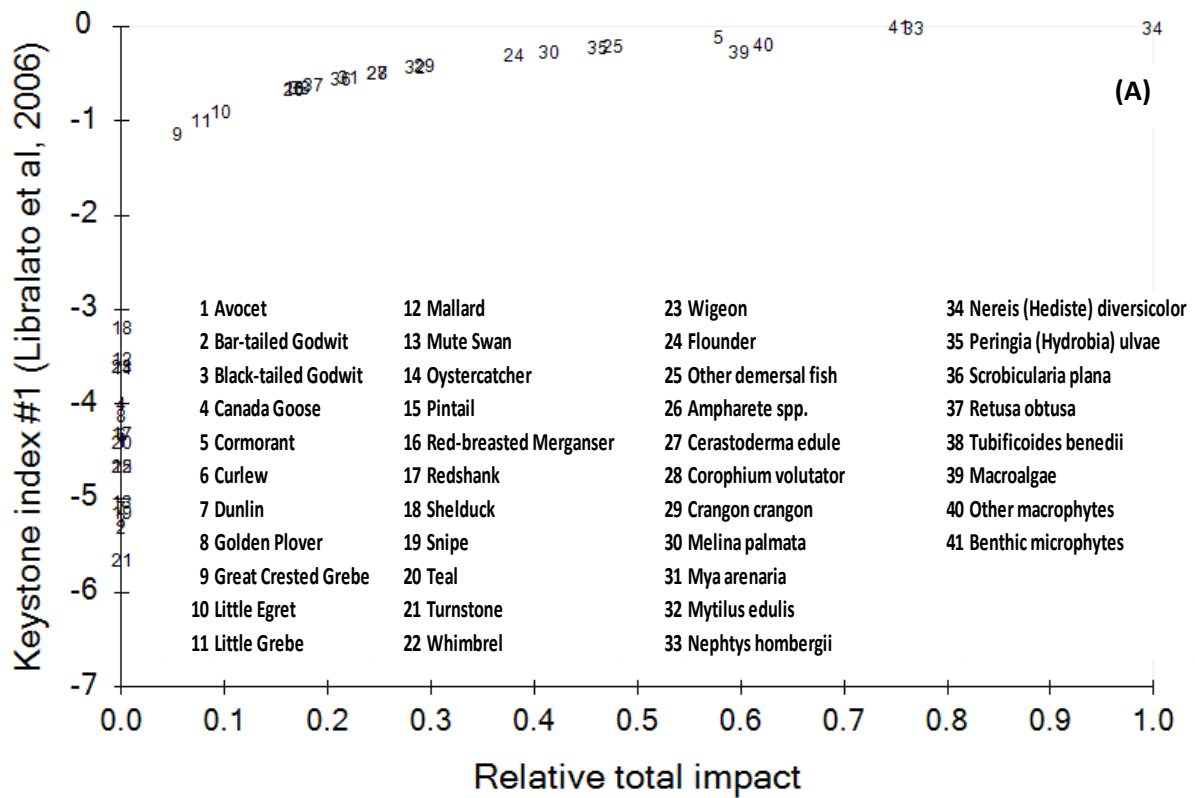


Figure 4. 7 Keystoneness for the functional groups of the Tamar trophic webs 1990 (A), 1992 (B) and 2005 (C). For each functional group, the keystone index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web. Within each trophic web the species are ordered by decreasing keystone, with keystone functional groups being those that have a value of the proposed index close to or greater than zero.

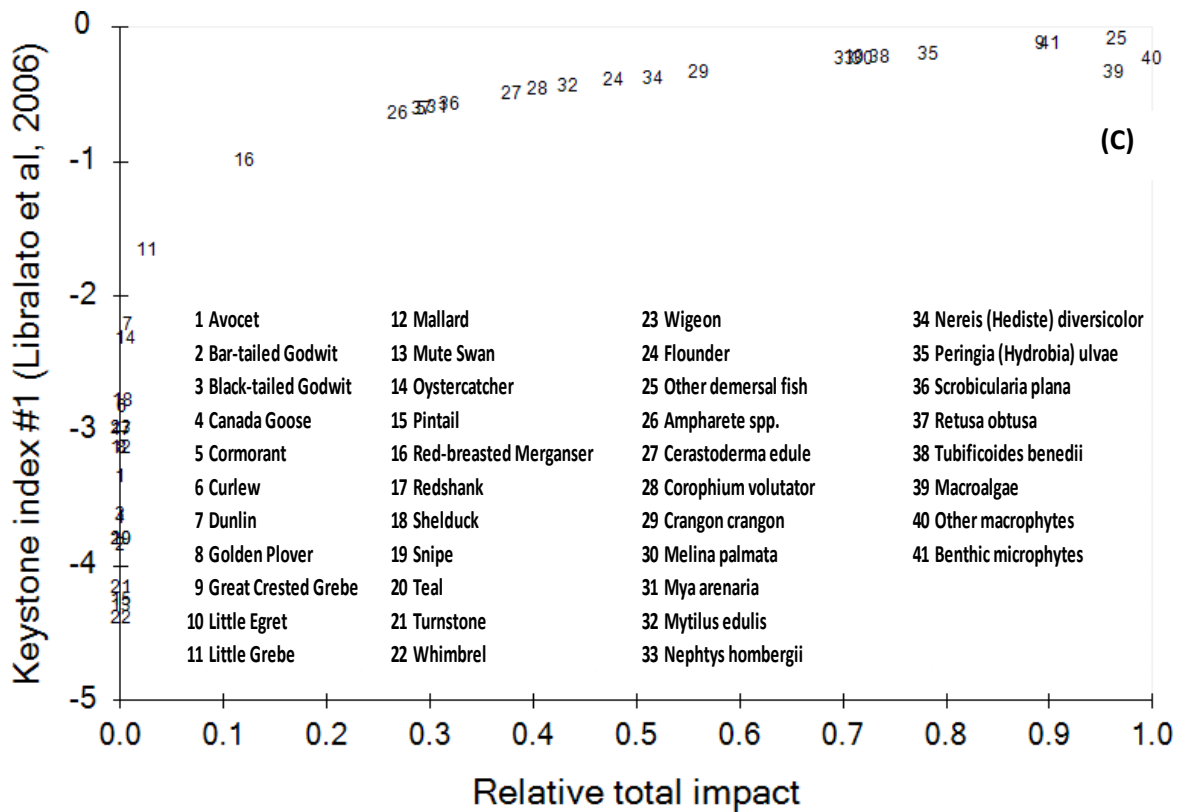


Figure 4. 7 (continued) Keystoneness for the functional groups of the Tamar trophic webs 1990 (A), 1992 (B) and 2005 (C). For each functional group, the keystone index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web. Within each trophic web the species are ordered by decreasing keystone index, with keystone functional groups being those that have a value of the proposed index close to or greater than zero.

Table 4.5 The first five functional groups ranking in decreasing order of keystone index

Model	Keystone index rank order				
	1	2	3	4	5
1990	Benthic microphytes (KS = -0.00891)	Hediste (Hediste) diversicolor (KS = -0.0255)	Nephtys hombergii (KS = -0.0293)	Cormorant (KS = -0.122)	Other demersal fish (KS = -0.209)
1992	Hediste (Hediste) diversicolor (KS = -0.0255)	Benthic microphytes (KS = -0.014)	Nephtys hombergii (KS = -0.0474)	Other macrophytes (-0.201)	Other demersal fish (KS = -0.114)
2005	Other demersal fish (KS = -0.0875)	Benthic microphytes (KS = -0.115)	Great Crested Grebe (KS = -0.118)	Peringia (Peringia) ulvae (KS = -0.196)	Little Egret (KS = -0.216)

4.4.3 How did changes in biodiversity affect ecosystem functioning and network characteristics of the Tamar estuary?

Total biomass in the system (or total system exergy see table 4.1 for definition) increased by 14.71 t km⁻² between 1990 and 1992 and fell by – 913 t km⁻² between 1992 and 2005, with the impact of these changes reflected by many of the system indices (Table 4.6) and network characteristics (Table 4.7).

Table 4.6 System indices of total and relative ecological functioning from the Tamar mass-balanced models.

Indices of total/relative ecological functioning	1990	1992	2005	Units	Difference (1992 relative to 1990)	Difference (2005 relative to 1992)
Sum of all consumption ($\sum C$)	27416	27790	12254	t km ⁻² yr ⁻¹	374.33	-15536.7
Sum of all respiratory flows ($\sum R$)	16474	16698	7373	t km ⁻² yr ⁻¹	223.46	-9324.77
Sum of all flows into detritus ($\sum FtD$)	6086	6227	2855	t km ⁻² yr ⁻¹	141.77	-3372.74
Sum of all production ($\sum P$)	10129	10205	6601	t km ⁻² yr ⁻¹	76.01	-3603.86
Calculated total net primary production (NPP)	4671	4671	4171	t km ⁻² yr ⁻¹	0	-499.3
Total biomass (excluding detritus) ($\sum B$)	2598	2612	1699	t km ⁻²	14.71	-913.098
Total primary production/total biomass (PP/B)	1.79	1.78	2.45	-	-0.01	0.66
Total primary production/total respiration (PP/R)	0.28	0.279	0.56	-	-0.003	0.28
Predatory cycling index (PI)	0.68	0.86	0.27	% of throughput w/o detritus	0.18	-0.59
Finn's cycling index (FCI)	1.93	2.02	4.32	% of total throughput	0.09	2.3
System Omnivory Index (SOI)	0.1121	0.1130	0.1119	-	0.0008	-0.0010

For instance, indices of total ecological functioning such as; consumption, respiratory flows, flows to detritus, and total production all increased slightly or not at all between the 1990 and 1992 period, but also decreased significantly between the 1992 to 2005 period. Total system throughput, a measure of the size of the system or flow of material through the system (Kay *et al.*, 1989), also followed a similar pattern increasing by 1033.36 t km⁻² yr⁻¹ then decreasing by -31864.8 t km⁻² yr⁻¹ respectively.

Table 4.7 Network characteristics from the Tamar mass-balanced models.

Network characteristics	1990	1992	2005	Units	Difference (1992 relative to 1990)	Difference (2005 relative to 1992)
Total system throughput (TST)	54040	55074	23209	t km ⁻² yr ⁻¹	1033.36	-31864.8
Ascendency (A)	75734	78565	29077	Flowbits	2831.5	-49488.2
Capacity (Ca)	252531	264262	96860	Flowbits	-66835.8	-88835.7
Overhead (O)	176797	185696	125938	Flowbits	87464.4	-138324
Relative ascendency (A/C)%	29.99	29.73	30.02	%	-0.25	0.28
Internal ascendency (IA)	46497	48385	20085	Flowbits	1887.6	-28300.2
Internal capacity (IC)	172084	181571	88255	Flowbits	9486.7	-93315.8
Internal overhead (IO)	125587	133186	68170	Flowbits	7599.2	-65015.7
Internal relative ascendency (A/C)%	27.02	26.64	22.75	%	-0.37	-3.89
Average Mutual Information(AMI)	1.40	1.42	1.25	Flowbits	0.026	-0.174

Associated with TST, the network characteristics (Table 4.4) ascendency capacity and overhead (calculated as the difference between the network indices capacity and ascendency), all increased marginally during the 1992 period but decreased substantially by the 2005 period, suggesting the system to now be less resilient, having less redundancy and therefore 'strength in reserve' to cope with future external stressors to the system in its lower nutrient state. However, relative ascendency (Ascendency/Capacity) was very similar in the two scenarios (-0.25 & 0.28 %), signifying that the Tamar as a system was able to accommodate (or resist) the large-scale changes in nutrient loading, primary production, and invertebrate biomass. When only the internal fluxes are concerned, the Tamar Estuary showed a decline of -0.37 in internal ascendency (Ai/Ci) relative to a larger change of (-3.98%) in total A/C during the 2005 period, indicating a higher dependency of this system on a few dominant exogenous connections to adjacent ecological and physical systems (e.g. the Western English Channel). Other natural capital stocks that may be derived from Ecopath, including total primary production/total biomass (PP/B) and primary production/respiration (PP/R), were similar during the 1992 period (-0.01 and 0.66 t km⁻² yr⁻¹ respectively) but increased by about 0.06 and 0.28 t km⁻² yr⁻¹ respectively during the 2005 period, indicating an improvement in water quality.

Considering the magnitude of mineral and nutrient cycling within the Tamar system, Finns Index increased between both periods by 0.09 & 2.3 t km⁻² yr⁻¹ respectively, while the Predatory cycling

index increased initially by $0.18 \text{ t km}^{-2} \text{ yr}^{-1}$ but then decreased by $-0.59 \text{ t km}^{-2} \text{ yr}^{-1}$. Taken together these changes would point to a general increase in the detrital process supporting the regulatory ESs of carbon and nutrient cycling following eutrophication, but a fall in the predatory species contribution to these processes. Networks of cycled flows for the Tamar system are illustrated in Table 4.8. The results show that the total number of cycles in the system is six, with these cycles distributed to varying degrees though three cycling nexuses.

Table 4.8 Cycle distributions of the Tamar system

Distribution (%) of cycles per nexus	1990	1992	2005
1	16.67	16.67	16.67
2	50	50	50
3	33.33	33.33	33.33
4	0	0	0
Number of cycles	6	6	6
Average path length (API)	2.631	2.616	2.865
Throughput cycled (including detritus) $\text{t km}^{-2} \text{ yr}^{-1}$	1045.67	1112.7	1003.4
Throughput cycled (excluding detritus) $\text{t km}^{-2} \text{ yr}^{-1}$	285.13	366.5	475.02
Throughput cycled (by detritus) %	72.73	67.06	95.31

The API of associated cycles, and throughput of material cycled (including detritus) was fairly consistent across the study period (2.6-2.8 and $1000\text{-}1100 \text{ t km}^{-2} \text{ yr}^{-1}$ respectively), indicating that flows of cycling were consistently occurring over short and fast loops. The percentage of material specifically cycled by the detritus compartment was also proportionately high (>65%), with increasing importance by the 2005 period (>95%).

Overall, the Tamar experienced relatively small changes in its natural capital stocks in the two years following the impact of eutrophication, with these changes reflected in the system indices and network characteristics. In contrast, following management interventions, the system experienced significant falls in many of its natural capital stocks including total biomass (exergy) and net primary production values. Despite this, the ability of these stocks to provide flows of ESs, such as the ratio of primary production to biomass (Pp/B) which is the flow of an ecosystem provisioning service (plant production) from a stock of natural capital and the flows relating to the regulating services of carbon and nutrient cycling, increased. There is also evidence that the size (TST) or ‘power’ of the system has decreased substantially between the 1990s and 2000s, with indications of reduced internal capacity to deal with future stressors based on system overhead and internal (Ai/Ci) ratios. However when taken in context with external factors (i.e. connectance with surrounding systems) these is evidence that system resilience has not been compromised.

4.4.4 Biodiversity changes between the periods 1999:2015 (Eden)

The biomass estimated for the two different years (1999 to 2015) and percentage differences with respect to the 1999 period are shown in Table 4. 9.

On the fringes of the estuary, species associated with the “other macrophyte” compartment changed in abundance (and hence biomass) on the Eden between 1999 and 2015, halving in number by 2008 (Fife Council, 2008). However their numbers in the two focal years 1999 and 2015 are similar due to significant restoration efforts of the habitats (Maynard, 2003; 2014). On the surface of the mudflats, macroalgal and benthic microphytic biomass was estimated to have decreased by -287.23 and -0.74 t km⁻² respectively, correlating with concomitant falls in riverine nitrite, nitrate and phosphates by similar amounts (chapter 3 section 3.4.1).

With the exception of the two polychaete species, *Capitella* (21.80 t km⁻²) and *Nephtys* (16.48 t km⁻²) all other invertebrate species were reduced in biomass relative to the 1999 period. The increased presence of *Capitella* and *Nephtys*, is likely a reflection of their opportunistic natures and tolerance to changes in nutrient availability (Dittman *et al.* 1999), with the former, known to vary its reproductive strategy to local conditions, facilitating quick exploitation of local concentrations of organic matter (Grassle & Grassle., 1974). Other changes in invertebrate biomass, are likely a consequence of the decreased organic and nutrient loading to the surrounding sediment, with many of the reduced species, characteristic of organically enriched environments e.g. *Ampharete sp* (-5.16 t km⁻²), *Cerastoderma*, (-26.78 t km⁻²), *Eteone longa* (-7.14 t km⁻²), *Mytilus* (-223.41 t km⁻²), *Macoma* (-34.96 t km⁻²), *Mya* (-7.37 t km⁻²), *Hediste* (-30.54 t km⁻²), *Peringia* (-40.41 t km⁻²), *Scrobicularia* (-114.28 t km⁻²) and *Tubificoides* (-44.88 t km⁻²) (Fahy *et al.*, 1975, Tubbs 1977, Pearson & Rosenberg 1978, van Impe 1985). A large decrease in relative biomass was also observed for the amphipod *Corophium* (-119.42 t km⁻²) consistent with historic observations for this species on the Eden (Blewer., 1993; SEPA 2006; Chocholek., 2013). The continued decline of *Corophium* is enigmatic, with studies from other Scottish estuaries such as the Ythan (Raffaelli *et al.*, 1991) suggesting that this species should benefit under the reduced impacts of nutrient enrichment. One explanation for this oracular decline, could be due to the largest concentrations of *Corophium* typically being found in the upper reaches of the Eden estuary (chapter 3 section 3.4.3), where the presence of algal mats is limited. Therefore the observed changes to this species is likely to have emanated from another source (e.g. increased predation), than the comparative influence of exclusion under algal mats.

Table 4.9 Biomasses of groups used in Eden mass-balance model

Group Name	1999 Biomass (t km ⁻²)	2015 Biomass (t km ⁻²)	Difference t km ⁻² (2015 relative to 1999)
Bar-tailed godwit	0.16698	0.2139	0.046
Black-tailed godwit	0.07595	0.05487	-0.021
Cormorant	0.0092	0.0345	0.025
Curlew	0.73632	0.54162	-0.19
Dunlin	0.055152	0.1068	0.051
Eider	0.5588	0.4774	-0.081
Golden plover	0.2112	0.6182	0.40
Grey plover	0.13944	0.1272	-0.01
Greylag goose	2.079	0.396	-1.68
Knot	0.1036	0.0294	-0.074
Mallard	0.2442	0.077	-0.16
Mute Swan	0.82	0.2255	-0.59
Oystercatcher	1.1124	1.1205	0.0081
Red-breasted merganser	0.0946	0.022	-0.072
Redshank	0.10872	0.11424	0.0055
Shelduck	0.7887	0.3685	-0.42
Teal	0.1089	0.07425	-0.034
Wigeon	0.983825	0.3857	-0.59
Demersal flatfish	4.16	4.22	0.056
Ampharete sp.	21.24007	16.07356	-5.16
Arenicola marina	11.25714	9.68	-1.57
Capitella capitata	2.616234	24.41818	21.80
Cerastoderma edule	139.2857	112.5	-26.78
Corophium volutator	145.5762	26.14762	-119.42
Crangon crangon	33.57143	13.36143	-20.21
Eteone longa	7.5	0.357143	-7.14
Eteone picta	0.535714	0.535572	-0.00014
Macoma balthica	110.1604	75.19929	-34.96
Mya arenaria	12.28571	4.914286	-7.37
Mytilus edulis	231.4286	8.014286	-223.41
Nephtys hombergii	3.497825	19.98757	16.48
Hediste diversicolor	65.11607	34.57071	-30.54
Peringia ulvae	85.56715	45.15097	-40.41
Scrobicularia plana	133.9286	19.64286	-114.28
Spio filicornis	38.07143	2.321429	-35.75
Tubificoides benedii	55.21071	10.32934	-44.88
Macroalgae	588.46	301.22	-287.23
Other macrophytes	220.00	220.00	0
Benthic microphytes	4.64	3.90	-0.74

Evidence for negative changes in the epi-benthic crustacean *Crangon crangon* were also noted (-151.26%) between the periods. While this trend would be consistent with parallel changes in its favoured prey species (Warwick *et al.*, 1987), caution in interpreting differences in *Crangon* density (and indeed all of the macro-invertebrate data) between the two surveys should be taken since they represent only two points in time. Nevertheless, as the species is well known to be an important keystone species in estuaries (Campos *et al.*, 2009), as long as it is still present, it will continue to play an important role in the ecosystems functioning. Ecopath estimates for demersal fish on the estuary suggested that benthic fish populations were relatively similar (0.056 t km^{-2}) between the investigated periods.

The responses of waterbirds between the 1999 and 2015 period, was generally unfavourable with twelve of the eighteen species recorded decreasing in biomass by the year 2015. Perhaps as expected, both of the main herbivorous species in the system, the wigeon (*Anas penelope*) and mute swan (*Cygnus olor*), decreased in biomass synonymously with the reduction in algal mats. These trends are consistent with the long term decline of the species recurring on the estuary (See Appendix 4C) since the late 1990's, with mute swan numbers in particular falling substantially at the onset of the estuary being designated a nutrient vulnerable zone in 2003. Minor population fluctuations were also observed by the bar-tailed (*Limosa lapponica*) 0.046 t km^{-2} and black-tailed godwit (*Limosa limosa*) - 0.021 t km^{-2} , but also by the curlew (*Numenius arquata*) -0.19 t km^{-2} , dunlin 0.051 t km^{-2} (*Calidris alpina*), eider (*Somateria mollissima*) -0.081 t km^{-2} , grey plover (*Pluvialis squatarola*) -0.01 t km^{-2} , oystercatcher (*Haematopus ostralegus*) 0.0081 t km^{-2} , redshank (*Tringa tetanus*) $0.0055 - 0.01 \text{ t km}^{-2}$ and the teal (*Anas crecca*) -0.034 t km^{-2} . All the aforementioned species displayed relatively consistent biomass patterns between the 1999 to 2015 period, suggesting the changes in prey resulting from reduced nutrients did not impact these species directly. Similarly the golden plover (*Pluvialis apricaria*) showed a relatively consistent population trend between the investigated periods, but numbers increased greatly in the three preceding years to the 2015 survey (65.84%), most likely as a result of enhanced recruitment from populations from the surrounding hinterland.

In a similar manner to the Tamar estuary, some of the greatest numerical declines in non-herbivorous waterbirds, were displayed by omnivorous wildfowl family *Anatidae*, such as by the greylag goose (*Anser anser*) -1.68 t km^{-2} , the mallard (*Anas platyrhynchos*) -0.16 t km^{-2} , the red-breasted merganser (*Mergus serrator*) -0.072 t km^{-2} and the shelduck (*Tadorna tadorna*) -0.42 t km^{-2} . These trends were indicative of longer term declines in biomass of each of these species recurring on the estuary (see Appendix 3) since the early 1990's, with the exception of the greylag goose which showed a disparate pattern of biomass throughout the periods, most likely due feeding extensively off-estuary. Large

declines in biomass were also recorded by the knot (*Calidris canutus*) -0.074 tkm^2 , which showed an irregular but cyclic pattern of biomass trends between the early 1990's and 2015 period. As these birds are a migratory species, it is likely that any interannual variation in population biomass is vulnerable to other *ex situ* changes such as barrages, sea-level rises and human disturbance.

In summary, it is clear with respect to the relative biomass of its major biodiversity elements that the Eden as a system has changed considerably between 1999 and 2015 periods, following the implementation of nutrient reduction measures and the designation of the estuary as a Nitrate Vulnerable Zone (NVZ) in 2003. The system became characterized in the 2015 period not only by a decrease in dense macroalgal mats, but also large-scale declines in many of the main prey invertebrates species associated with them. These changes in the prey base were reflected in shifts in the relative biomasses of several waterbird species.

4.4.5 Keystone species (Eden)

Figure 4.8 represents the estimated keystone index for the functional groups of the two selected models, representing the Eden system. As with the Tamar, all three benthic primary producers (macroalgae, other macrophytes and benthic microphytes) showed high keystone index.

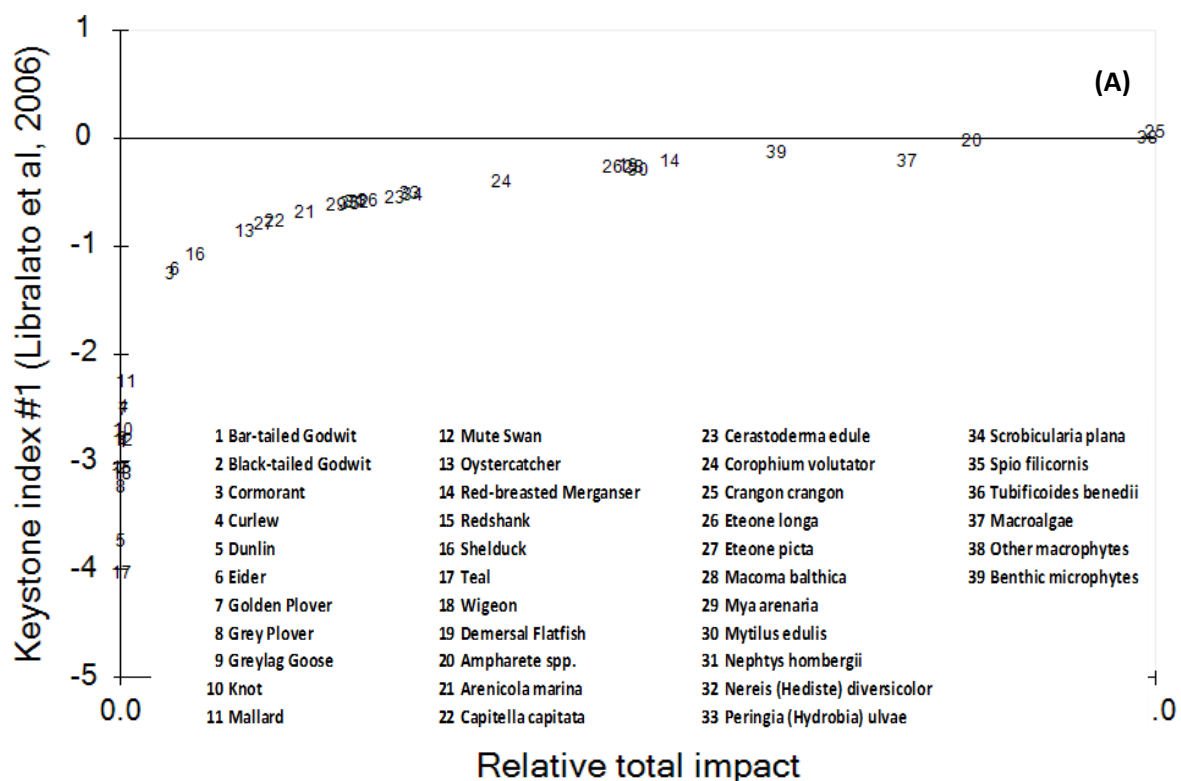


Figure 4. 8 Keystone index for the functional groups of the Eden trophic webs 1999 (A), 2015(B). For each functional group, the keystone index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web. Within each trophic web the species are ordered by decreasing keystone index, with keystone functional groups being those that have a value of the proposed index close to or greater than zero

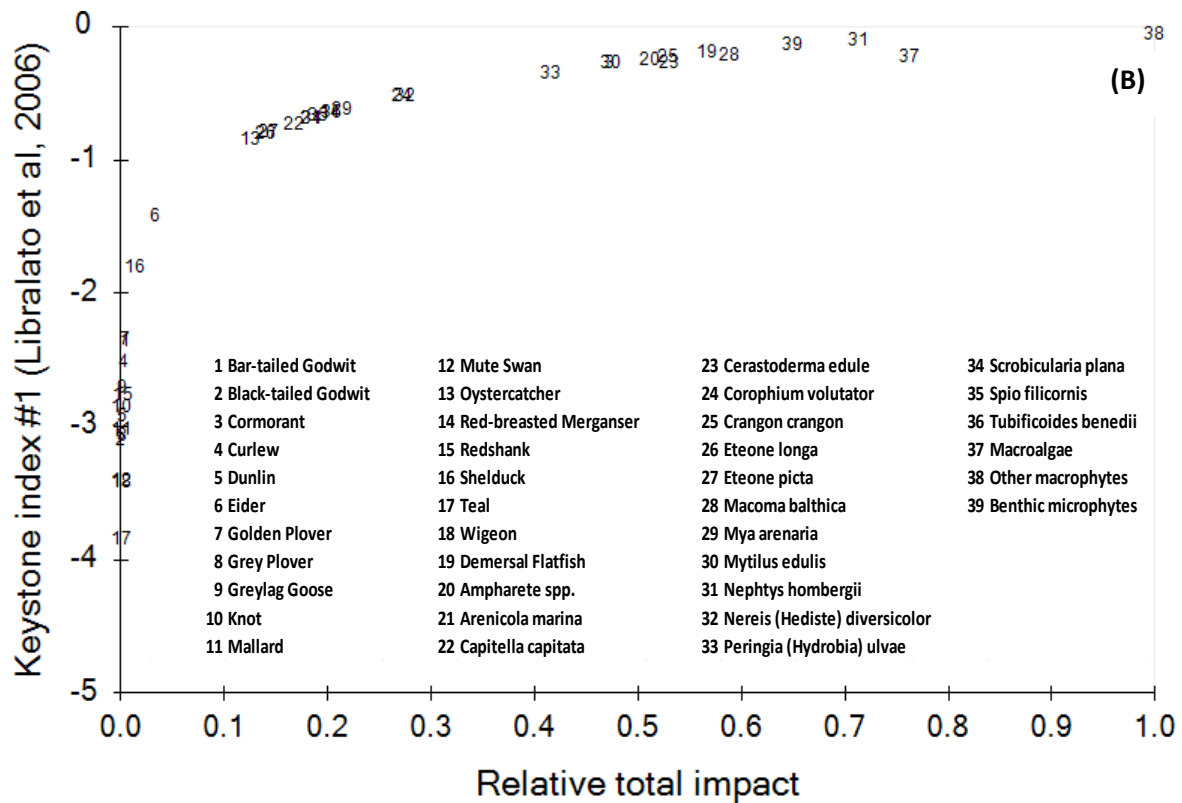


Figure 4. 8 (continued) Keystoneness for the functional groups of the Eden trophic webs 1999 (A), 2015(B). For each functional group, the keystone index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web. Within each trophic web the species are ordered by decreasing keystone index, with keystone functional groups being those that have a value of the proposed index close to or greater than zero.

Table 4.10 The first five functional groups ranking in decreasing order of keystone index

Model	Keystone index rank order				
	1	2	3	4	5
1999	Crangon crangon (KS=0.0564)	Other macrophytes (KS=0.00803)	Benthic microphytes (KS=-0.135)	Ampharete spp. (KS=-0.0255)	Red-breasted Merganser (KS=-0.212)
2015	Nephtys hombergii (KS=-0.0953)	Other macrophytes (KS=-0.053)	Benthic microphytes (KS=-0.221)	Demersal fish (KS=-0.188)	Crangon crangon (KS=-0.222)

The epi-benthic predator *Crangon crangon* was also identified as the most important keystone species during the 1999 period (Table 4.10), while the later period showed higher keystone index for the opportunistic polychaete *Nephtys hombergii*. Other benthic species, such as *Ampharete spp*; demersal fish and the piscivorous, red-breasted merganser, also ranked within the top five key species during the principal periods. Similarly to the Tamar system, most species of waterbird species expressed low keystone index values, relative to low total impact scores, suggesting pressure from higher trophic levels was less important for the structuring of this system.

4.4.6 How did changes in biodiversity affect ecosystem functioning and network characteristics of the Eden estuary?

Total biomass in the system (or total system exergy) decreased by between 1999 and 2015 by $-965.35 \text{ t km}^{-2} \text{ yr}^{-1}$ and as with the Tamar, the impact of these changes was reflected by many of the system indices (Table 4.11) and network characteristics (Table 4.12).

Table 4.11 System indices of total and relative ecological functioning from the Eden mass-balanced models.

Indices of total/ relative ecological functioning	1999	2015	Units	Difference (2015 relative to 1999)
Sum of all consumption ($\sum C$)	26122	9386	$\text{t km}^{-2} \text{ yr}^{-1}$	-16736.2
Sum of all respiratory flows ($\sum R$)	15696	5648	$\text{t km}^{-2} \text{ yr}^{-1}$	-10048.8
Sum of all flows into detritus ($\sum \text{FtD}$)	5644	2075	$\text{t km}^{-2} \text{ yr}^{-1}$	-3569.16
Sum of all production ($\sum P$)	8042	3660	$\text{t km}^{-2} \text{ yr}^{-1}$	-4382.66
Calculated total net primary production (NPP)	2841	1799	$\text{t km}^{-2} \text{ yr}^{-1}$	-1042.49
Total biomass (excluding detritus) ($\sum B$)	1922	957	t km^{-2}	-965.35
Total primary production/total biomass (PP/B)	1.47	1.87	-	0.40
Total primary production/total respiration (PP/R)	0.18	0.31	-	0.13
Predatory cycling index (PI)	0.03	0.25	% of throughput w/o detritus	0.22
Finn's cycling index (FCI)	2.84	4.33	% of total throughput	1.49
System Omnivory Index (SOI)	0.112	0.119	-	0.007

Together with total system biomass (exergy see table 4.1 for definition), all other indices of total ecological functioning such as: consumption, respiratory flows, flows to detritus, total production and net primary production decreased between the focal periods. In parallel, total system activity or throughput also decreased substantially $-31749.9 \text{ t km}^{-2}$ (Table 4.12).

Based on the network characteristics for of the whole system, ascendancy capacity and overhead all decreased in values by the 2015 period suggesting the system now is less resilient, with a reduced capacity or redundancy to deal with future stressors. Relative ascendancy (A/C)% between the periods did however increase (6.14%) indicating that the Eden as a system has been able to accommodate the large-scale changes in nutrient reductions, primary production, and invertebrate biomass. Regarding internal fluxes of material, the Eden also displayed reduced internal stability, exhibited by ascendancy (-41451), capacity (-201528) and overhead (-114116). Internal relative ascendancy

remained relatively similar between the periods (0.54) indicating that this system has/can maintain its activity without too much dependence on external inputs.

Table 4.12 Network characteristics from the Eden mass-balanced models.

Network Characteristics	1999	2015	Units	Difference (2015 relative to 1999)
Total system throughput (TST)	49184	17434	$\text{t km}^{-2} \text{ yr}^{-1}$	-31749.9
Ascendency (A)	64431	22980	Flowbits	-41451
Capacity (Ca)	280453	78924	Flowbits	-201528
Overhead (O)	216021	101905	Flowbits	-114116
Relative ascendency (A/C)%	22.97	29.11	-	6.14
Internal acendency (IA)	44641	16934	Flowbits	-27707.7
Internal capacity (IC)	191630	71035	Flowbits	-120596
Internal overhead (IO)	146988	54101	Flowbits	-92887.8
Internal relative ascendency (A/C)%	23.29	23.83	-	0.54
Average Mutual Information (AMI)	1.31	1.31	Flowbits	0.008

Regarding proxies from natural capital stocks (Table 4.8), total primary production/total biomass (PP/B) and total primary production/total respiration (PP/R) both increased between the two periods by 0.40 and 0.13 respectively. Indices representing the regulating ESs of carbon and nutrient cycling all increased during the 2015 period, suggesting greater system retentiveness and a greater proportion of material cycled across both higher and lower trophic levels (Odum, 1969). Networks of these cycled flows are illustrated in Table 4.13.

Table 4.13 Cycle distributions of the Eden system

Distribution (%) of cycles per nexus	1999	2015
1	10	10
2	40	40
3	30	30
4	20	20
Number of cycles	10	10
Average path length (API)	2.82	2.91
Throughput cycled (including detritus) $\text{t km}^{-2} \text{ yr}^{-1}$	1395	754
Throughput cycled (excluding detritus) $\text{t km}^{-2} \text{ yr}^{-1}$	12.67	33.36
Throughput cycled (by detritus) %	99.09	95.57

The cycling structure of the Eden estuary consisted of a total of ten cycles, distributed to varying degrees though four cycling nexuses. The API of associated cycles, was fairly consistent between the study periods (2.8-2.9) indicating that flows of cycling were occurring over short and fast loops. The

percentage of material specifically cycled by the detritus compartment was also proportionately very high (>95%), with around about a 4% shift towards non-detritus based cycling during the 2015 period.

Overall, following management measures the Eden Estuary has experienced significant falls in many of its natural capital stocks including total system biomass (exergy) and net primary production values. Despite this, the ability of these stocks to provide flows of ESs, such as the ratio of primary production to biomass (Pp/B) and the flows relating to the regulating services of carbon and nutrient cycling, appear to have increased. There is also evidence that the size (TST) or 'power' of the system has decreased substantially between the 1990s and 2010s, with indications of reduced internal capacity to deal with future stressors based on system overhead and internal (Ai/Ci) ratios. However when taken in context with external factors (i.e. connectance with surrounding systems) these is evidence that the resilience of the system has not been compromised.

4.5 Discussion

The two case studies investigated here clearly demonstrate the effects of biodiversity change on ecosystem functioning in seascape-scale systems. These changes were almost certainly attributed to the direct bottom up-effects of nutrient diminution which altered the abundance of benthic primary producers, with cascading consequences on invertebrate and waterbird species at higher trophic levels. These changes were also responsible for changes in secondary production and a number of higher level systems metrics. The effects are believable, not because of a statistically rigorous experimental design, but because the effect sizes are very large, and the altered biodiversity and ecological functioning are clearly different relative to the post management periods. Due to the weaker inferential power of observational and modelling studies it is always important to consider alternative explanations for the observed effects (Underwood *et al.*, 2000; MacNeil, 2008). A range of these have been considered during the timeframe for these two case studies (Chapter 3), with the most parsimonious and persuasive explanations for the observed changes in functioning remain the changes in biodiversity observed.

As such, for both the Tamar and the Eden estuaries, an argument can be made for a qualitative regime shift (i.e. large, abrupt, persistent changes in the structure and function of a system) occurring at critical changes in biodiversity, where the system continues to function but as a very different system, and in a very different way. For instance, ecosystem-scale metrics in both case studies, indicate that many aspects of functioning (e.g. biomass, flow of material, net primary production) have decreased under the impact of nutrient reductions. However, other proxies for functioning such as mineral and nutrient cycling (Finns index) and plant production (PP/B) increased under the same scenarios, highlighting the potential for trade-offs in ecosystem functions under different environmental states.

Intrinsically, this rises fundamental questions about management goals, societal choice, and what kind of system is desirable or acceptable. Such choices, are ultimately a consequence of stakeholder perceptions of what the system should be like (Wicklum & Davies, 1995), with the task of management ultimately be to maintain the stability of the overall system for combinations of biodiversity and functions that produce desirable bundles of ESs.

In managing for marine biodiversity, it is also worth recognising that, whilst every species contributes to biodiversity, each contribution is not of equal importance. As such, the keystone species identified here might be of particular relevance for the marine biodiversity characterisation within the assessment of Good Environmental Status (GES), for the Marine Strategy Framework Directive (MSFD) at each of the case study sites (Valls *et al.*, 2015). More generally, the Ecopath approach used here has been highlighted as one of the most widely used and one of only a few modelling techniques available to identify keystone species in marine environments at large spatial scales (Smith *et al.*, 2015). There are however, limitations associated with the selection of keystone species following this approach regarding in particular the cut off point for a species to be defined keystone. Although some authors have identified keystone index values higher or around zero as indicative of a keystone role (Libralato *et al.*, 2006; Heymans *et al.*, 2011), several species or functional groups in the food web may fulfil this criterion.

This analysis also has implications for the way biodiversity–ecosystem processes–ecosystem services relationships are evaluated at large spatial scales. Here, the Ecological Network Analysis tools available within the Ecopath software, allowed a detailed understanding of the various biophysical processes that generate the flows of several of the ESs (*sensu* the VECTORS scheme shown chapter 1 section 1.3.2) that each of the estuaries potentially provides. These included flows of provisioning services, such as the yield of plant material, wildfowl, mussels or fish, for their underlying biomass stocks and the relative flows of the regulating services, climate regulation (*via* carbon cycling) and waste remediation (*via* nutrient cycling). Similarly, density-dependent relationships for the quantification of many cultural services were also calculated including demersal fish stocks for recreational angling and waterbird stocks for birdwatching, from which cultural benefits could have been derived. By evaluating and valuing stock elements in this way, it allowed a greater understanding and appreciation of the connections within which ESs are delivered and the context within which they operate.

Additionally as trophic networks can be studied in a quantitative and systematic fashion at several organisational levels: species–population- community and ecosystem (Ulanowicz, 2004), information can be interpreted and examined at the spatial level of interest to the user (e.g. single keystone species

vs. ecosystem level metrics). In the context of ESs such as climate regulation (Beaumont et al., 2014) and waste remediation (Watson *et al.*, 2016) this is important because the ecosystem processes that provide the service (e.g. primary production and nutrient cycling) are not delivered by species alone, but by many facets of natural capital of which species are only one component (Jones *et al.*, 2016). Therefore a focus on a systems emergent properties rather than its individual parts are particularly important in understanding the effects of change on ES provisioning. At the level ecosystem level, the consequential flow of an ESs resulting from the stocks of many different sources of natural capital, may be best captured using ecosystem-scale metrics, without the loss of information commonly associated with scaling from small-scale experimental systems (Raffaelli & Moller, 2000). Put in the context of this study, the relative abundant changes between the eutrophic and undisturbed states represent an overall shift in the community or ecosystem dimension of biodiversity, an expression of biodiversity that is likely to resonate more with local stakeholders than species richness, being closer to the concept of natural capital.

In addition to the quantity of the stocks and their flows, this study also measured several system properties, which consist of the attributes or characteristics of the system. These properties were categorised in two ways either 1) comprising the properties of the stocks themselves (e.g. exergy and many of the network characteristics- ascendancy, capacity, overhead) or 2) relate to their spatial and temporal arrangement in the system (e.g. cycling structure). In the first instance, many of the topological properties of both case study networks are consistent with Ulanowicz's (1986) view that the impacts of eutrophication can be described as any increase in system ascendancy that causes a rise in total system throughput (and the opposite in the case of nutrient reduction), which more than compensates for any concomitant fall (in this case none) in the average mutual information content.

Based on the same system resilience measures, there is also evidence that the stability or resilience of both systems has been reduced under the impact of nutrient reductions, based on the network characteristics calculated here. However relative ascendancy (A/C), a dimensionless ratio that excludes the influence of system size, suggested that both estuarine systems were highly resistant to negative changes in nutrient loading over the study periods, collaborating with the assumption that the high natural variability within estuaries may have conferred an ability to withstand stress, (in this case anthropogenic), thus showing a resilience created by Environmental Homeostasis (Elliott & Quintino., 2007). The same index also proved useful in determining the relative dependence of each system to external inputs, with the Tamar estuary evaluated as having a greater dependence on connecting ecosystems, in comparison to the relatively isolated Eden estuary. As the degree to which environmental change is likely to influence ecosystem resilience will depend on metacommunity structure and connectance (Dunne *et al.*, 2002; Fung *et al.*, 2015), the (A/C) index could therefore be

a suitable indicator to compare ecosystems of different sizes (Mann *et al.*, 1989, Baird *et al.*, 1991) and in understanding the potential for cumulative effects to impact upon diversity (Thrush *et al.*, 2008).

From the cycling analysis, both estuaries were found to recycle a large proportion of their material through short-fast cycles, with the preponderance of a unit of matter (e.g. carbon) being retained for approximately 2-3 cycles. The increasingly high FCI index also indicates both estuaries have a relatively simple cycling structure with both FCI and API of a similar order as other estuaries with a legacy of nutrient contamination e.g. the Ythan Scotland (Baird *et al.*, 1993), with a study by Raffaelli (2011) also showing a similar increase in the FCI index under a period of nutrient reduction. The higher FCI and longer path lengths presented under lower nutrient conditions, are also consistent with Ulanowicz (1984) hypothesis that systems with longer cycles and low proportions of cycling are indications of less stressed systems.

4.6 Conclusions

In conclusion, the process of constructing an Ecopath model provides a valuable end product in itself through explicit synthesis of work from many researchers (Christensen *et al.*, 2000). EwE-based studies can help with understanding the general structure and functioning of aquatic ecosystems, deriving its various system properties, and comparing them to other ecosystems (Walters *et al.*, 1997). Further in this chapter I have demonstrated that the mass-balance modelling approach can capture aspects of natural capital and seems to have potential for exploring biodiversity–ecosystem processes-services relationships in quite a different way to the experimental approaches that have dominated this field to date (see Crowe *et al.*, 2012). While not all ecosystem ecologists will be comfortable with the thermodynamic or cybernetic perspective on ecosystems accosted with network analysis tools, the stock–flow relationships and dynamics outlined here have been central to much of ecosystem research (Raffaelli & White, 2013) and their application therefore have much to contribute to the development of an ecosystem service science.

Bearing such tools down on the seascape scales at which environmental management policies are implemented and at which ESs are delivered, may however be more challenging. EwE models are easy to construct and manipulate, and there is an acknowledged need to raise the standards of use for these models in a management context (Heymans *et al.*, 2011; 2016), with similar standards needed in exploring ecosystem theory (Pocock *et al.*, 2016). To be executed correctly, one needs to have an understanding of both 1) the uncertainty of the input data (e.g. though the pedigree routine in EwE) and 2) be able to assess the confidence in the model outputs, before the model should be considered (if at all) for use in management purposes (Heymans *et al.*, 2016). In the case of Ecopath models,

ongoing quality assurance measures such as the application diagnostic checks (PREBAL) and 'key-runs', which refers to a model parameterization and output (ICES, 2012; 2013; 2016), are increasingly being implemented in mass balanced models to provide a quality assured source for scientific input in the provision of advice for management. However, although key features inherent within these models (e.g. identification keystone species) have proven useful in ascertaining information in the assessment of Good Environmental Status (GES), for example in the Marine Strategy Framework Directive (MSFD), there remains significant challenges in "operationalising" (Hines *et al.*, 2015; Truchy *et al.*, 2015) and accepting (Rombouts *et al.*, 2013; Niquil *et al.*, 2014) the use of many of the highlighted Ecological Network Analysis techniques in these same policy practices.

Nonetheless, as a mode of scientific inquiry ecological networks provide an ideal vehicle to explore the possible effects of global change and biodiversity loss on communities and ecosystems (Raffaelli, 2006), and the inevitable repercussions on ESs (Bennett *et al.*, 2009 and Bohan *et al.*, 2013). Further, understanding how a system and its constituents might change under the impact of multiple anthropogenic stressors in the future and establishing how near a system is to thresholds of change, and thus how much biodiversity change is permissible to maintain functioning is an urgent area of research for the sustainable management of marine systems (Cardinale *et al.*, 2012; Elliott *et al.*, 2015; Oliver *et al.*, 2015). As such, the following two chapters of this thesis aim to address these questions, building on the mass-balance approach codified here.

Chapter 5 Modelling the effects of multiple stressors on estuarine benthic food webs.

Chapter Summary

In the last few decades, the scientific community has made substantial progress in the identification and quantification of multiple human threats that impact marine biodiversity, habitats, and ecosystems (Breitburg *et al.*, 1998; Rudd, 2014; Gunderson *et al.*, 2016). However, as stressors often interact in many ways, and their interactions do not occur the same way everywhere, future changes of current human activities (such as climate change and local anthropogenic impacts) will continue to challenge our current understanding of how anthropogenic stressors impact on marine and coastal systems (Lotze *et al.*, 2006; Halpern *et al.*, 2008a). To untangle some of these challenges, there is an increasing need to develop novel methodologies of data integration, assimilation and modelling at different scales, taking into account uncertainties in data and processes (Barange *et al.*, 2010; Coll *et al.*, 2015; Payne *et al.*, 2015).

Food webs or ecological networks provide a particularly good framework in this regard, acting as useful tools for representing the complexity of communities and ecosystems (Elton., 1927; Cohen *et al.*, 2003; Emmerson & Raffaelli, 2004). While they often appear confoundingly complex, they can be easily summarized by a number of key explanatory properties that represent overall system health or status (i.e. system structure, functioning and resilience see chapter 4 section 4.3.9 for a detailed explanation of indices). As many of these properties have been shown to play an important role in the persistence of marine communities (Dunne *et al.* 2002, Montoya *et al.*, 2006), it is important that we combine the studies of multiple stressors and food webs to anticipate the long term system-wide consequences of anthropogenic influences in nature (Gorman *et al.*, 2012). While a number of modelling techniques are now available to simulate interacting stressors (Baird *et al.*, 2015; Chariton *et al.*, 2015; Van den Brink *et al.*, 2016), modelling experiences that include greater than two factors are still scarce in ecological research (Dafforn *et al.*, 2015). The Ecosim component of the Ecopath (EwE) for example was initially developed specifically to provide a method for predicting cumulative changes in the context of fisheries management (Christensen & Walters, 2004), and recently a number of studies (Booth & Zeller, 2005; Guénette *et al.*, 2006; Ainsworth *et al.*, 2011) have emerged that attempt to model interacting stressors with temporal–spatial variability. As there has been an dramatic growth of interest in modelling ecosystem dynamics and cumulative effects, applying spatial–temporal studies into other environments (e.g. estuarine systems) is foreseen as a major development goal for the scientific community (Coll *et al.*, 2015) and will therefore be the primary focus of this chapter.

5.1 Introduction

As discussed in the previous chapter, marine ecosystems are sustained by the autocatalytic flow of energy from primary producers at the base of food webs through to intermediate consumers, followed by consumption by top predators and then back again through decomposition and detrital pathways (Paine, 1980; Ulanowicz, 1997). Thus, marine communities can be considered as ecological networks (Proulx *et al.*, 2005; Ings *et al.*, 2009), that depend directly or indirectly on the performance of other species within the network (e.g., predator-prey relationships, competition, facilitation and mutualism). While many of these interactions may occur at very small scales (sub-millimetre), the aggregate effect of large numbers of small interactions can produce transfers of energy or material (e.g. nutrient cycling, primary and secondary productivity) recognised as ecosystem functioning (Paterson *et al.*, 2012), resulting in the flow of ocean and coastal ecosystem services (ESs) and benefits on which society depends (De Groot *et al.*, 2002; Beaumont *et al.*, 2007; Fisher *et al.*, 2009).

Human induced stressors affecting the marine ecological networks and the ESs they provide have been increasingly reported within the scientific literature (Brierley & Kingsford., 2009; Hoegh-Guldberg *et al.*, 2010; Doney *et al.*, 2012; Poloczanska *et al.*, 2013; Staudt *et al.*, 2013), often with an increased emphasis on co-occurring stressors (Crain *et al.*, 2008; Darling & Côté, 2008; Halpern *et al.*, 2008a; Griffen *et al.*, 2016; Gunderson *et al.*, 2016), especially in ecosystems adjacent to centres of human populations where the likelihood of stressor overlap is greatest (Harley *et al.*, 2006; Halpern *et al.*, 2008b; Crain *et al.*, 2009). These concerns are compounded by expectations that localised anthropogenic pressures such as changes in freshwater environmental flows operating within trans-boundary systems such as estuaries, are increasingly modulated by complex interactions with other more pervasive abiotic factors such as global warming and ocean acidification (Pörtner, 2008; Gibson *et al.*, 2011; Gruber, 2011; Tyrrell, 2011). This is important because, the cumulative action of several stressors has the potential to induce sudden, nonlinear regime shifts that drive ecosystems into novel, alternative states with fundamentally different structures, dynamics and capacity to deliver ES's (Standish *et al.*, 2014). Therefore, if we are to understand or predict how the consequences of ongoing environmental change are likely to impact on the structure, functioning and/or resilience of ecological networks, it is imperative that we work to understand how the cumulative impact of several stressors combine to produce effects at societally relevant seascape scales (Ellis *et al.*, 2015).

5.1.2 The impact of multiple stressors at seascape scales

Anthropogenic pressures can affect biota at different levels of biological organisation and can have profound influences on marine ecosystems including; changing the physiological performance of

individuals, dynamics of populations, patterns of species, community interactions and ecosystem structural components or functional processes (Martínez-Crego *et al.*, 2010). The rates of biological response to stressors can also vary at different levels of organisation with individuals and populations responding quickly often to low levels of stress, while community and ecosystems response times can be slower to manifest, even under high levels of stress (Figure 5.1). While the effect at one level of biological organisation can clearly underpin changes at other levels, predicting the ultimate effect a stressor or series of stresses will have at a specified organisational level is difficult because anthropogenic stressors do not produce uniform or consistent impacts on biodiversity and ecosystem functioning (Attrill & Delpledge., 1997). Thus impacts at lower levels of organisation may not necessarily translate into impacts at higher levels (Duffy, 2008; Stachowicz *et al.*, 2008; Kozlov & Zvereva, 2011). It is therefore imprudent to predict the effects of stressors at higher levels of organisation from existing knowledge of impacts at lower levels of organisation (Farrell & Crowe, 2007).

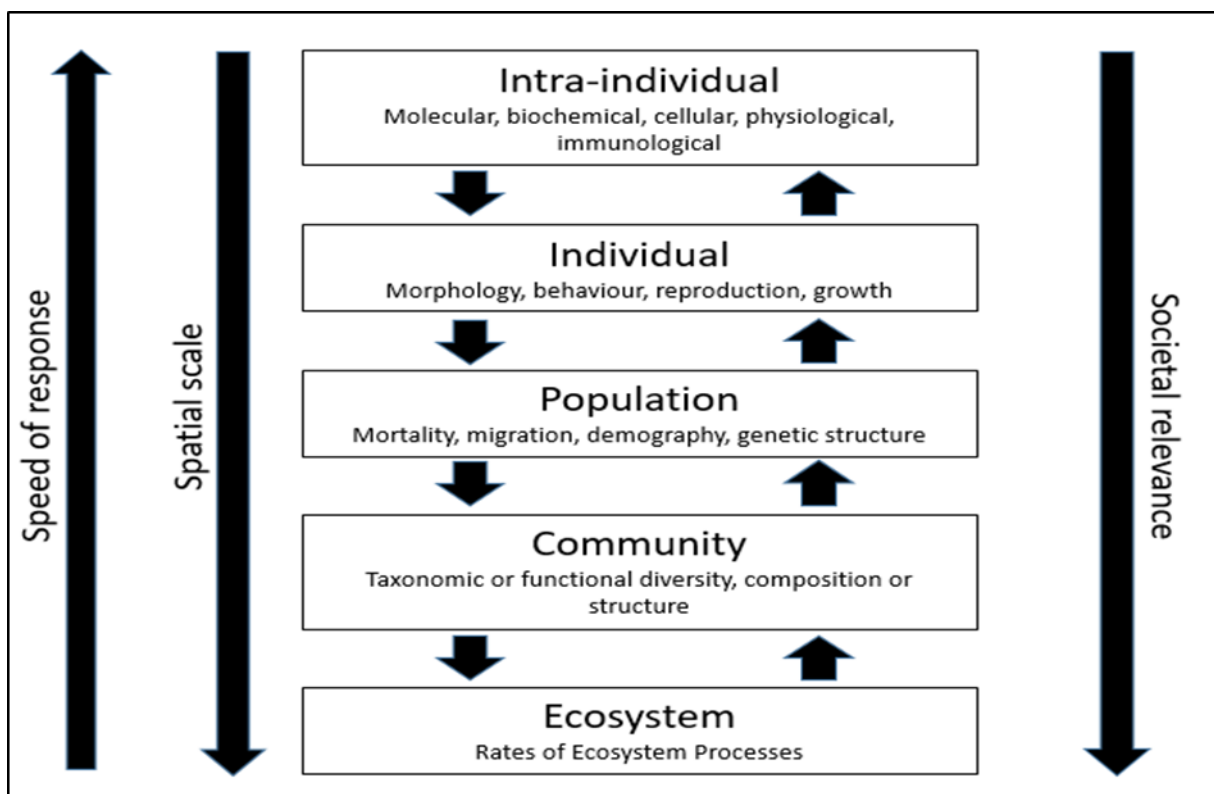


Figure 5.1 Levels of biological organisation at which impacts may occur and indications of variations speed scale of responses and degree of societal relevance at different scales of hierarchy. Arrows between levels indicate the effects at one level of organisation can have implications for others, both below and above them in the hierarchy. Adapted from Crowe & Frid (2015).

At the ecosystem level, stressors can influence ecosystem properties (i.e. structure, functioning, and resilience) by their effects on the biota, but also by modifying surrounding abiotic conditions altering the context which ecological and chemical processes occur (Stanseth *et al.*, 2002; 2003), for example through differences in water temperature, river-flow, nutrient supply and cycling. Ultimately, the degree to which an ecosystem is impacted by a particular stressor (of combination thereof) will depend upon: 1) the particular properties of the stressors and 2) the context of the receiving ecosystem (Sousa, 1984). One reason for this is that, both natural and anthropogenic stressors can operate under different disturbance regimes and are subject to a series of potential higher order interactions including: varying in their intensity (e.g. low vs. high), timing (e.g. seasonal vs annual), spatial extent (e.g. local vs. global) frequency (e.g. simultaneous vs. consecutive), duration (e.g. short vs. long) and/or temporal patterning of occurrence (e.g. press vs. pulse) (Miller, 1982; Pickett & White, 1985; Easterling *et al.*, 2000; Boyce *et al.*, 2006; Glasby & Underwood, 1996; Anthony *et al.*, 2008; Crain *et al.*, 2008). Depending on the disturbance regime, specific combinations of stressors can interact in different ways having different effects. However, even if two ecosystems are subjected to a similar set of stressors, operating under the same disturbance regime, they are unlikely to exhibit the same ecological impacts because each set of stressors will directly interact with local environmental conditions and are qualitatively changed as a result (Lyons *et al.*, 2015).

Ecosystems and its constituent parts that are subjected to multiple stressors, may exhibit one of three types of responses (Todgham & Stillman, 2013; Piggott *et al.*, 2015): additive (= to the individual effects), antagonistic (< the sum of their individual effects) or synergistic (> the sum of their individual effects). In the absence of interactions between stressors (i.e. two effects would combine additively in the absence of an interaction), scientists, policy makers and managers are often concerned with stressors that interact synergistically to produce larger or more potent net impacts than would have been predicted from their individual effects (Darling *et al.*, 2008; Brown *et al.*, 2013) These types of interactions are of immediate concern because if left unnoticed, the enhanced impacts of such associations can leave entire ecological networks more vulnerable to future stressors resulting in management failure and insufficient biodiversity reserves to promote ecosystem functioning and the delivery of ESs. In contrast, antagonistic interactions occur when stressors induce changes that mitigate or reduce the net impact of two or more stressors, thereby making the subsequent system more resilient to further stressors (Breitburg *et al.*, 1999; Wulff *et al.*, 2000). An understanding of such antagonisms therefore, has the potential to provide opportunities for management to reduce the net impact of human activities.

In assessing the significance of the impacts of anthropogenic stressors on the environment, it is also important to consider the systems inherent ability to resist change and ability to recover following

damage (i.e. resilience). While concept of resilience is a multifaceted concept with several definitions and classifications (see Chapter 1 section 1.4), understanding resilience and its components (recovery, resistance etc.) can help us to understand not only the extent to which systems may persist in the face of multiple stressors, but can also aid in promoting a range of adaptive management strategies (Gunderson *et al.*, 2002; Leslie & Kinzing, 2008). From a management perspective, systems may be classified as having 'specific' or 'general' resilience to a particular set of stressors (Levin, 1999; Anderies *et al.*, 2006; Carpenter *et al.*, 2012). Specific resilience refers to the capacity of a system to absorb a specific stressor and continue to function in a similar state. In this way a system may have high resilience to some stressors but not others. Alternately, general resilience, refers to the capacity to absorb a broader range of stressors including emerging or unexpected ones (Folke *et al.*, 2010). Careful consideration must therefore be taken by environmental managers as to which kind of resilience to invest in, as the underlying ecosystem properties responsible for each type of resilience are often unrelated e.g. general resilience (adaptive capacity) vs. specific resilience (resistance). Thus, there is a pressing need for studies that investigate the combined impact of stressors on natural communities in order to facilitate future prediction of the consequences of increased anthropogenic pressure on the performance of ecosystems.

5.1.3: Study aim

As both the Tamar and Eden estuaries have been extensively studied for over the past 30+ years, they provide an excellent case study for modelling the dynamics of coastal systems under stress from multiple anthropogenic pressures. Having in the previous chapter attempted to answer the question: how did the structure and functioning of the associated food webs change under historic nutrient management measures? The aim of this chapter was to investigate the effects of periodic, stochastic, sequential and/or cyclical variations in the future climate and nutrient cycles of the Tamar and Eden estuaries.

Three common stressors in estuarine systems (river flow, nutrient inputs and thermal stress) were chosen based on previous evidence for potential cumulative and/or interactive effects (e.g. Cloern, 2001; Paerl, 2006; Crain *et al.*, 2008; Hoegh-Guldberg & Bruno, 2010; Fitch & Crowe, 2011; Alsterberg *et al.*, 2012; Baron *et al.*, 2012; Bijma *et al.*, 2013; Crossman *et al.*, 2013; Elbrecht *et al.*, 2016; Hanson *et al.*, 2016; Jackson *et al.*, 2016; Nöges *et al.*, 2016) and their known prevalence of impact within the case study systems (evidenced in chapters 2/3). In practice, each of the stressor combinations were imposed on each system using the Ecosim component of the most recent Ecopath models developed in chapter 4, to investigate the effects of long-term (50 years) changes in each systems emergent properties (i.e. structure, functioning and resilience) and each systems capacity to provide ESs under the impact of multiple stressor scenarios.

Since all stressors have the potential to alter the available energy within the systems, the two formal questions were proposed as follows:

Q1: Would the combination of stressors act to negatively alter the future structure, functioning and/or resilience of the respective food chains? (Tamar/Eden).

Q2: Do different combinations of stressors (river flow, nutrient inputs and thermal stress) act in a non-additive manner? And is there a difference between each system? (Tamar/Eden)

The results of this chapter will therefore have implications for the prediction of multiple stressor effects on ecosystems based on a knowledge of individual effects. While limited to impacts of three stressors in two systems, this study aims to place multiple stressor research in a broader context by demonstrating an approach to examine potential impacts of multiple stressors on the underlying health of real systems.

5.2 Modelling approach

Using the same computational food webs and key initial parameters used in the base 2005 (Tamar) and 2015 (Eden) Ecopath models (Chapter 4. Section 4.3) long term (50 year) time-dynamic simulations were performed using Ecosim at the ecosystem level.

5.2.1 Ecosim: temporal simulations

Ecosim bases its critical ‘mass action’ assumptions on a substantiated Lotka-Volterra ‘foraging arena’ principle whereby predator prey interactions are moderated by prey behaviour to limit exposure to predation (e.g. by hiding in the crevices of rocks or in the substrate). Biomass flux rates are represented by a series of coupled differential equations:

$$\frac{dB_i}{dt} = g_i \sum_j j_i - \sum_j j_i + I_i - (M_i + F_i + e_i)B_i \quad \text{Equation 5.1}$$

Where $\frac{dB_i}{dt}$ represents the growth rate in biomass of group i , while B_i = biomass, g_i = the net growth efficiency (production/consumption ratio), M_i = natural mortality, F_i = fishing mortality, e_i = emigration, I_i = immigration rates (and $e_i \cdot B_i - I_i$ the net migration rate) of group i . The two summations of Q_{ji} and Q_{ij} are a function that predicts the total consumption rate of for a given predator j feeding on a prey i and is predicted from:

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i P_j T_j S_{ij} I D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} P_j S_{ij} T_j I D_j} \quad \text{Equation 5.2}$$

With Q = consumption, a = effective search rate, v = vulnerability, B = biomass, P = predator biomass/number, S = seasonality or long-term forcing, M = mediation, T = search time, D = handling time. See Walters *et al.*, (1997; 2000), Walters & Kitchell (2001) and Christensen & Walters (2004) for further information on these algorithms.

Predator prey interactions are moderated by prey behaviour to limit exposure to predation, such that biomass flux patterns can show either bottom-up or top down (trophic cascade) control (Walters *et al.*, 2000). Within Ecosim such relationships are controlled by attributing a “vulnerability” term for each of these interactions, indicating how the biomass of different groups in the ecosystem is controlled (Christensen *et al.*, 2001). Low vulnerability (close to 1) means that an increase in predator biomass will not cause any noticeable increase in the predation mortality the predator may cause on the given prey. A high vulnerability (e.g. 100) indicates that the predator biomass is low compared with its carrying capacity (Guénette *et al.*, 2008) and so the predator will be capable of inflicting greater mortality, increasing its consumption and will recover more quickly (Araujo *et al.*, 2008). Initially the default value of 2 (indicating neither a top-down nor bottom-up control of a predator–prey interaction) was used, prior to a standardised procedure being undertaken that allows the user to undertake a “fitting” procedure namely: to search for vulnerability estimates which give better “fits” of the model to time-series data; and to search for time series values of annual relative primary productivity which may represent how productivity has impacted biomass throughout the ecosystem. By doing repeated simulations, Ecosim therefore allows hindcasting of predicted biomasses to historic time series data.

5.2.2: Ecosim: Fitting procedure

The next critical step in the development of a credible ecosystem model is calibration, which is done by showing that the model can reproduce observed historical trends (Alexander *et al.*, 2015). To fit an Ecosim model, time series data are required to: (a) affect a change in the model, and (b) to compare the modelled output to reference data using statistical diagnostics (Coll *et al.*, 2008; Mackinson, 2014). Similar to the formal ad-hoc exploratory fitting methodology suggested by Mackinson *et al.* (2009), and using an automated fitting software designed by Scott *et al.*, (2016) the following procedure was used to “fit” both the Tamar and Eden models to observed waterbird time-series data (1990-2015 see chapter 4.2.4 and 4.2.8 for data collection methods). Unfortunately historical biomass data for other groups including the: primary producers, macrofauna and demersal fish groups were too disparate in time to include in the fitting procedure.

Eight alternative hypotheses (or models) were parameterised and compared (each alternative hypothesis starts from a point where all “fitting factors”—vulnerabilities and PP anomaly—are reset) as described in Table 5. 1 and below:

Table 5.1 The eight alternative hypotheses and changing factors parameterised and compared by the Stepwise Fitting Procedure. ✓ and X indicate if a factor is included and not included respectively.

Hypothesis	Trophic effects (Vulnerabilities)	PP anomaly
(1) Baseline model	X	X
(2) Baseline and trophic effects	✓	X
(3) Baseline and PP anomaly	X	✓
(4) Baseline, trophic effects and PP anomaly	✓	✓
(5) Forced riverflow	X	X
(6) Forced riverflow and trophic effects (15v)	✓	X
(7) Forced riverflow and PP anomaly (5PP)	X	✓
(8) Forced riverflow and trophic effects and PP anomaly (15v, 5PP)	✓	✓

1. Baseline model: no environmental data were used to drive the model. All vulnerabilities were set to 2
2. Baseline and trophic effects: no environmental data were used to drive the model. The optimal numbers of vulnerabilities (for predator–prey interactions) were identified using the “sensitivity to vulnerabilities” subroutine of the “fit to time series” algorithm. This algorithm incremented one vulnerability value slightly in each run, so as to calculate the “Jacobian matrix” of sensitivities of each of the predicted time-series observations to each of the parameters. After N +1 checks (N is the number of parameters with non-zero variances), the Jacobian matrix is used to estimate an initial best step change for each parameter (Christensen *et al.*, 2001).
3. Baseline and environmentally driven changes in PP: no environmental data were used to drive the model. The “PP anomaly” procedure was used to search for time-series values of annual relative primary productivity that may represent historical productivity trends impacting biomasses. The same procedure as that for identifying the optimal vulnerabilities is used but, in this instance, the annual PP value is changed slightly in each run until a best fit to the time-series data is achieved.
4. Baseline and trophic effects and environmentally driven changes in PP: no environmental data were used to drive the model. Vulnerabilities and a PP anomaly were estimated using the “fit to time series” algorithm.

5. Forced river flow: Historic river flow (see collection methods below) was included as a model driver (primary producers) on the *a priori* assumption that it is a key modulator of abiotic/biotic interactions in estuaries.
6. Forced river flow and trophic effects: Forced river flow was included in the model. The optimal vulnerabilities were identified using the same procedure identified in model scenario two and included in the model.
7. Forced river flow and environmentally driven changes in PP: Forced river flow was included in the model. A PP anomaly was estimated using the “fit to time series” routine described in model scenario three.
8. Forced river flow, trophic effects, and environmentally driven changes in PP: Forced river flow was included in the model. Vulnerabilities and a PP anomaly were estimated using the “fit to time series” algorithm.

Model 5-8 simulations were driven by historic river flow data (Tamar 1980-2005 & Eden 1980-2015), measured from gauging stations at the major confluences of each estuary (i.e. Gunnislake Tamar see section 2.4.1) and Kembeck (Eden see section 2.5.1 for protocols). Initially, baseline monthly values of the river flow forcing variable were estimated (to represent seasonal trends in river flow), by dividing total annual average flow by average flow per month over each of the periods (Figure 5.2). An annual baseline simulation using the resulting seasonal river flow forcing variable was then used to drive the respective models (years 1 to 10 shown in Figure 5.3).

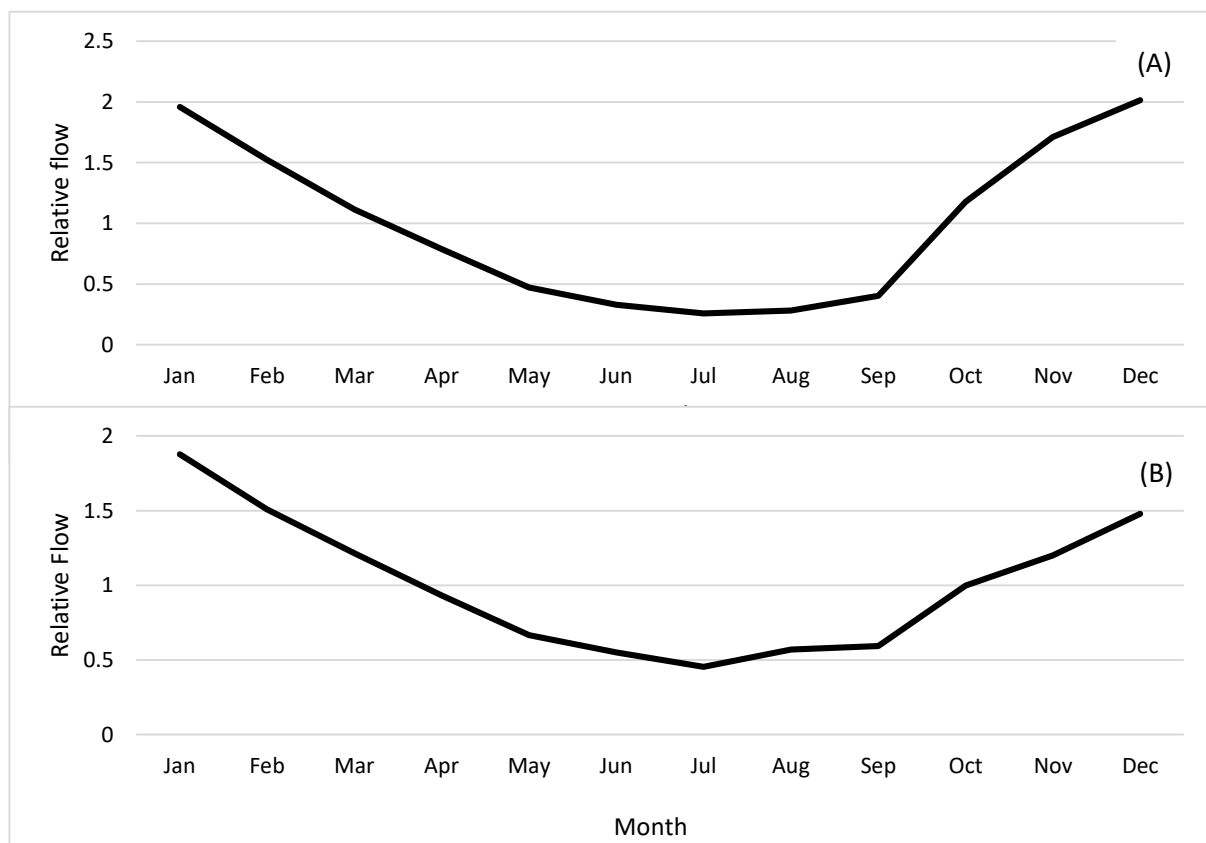


Figure 5.2 Monthly river flow driving variable derived from flow data (A) Tamar & (B) Eden. River flow is the monthly average flow divided by the total average annual flow.

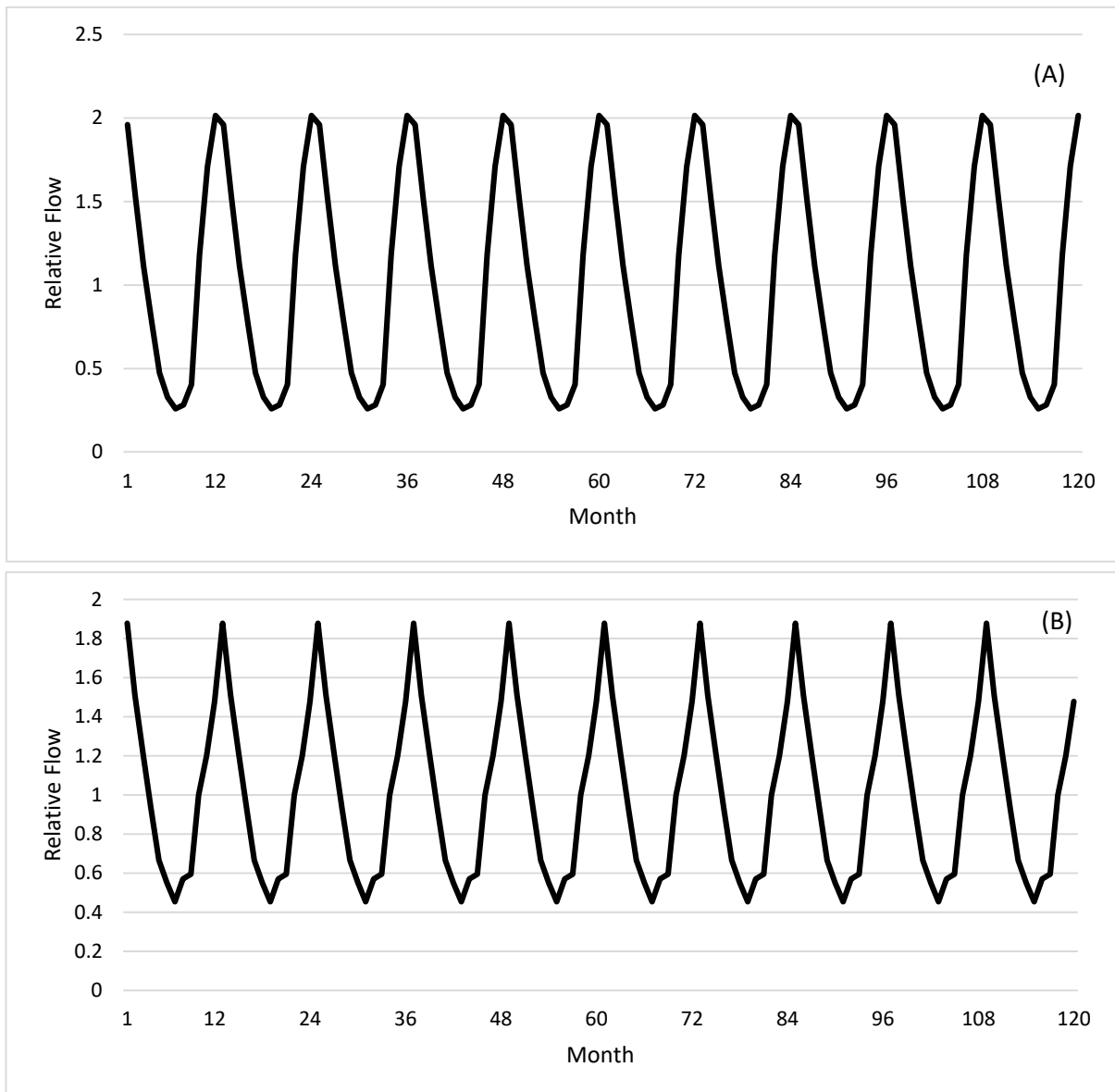


Figure 5.3 Baseline river-flow driving variables for the long-term simulations (A) Tamar (B) Eden. Years 1 to 10 are shown

At each step of the fitting process, the goodness-of-fit (SS) of the model was assessed using Akaike's Information Criterion (AICc) (Akaike, 1974), a tool for model selection which takes into account the predictive accuracy (SS) and complexity (number of parameters), and was applied as proposed by Mackinson *et al.* (2009). The AICc is defined as:

$$\text{AICc} = \text{AIC} + 2K(K - 1)/(n - K - 1) \quad \text{Equation 5.3}$$

where n is the number of observations, or time series values, i.e. the number of series used multiplied by the number of years for each parameter and K is the number of parameters estimated. The hypothesis that obtains the lowest AICc is therefore the best hypothesis having obtained best fit of

the model to the data while using the least number of parameters to do so (Burnham & Anderson, 2004). In the Ecosim scenarios described here the effects of fishing and mediation functions were not included.

In a final step of the fitting procedure, the Monte Carlo routine in Ecosim was used to perform sensitivity analyses for both the best fitted Tamar and Eden models. This routine tests the sensitivity of Ecosim's output to the initial Ecopath input parameters (e.g., P/B, Q/B, EE) by drawing input parameters from a uniform distribution centred on the base Ecopath value with the coefficient of variation set to 0.1 (Christensen *et al.*, 2009).

5.2.3 Ecosim: Long term (50 year) temporal simulations

Having parameterised each model, long-term (50 year) simulations were performed to address the research question. To represent physical or environmental parameters that may influence the trophic interactions thus described, a number of 'forcing function' routines were implemented within Ecosim. These forcing functions were imported from a spreadsheet and represent seasonal (cycles that repeat annually) or long-term (monthly) environmental oscillations. Functions of interest included variations in river flow, nutrient availability and water temperature, with the procedure for defining each function described henceforth.

To investigate the impact of variation in the amount of precipitation delivered to the watersheds, the baseline river flow forcing variable was modified to produce extremes of high and low flow conditions for each year of the 50 year simulation representing the effects of within-year extremes of high-flow (winter) and low-flow (summer) conditions (years 1 to 10 shown in Figure 5.4). Flow during the wettest months of the year was increased by approximately 40%, and flow during the driest months of the year was decreased by approximately 40%. Extreme high and low period values were validated against river flow measurements from the National River Flow Archived database (<http://nrfa.ceh.ac.uk/derived-flow-statistics>) for each catchment. Two specific flow percentiles were investigated to validate if the high (Q10- the flow in m^3s^{-1} which was equalled or exceeded for 10% of the flow record) and low (Q95 - the flow in m^3s^{-1} which was equalled or exceeded for 95% of the flow record) flow scenario values were realistic. For the Tamar periods Q10= ($2.507\text{m}^3\text{s}^{-1}$) and Q95= ($0.098\text{m}^3\text{s}^{-1}$) and for the Eden periods Q10= ($1.925\text{m}^3\text{s}^{-1}$) and Q95= ($0.230\text{m}^3\text{s}^{-1}$), suggesting the extremes used here were representative of the highest and lowest river flow values recorded in both catchments.

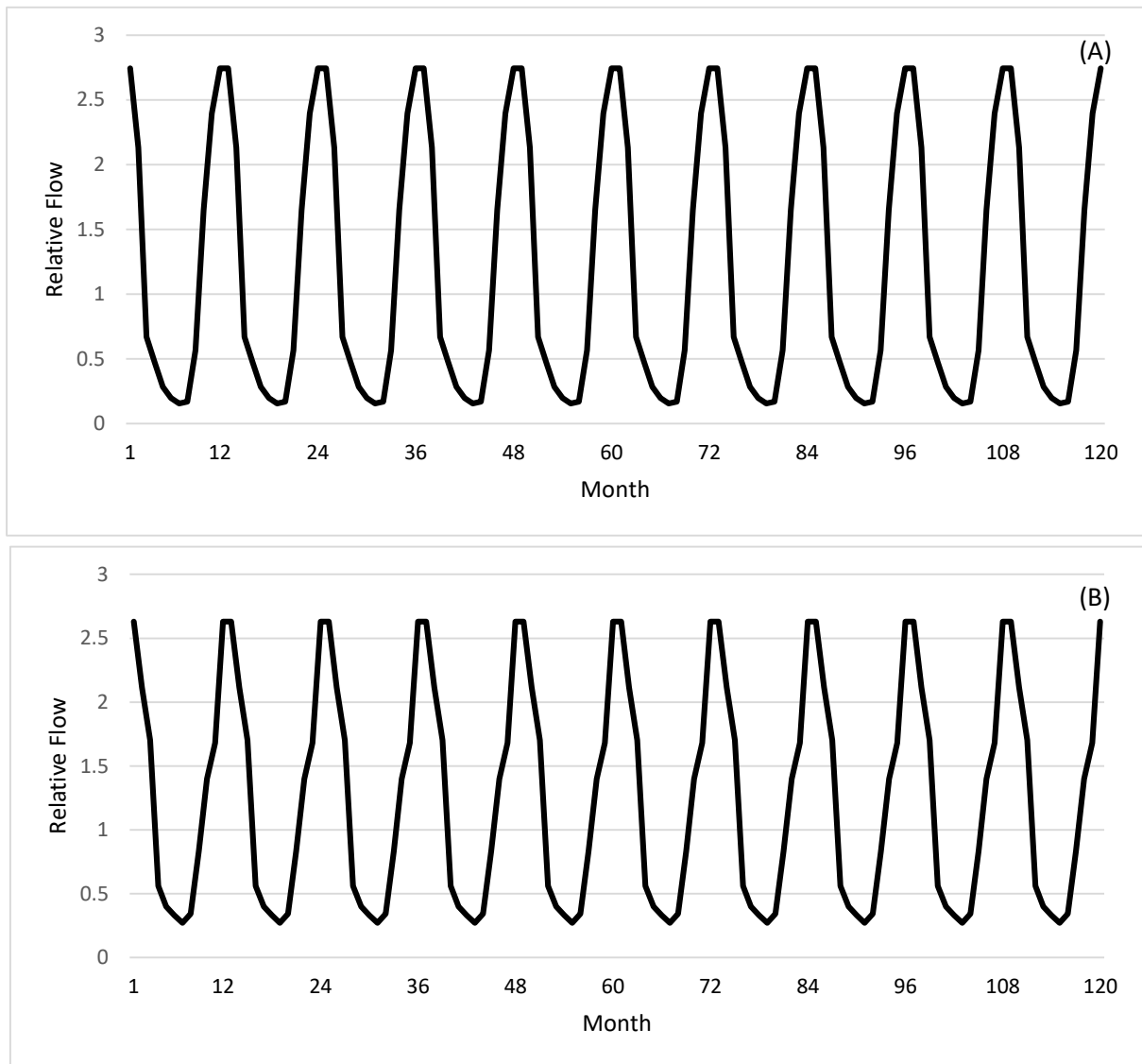


Figure 5.4 Extreme river flow driving variables for the long-term simulations (A) Tamar (B) Eden. Years 1 to 10 are shown.

Changes in nutrient loading on each system, were simulated by assigning a time forcing function to the free nutrient concentration pool within the system. It is assumed by Ecosim that at any instant in time the system has a total nutrient concentration (N_T), which is partitioned between nutrient 'bound' in biomass versus free in the environment (N_f) accessible to primary producers for nutrient uptake,

Or more formally

$$N_T = \sum i n_i B_i + N_f \quad \text{Equation 5.4}$$

Where i is (fixed) nutrient content per unit of pool i biomass, and N_f is free nutrient concentration. By manipulating the default free nutrient pool, the effects of 1) baseline conditions (i.e. N_f constant over time), 2) nutrient limitation (N_f 25% less than baseline unity) and 3) nutrient enrichment (N_f 25% greater than baseline unity) could be investigated.

The influence of increasing water temperature in each system was characterised by a linear forcing function (Figure 5.5) based on the evidence from the IPCC 5th WG1AR5 assessment report that warming in the upper 75 m of the ocean is likely to increase by an average of 0.11 [0.09 to 0.13]°C a decade (Rhein *et al.*, 2013).

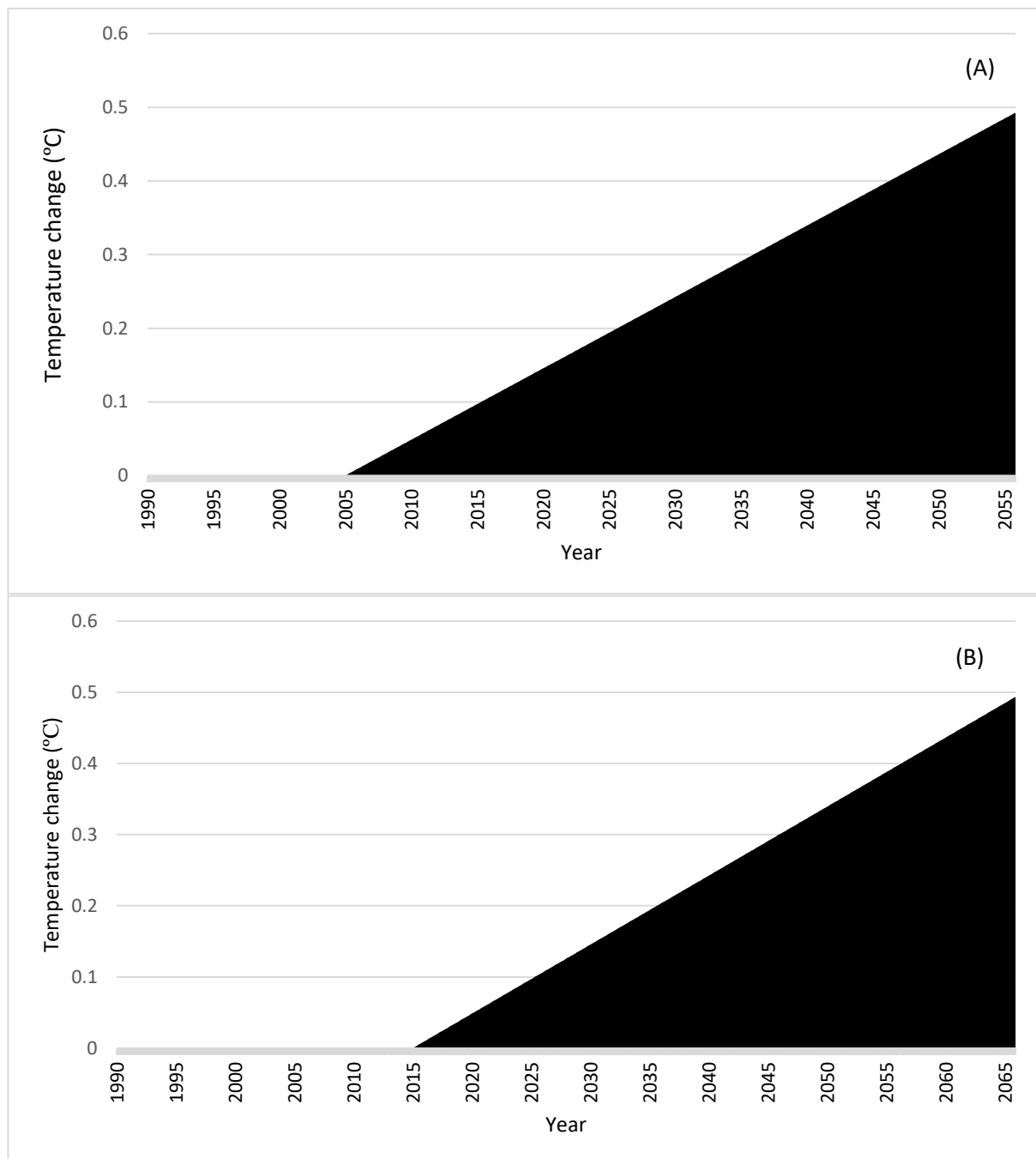


Figure 5.5 Temperature driving variables for the long-term simulations (A) Tamar (B) Eden.

Having defined the forcing functions, the models with the best fit to historic biomass data (Section 5.2.3) were subjected to environmental variation in a stepwise manner to test twelve alternative hypotheses (Table 5.2).

Table 5.2 The twelve alternative hypotheses and changing factors parameterised and compared by the long-term simulations ✓ and X indicate if a factor is included and not included respectively.

Hypotheses	Extreme river low	Nutrients high	Nutrients low	Temperature high
Baseline river flow	X	X	X	X
Baseline river flow and nutrients high	X	✓	X	X
Baseline river flow and nutrients low	X	X	✓	X
Baseline river flow and temperature	X	X	X	✓
Baseline river flow and nutrients high and temperature	X	✓	X	✓
Baseline river flow and nutrients low and temperature	X	X	✓	✓
Extreme river flow	✓	X	X	X
Extreme river flow and nutrients high	✓	✓	X	X
Extreme river flow and nutrients low	✓	X	✓	X
Extreme river flow and temperature	✓	X	X	✓
Extreme river flow and nutrients high and temperature	✓	✓	X	✓
Extreme river flow and nutrients low and temperature	✓	X	✓	✓

In each year of the simulations, single or multiple forcing functions were used to modify the Q/B ratios of each consumer group and/or force the production of the primary producer groups. For example, each of the river flow and nutrient forcing functions were applied to the production rate of the main primary producer groups having assumed *a priori* that the major effect of river flow, is the delivery of nutrients that drives benthic primary production (Day *et al.*, 1989) and hence acts a suitable proxy for changes in benthic system functioning. The forcing variable for temperature in contrast, was forced on all component groups.

After each simulation was run, model estimates were analysed by comparing the observed and simulated biomass. Additionally the simulated trajectories of each scenario was subjected to network analysis and the results compared. The network analysis indicators used to examine the status of the two ecosystems as depicted by their Ecosim models include total systems throughput (TST, t km⁻¹ year⁻¹), systems average mutual information (AMI, ‘flowbits’), ascendancy (A, ‘flowbits’), overhead (O, ‘flowbits’) and Finns cycling index (FCI, %.) A synopsis of each of these indicators is given in the previous chapter (4 section 4.3.9), but to recapitulate: TST is the sum of all flows in the model (Finn 1976), AMI measures the organization of the exchanges among components (Abarca Arenas &

Ulanowicz, 1997), ascendancy and overhead can be considered as indices of the system’s resilience (Christensen, 1995; Heymans, 2003) , while Finn’s Index quantifies the relative amount of carbon and nutrient recycling and is an indication of stress and structural differences either within or among models (Finn, 1976).

5.3 Results

5.3.1 Model fitting and choice of best model

The most statistically significant results (based on Akaike’s information criterion) from fitting both of the Tamar and Eden were obtained when forced historic river flow, trophic effects, and a PP anomaly search were included together in the model (Model 8, last row in Table 5.3 &5.4)

The final models improved the fit by 111.03% (Tamar) and 159.3% (Eden) over the baseline models. In the case of the Tamar, the addition of customised trophic interactions (model scenarios 2 & 6) and a primary production anomaly (model scenarios 3 & 7) had a greater influence in improving model fit (AICc reduced by 87-103% against baseline) than in case of the Eden estuary (AICc reduced by 4-36 % against baseline). In contrast when the two variables were combined (model scenarios 4 and 8), these interactions provided the second and largest advance in the fit in both models (AICc reduced by > 100% both models), with inclusion of trophic effects and a PP anomaly providing the largest improvement of overall fit in the Eden models.

Table 5. 3 Comparison of model fits for the Tamar Estuary. AICc is Akaike information criterion with a second-order correction for small sample sizes ($AICc = AIC + 2 K(K - 1)/n - K - 1$, where n is the number of observations and K the number of parameters). V is the number of vulnerability parameters, minSS is the predictive accuracy derived from Ecosim and PP the number of primary production spline points (for smoothing).

Model	Description	n	minSS	K	AICc	% improved fit
1	Baseline model	822	570.9	0	-130.13	0
2	Baseline and trophic effects (5v)	822	388.05	5	-257.91	98.19
3	Baseline and PP anomaly (5PP)	822	388.01	5	-257.94	98.21
4	Baseline and trophic effects and PP anomaly (5v, 5PP)	822	368.1	10	-266.57	104.85
5	Forced river flow	822	571.6	0	-129.69	-0.33
6	Forced river flow and trophic effects (15v)	822	380.6	15	-244.35	87.77
7	Forced river flow and PP anomaly (5PP)	822	380.55	5	-264.87	103.53
8	Forced river flow and trophic effects and PP anomaly (15v, 5PP)	822	339.6	20	-274.62	111.03

Table 5. 4 Comparison of model fits for the Eden Estuary. AICc is Akaike information criterion with a second-order correction for small sample sizes ($AICc = AIC + 2 K(K - 1)/n - K - 1$, where n is the number of observations and K the number of parameters). V is the number of vulnerability parameters, minSS is the predictive accuracy derived from Ecosim and PP the number of primary production spline points (for smoothing).

Model	Description	n	minSS	K	AICc	% improved fit
1	Baseline model	750	576.4	0	-85.75	0
2	Baseline and trophic effects (5v)	750	507.63	5	-117.08	36.53
3	Baseline and PP anomaly (5PP)	750	548.9	5	-91.62	6.84
4	Baseline and trophic effects and PP anomaly (5v, 5PP)	750	361.79	10	-217.21	153.29
5	Forced river flow	750	603.9	0	-70.57	-17.7
6	Forced river flow and trophic effects (15v)	750	494.92	15	-104.82	22.23
7	Forced river flow and PP anomaly (5PP)	750	552.4	5	-89.55	4.43
8	Forced river flow and trophic effects and PP anomaly (15v, 5PP)	750	334.08	20	-222.36	159.3

Using the “best-fit” models (the models with the lowest AICc), the Ecosim estimations emulated the historic biomass trends well for the majority of the waterbird species (Figures 5.6 & 5.7). However, the final fitted models did not represent trends well for a few species such as: the Bar-tailed godwit (SS, 50.63), Dunlin (SS, 49.24) and Redshank (SS, 32.62) in the case of the Tamar or the Golden plover (SS, 111.3) and Greylag goose (SS, 66.23) in the case of the Eden.

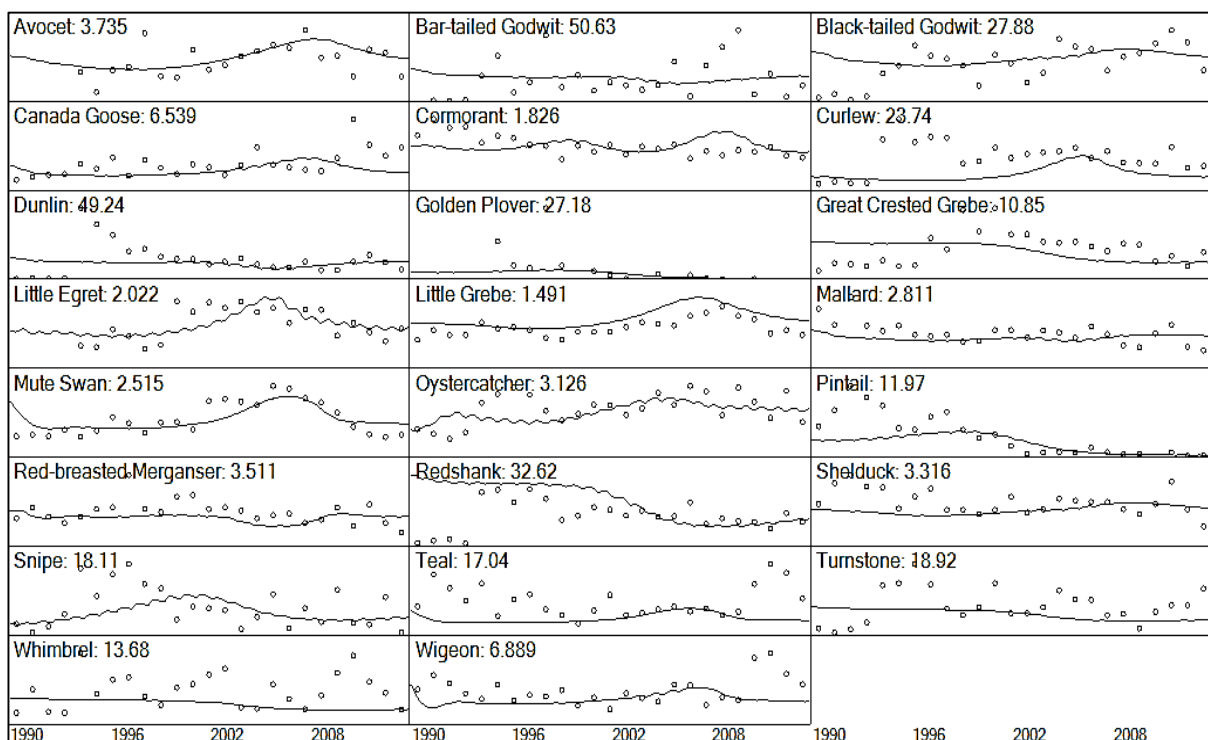


Figure 5.6 Predicted historic waterbird biomass trends for the Tamar estuary following fitting procedure showing the the goodness-of-fit (SS) of the model .The dots are observed calibration data and the line shows the model simulation for the different functional groups.

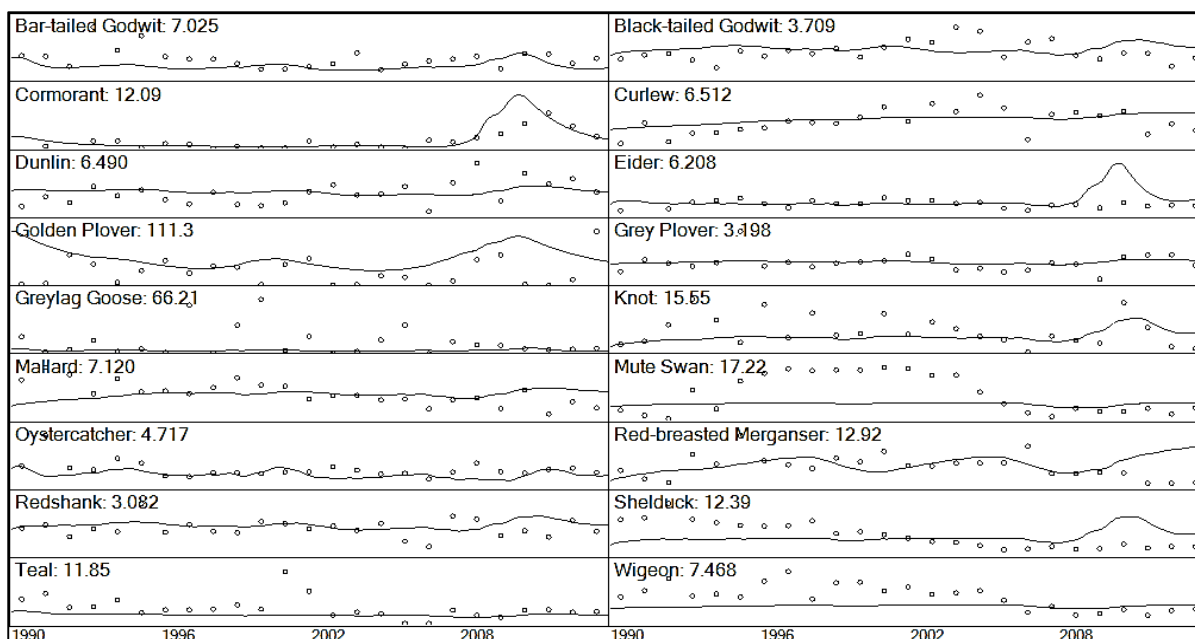


Figure 5.7 Predicted historic waterbird biomass trends for the Eden estuary following fitting procedure showing the goodness-of-fit (SS) of the model. The dots are observed calibration data and the line shows the model simulation for the different functional groups.

5.3.2 Regional responses to climate change impacts: ecosystem and community biomass

In the Tamar system, ecosystem biomass responded strongly to changes in river flow and nutrient inputs (high or low) when these effects were applied individually (Figure 5.8). At this aggregate scale, these effects perturbed the ecosystem reducing total system biomass by approximately -17.5% (extreme river flow) and -25% (high and low nutrient scenarios) against baseline conditions. In contrast, thermal stress had the least effect (-9.5%) on ecosystem biomass as an independent variable.

When the variable of nutrient availability and extreme river flow were combined with each other, there was little additional impact on already predicted biomass, suggesting that under these particular circumstances, these effects were additive in effect. Similarly, upon adding the variable of thermal stress to the model, there was little cumulative interaction detected among variables, with the exception of high nutrients combined with increased water temperature under baseline river flow conditions. Under this scenario, cumulative impacts, accounted for an increase in ecosystem biomass greater than the sum of all the reductions caused by constituent effects. This suggests that antagonistic interactions between increasing thermal stress and high nutrient concentrations can occur through the Tamar food-web dynamic.

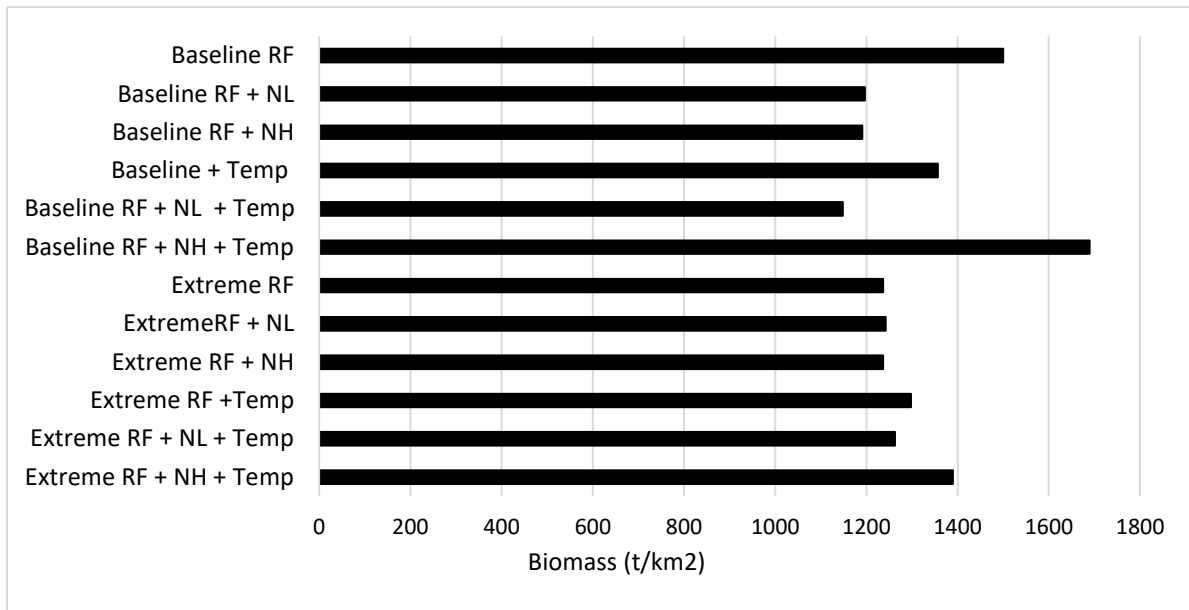


Figure 5.8 Projected Tamar ecosystem biomass in 2055 under different climate change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High).

As with changes in overall ecosystem biomass, only the addition of thermal stress in combination with other variables had a clear impact on community biomass, generally reducing demersal fish biomass, but increasing invertebrate and waterbird biomass (Figure 5.9). In particular, under the combination of river flow, higher water temperatures and altered nutrient availability (high or low), demersal fish biomass was severely reduced in the model, suggesting an inability for these spaces to adapt to heat induced stressor combinations.

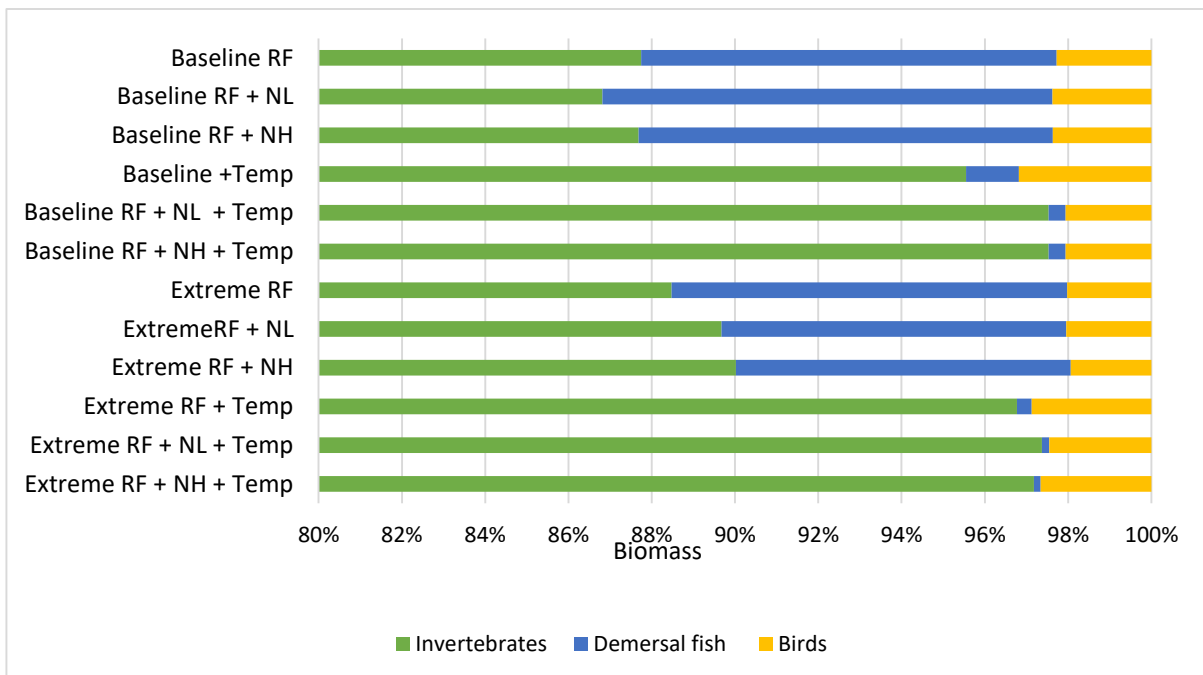


Figure 5.9 Projected Tamar community biomass in 2055 under different climate change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High).

In contrast to the Tamar, Eden ecosystem biomass did not respond strongly to changes in extreme variations in river flow or nutrient inputs (high or low) when these effects were applied individually (Figure 5.10). At this level, none of these effects perturbed the ecosystem far from the condition expected without climate change; with both variable scenarios corresponding within 5% of the predicted baseline biomass estimates. However, when a third variable of thermal stress was added to each scenario, cumulative impacts caused a substantial increase (Baseline RF-NH/L-Temp 36-39%; Extreme RF-NH/L-Temp 41-45%) in biomass over baseline conditions. Similarly, when applied independently, thermal stress had a strong positive effect on ecosystem biomass under baseline (30%) and extreme river-flow conditions (36%). As the addition of thermal stress accounted for an increase in ecosystem biomass greater than the sum of all the reductions caused by constituent effects in all trivariate scenarios, this suggests that antagonist reactions between the abiotic environment and biodiversity are likely to be a predominant feature of the Eden Estuary if water temperatures increase by the predicted amount of 0.5°C in the near future.

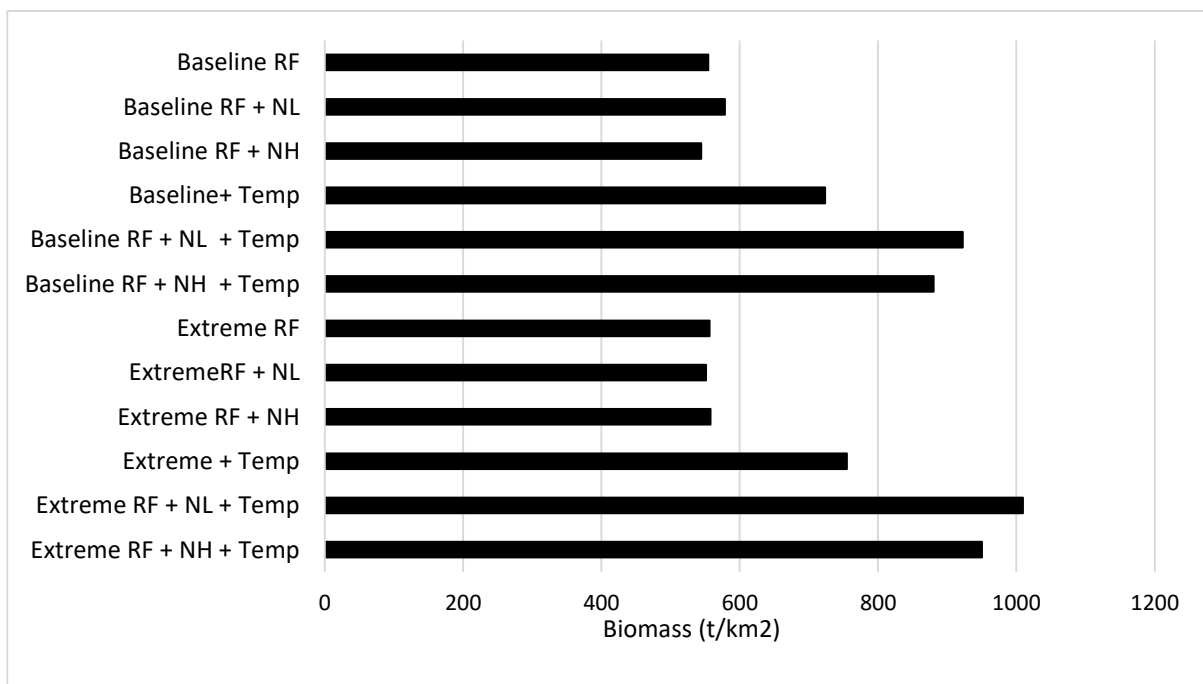


Figure 5.10 Projected Eden ecosystem biomass in 2065 under different climate change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High).

At the community level, only the individual impacts of low nutrient conditions and thermal stress had a negative impact on the different consumer groups (Figure 5.11) , acting to reduce invertebrate (NL-59%; Temp -135%) and bird biomass (NL-153%; Temp -407%) while increasing demersal fish biomass (NL 18.4%; Temp 34.5 %). However, when thermal stress was combined with the other variables (Extreme RF, NL/NH), it improved the biomass of every group in every model.

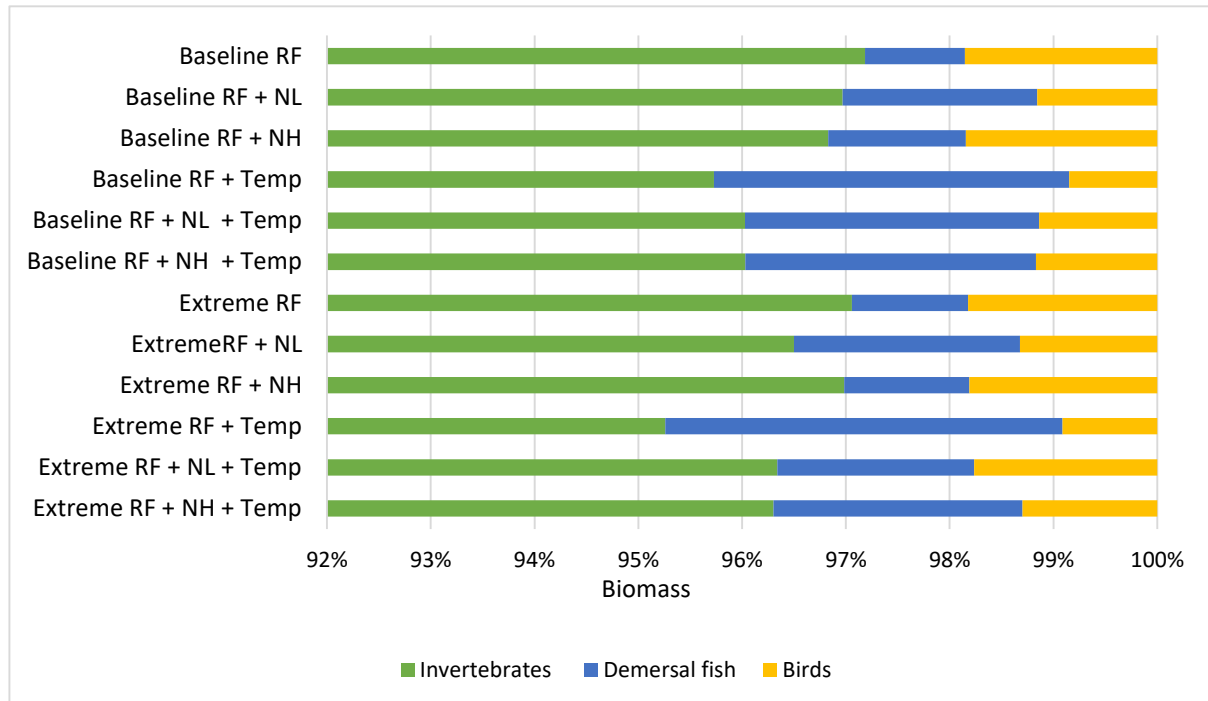


Figure 5.11 Projected Eden community biomass in 2065 under different climate change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High).

To easily visualise the directional changes in key consumer groups between the two systems a supplementary table is provided below (Table 5.4).

Table 5.4 Direction of impacts on key consumer groups in the Tamar and Eden estuaries. Arrows indicate direction of effect relative to the baseline RF simulation with no anthropogenic drivers. RF (River flow), NL (nutrients low), NH (nutrients high).

Scenario	Species groups	Tamar	Eden
Baseline RF + NL	Invertebrates	↓	↓
	Demersal Fish	↓	↑
	Birds	↓	↓
Baseline RF + NH	Invertebrates	↑	↓
	Demersal Fish	↑	↑
	Birds	↑	↓
Baseline +Temp	Invertebrates	↑	↓
	Demersal Fish	↓	↑
	Birds	↑	↓
Baseline RF + NL + Temp	Invertebrates	↑	↑
	Demersal Fish	↓	↑
	Birds	↑	↑
Baseline RF + NH + Temp	Invertebrates	↑	↑
	Demersal Fish	↓	↑
	Birds	↑	↑
Extreme RF	Invertebrates	↑	↓
	Demersal Fish	↑	↑
	Birds	↓	↓
Extreme RF + NL	Invertebrates	↑	↓
	Demersal Fish	↑	↑
	Birds	↑	↓
Extreme RF + NH	Invertebrates	↑	↓
	Demersal Fish	↑	↑
	Birds	↑	↓
Extreme RF Temp	Invertebrates	↑	↓
	Demersal Fish	↓	↑
	Birds	↑	↓
Extreme RF + NL + Temp	Invertebrates	↑	↑
	Demersal Fish	↑	↑
	Birds	↓	↑
Extreme RF + NH + Temp	Invertebrates	↓	↑
	Demersal Fish	↑	↑
	Birds	↓	↑

5.3.3 Regional responses to climate change impacts: ecosystem attributes

In the Tamar system, anthropogenic effects had mixed but definitive impacts on ecosystem structure, functioning and resilience (Figure 5.12). When considered individually and together the effects of each of the three stressors acted unanimously to increase ecosystem structure (AMI), vigour (TST) and organisation (Ascendency) while also acting concordantly to reduce system resilience (Overhead) and nutrient cycling capabilities (Finns cycling index). Generally, the greatest of these effects occurred when all three stressor variables were combined (i.e. extreme RF, NH/NL and temperature) with two noticeable exceptions: overhead (baseline +temp) and Finns cycling index (baseline + NL + temp).

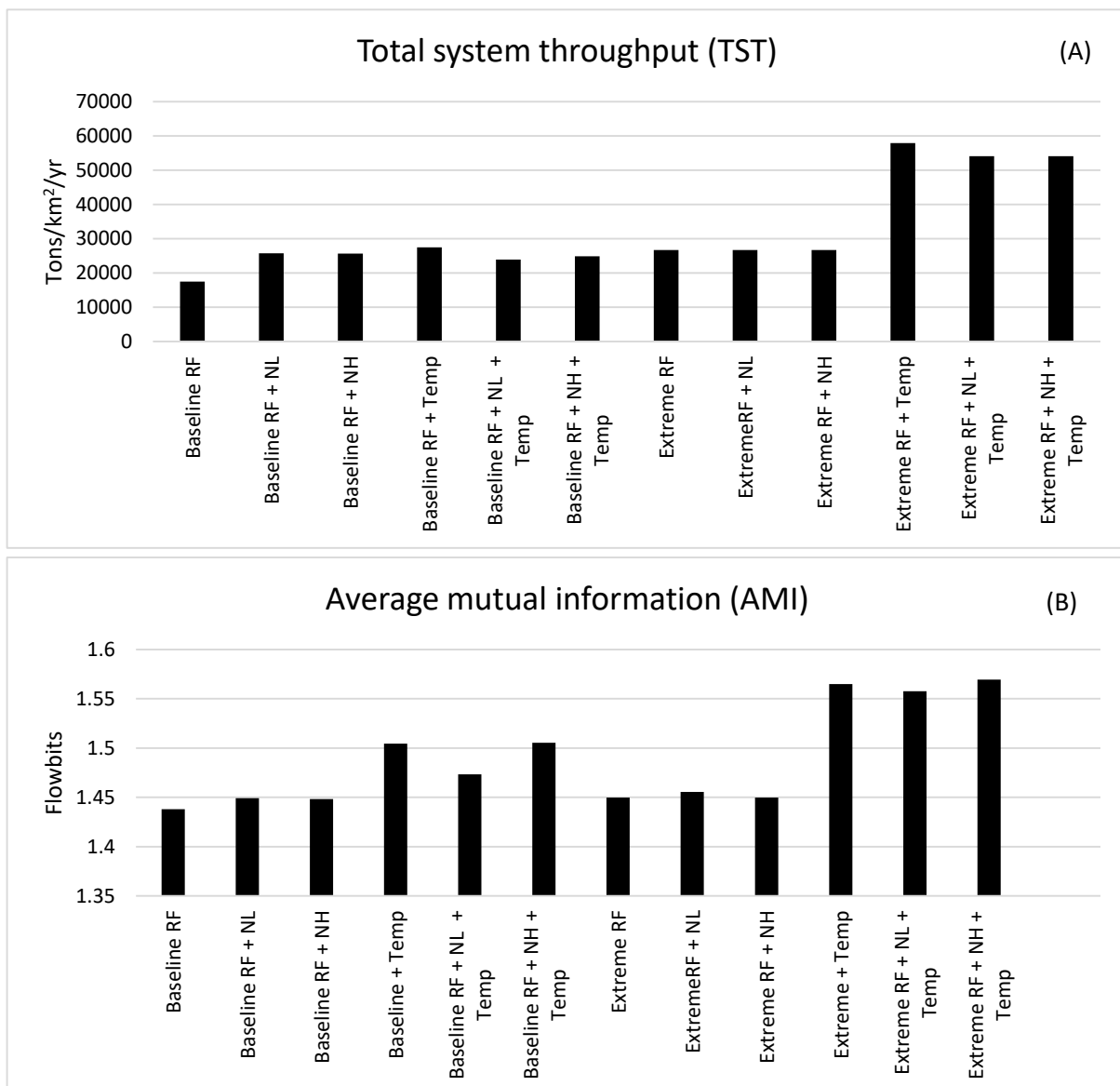


Figure 5.12 Tamar projected ecosystem attributes from network analysis in 2055 under anthropogenic change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High). (A) Total system throughput, (B) Average mutual information.

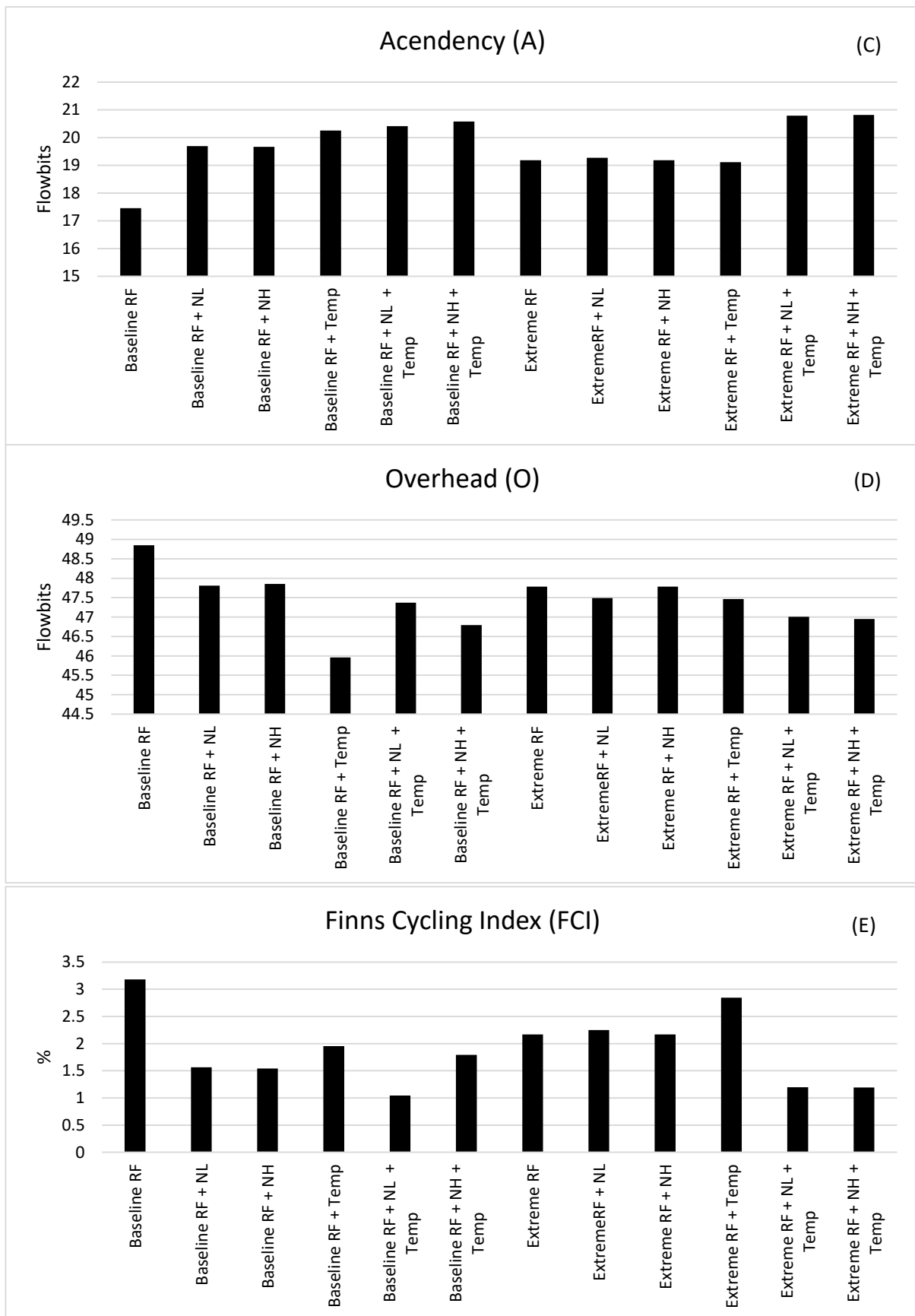


Figure 5.12 (continued) Tamar projected ecosystem attributes from network analysis in 2055 under anthropogenic change scenarios .RF (River flow), NL (nutrients low), NH (nutrients high). (C) Ascendency, (D) Overhead, (E) Finns Cycling Index.

Considered in more detail, the variable of temperature singly and in combination had the most significant impact on ecosystem activity (TST), structure (AMI) and efficiency (Ascendency), particularly in combination with the extreme river flow variable (TST ~ 209%, AMI, ~ 2.1, A ~ 19% increase), suggesting a greater degree of energy flowing through the system, though a smaller number of more efficient compartments when temperature and extreme river flow variables are combined. While intuitively increased structure and efficiency can be thought of as a good thing, too much of either variable can also lead to ecosystems becoming more 'brittle' (Ulanowicz, 2002). Therefore as system ascendency (scaled by TST and AMI) increases under the impact of greater stress, by means of pruning of the systems less efficient or cooperative elements, it also depletes the systems inherent reservoirs of sundries and unfit processes that comprise the overhead of the system that can be drawn upon to create an adaptive response to a new threat (Ulanowicz, 1997). Hence, concomitantly with increasing ascendency the Tamar system would experience a reduction in system resilience (overhead) under any of the future scenarios investigated here. Similarly the Tamar system as a whole exhibited a greatly reduced cycling capacity, particularly under the combined influence of higher temperatures and low nutrient conditions. As the cumulative effects of three separate scenarios (1) baseline RF + NL+ temp 2) extreme RF + NL+ temp and 3) extreme RF+NH+temp) accounted for a reduction in ecosystem cycling greater than the sum of all the reductions caused by constituent effects, this suggests that synergies may be likely to occur between temperature and nutrients in the Tamar ecosystem and may be exacerbated by increased river flow.

In the Eden ecosystem, cumulative and individual impacts also produced noticeable changes on a number of ecosystem attributes (Figure 5.13). Considering the structure and flow of energy through the network, the addition or limitation of nutrients had relatively little effect on system dynamics (AMI and TST) in comparison to future baseline conditions. However the addition of thermal stress to the models reduced both system metrics under all baseline conditions and in the case of AMI under all extreme river flow conditions. Despite the reduction in flow and structure under these scenarios, the addition of the extreme river flow variable had an ameliorative effect on TST (e.g. baseline + NL vs. extreme + NL = 3.96%).

The response of system ascendency, which denotes how well organised the system is at processing medium, was fairly ambiguous under all individual and cumulative stressor scenarios. Hitherto, the largest rise in ascendency was observed under all trivariate model scenarios, which also correlated with the largest falls in system overhead (resilience), suggesting that the greatest future reductions in system resilience are likely to occur when three (or more) stressors combine. The greatest of these effects were observed when the extreme river flow events coincide with increased thermal stress (0.5°C) and lower (-3.31%) or higher (-5.33%) nutrient availability (Figure 5.12).

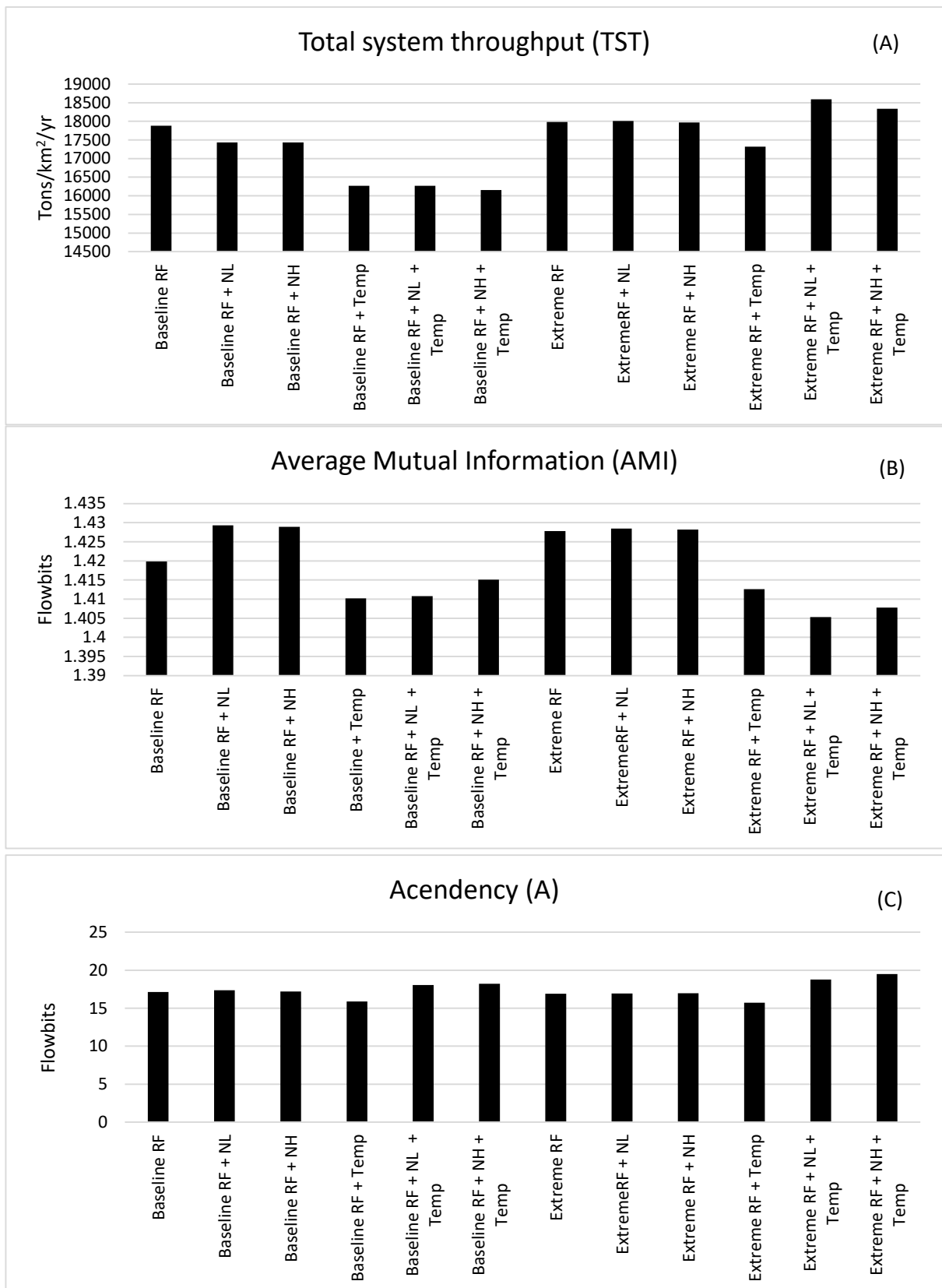


Figure 5.13 Eden projected ecosystem attributes from network analysis in 2065 under anthropogenic change scenarios. RF (River flow), NL (nutrients low), NH (nutrients High). (A) Total system throughput, (B) Average mutual information (C) Ascendency.

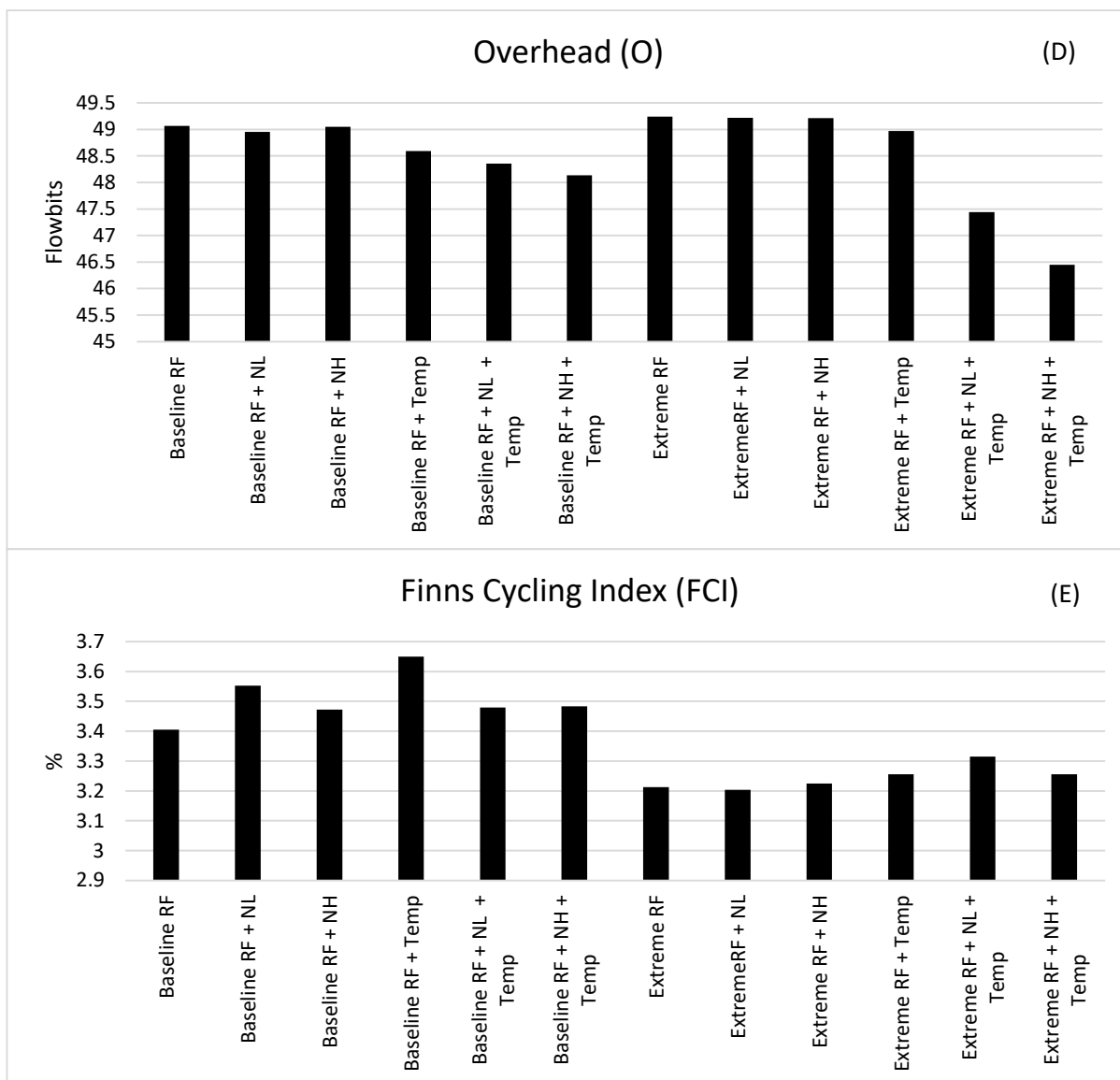


Figure 5.13 (continued) Eden projected ecosystem attributes from network analysis in 2065 under anthropogenic change scenarios. RF (River flow), NL (nutrients low), NH (nutrients high). (D) Overhead, (E) Finn’s Cycling Index.

Changes in the Finn’s Cycling Index also revealed two separate trend patterns between stressors applied to predicted baseline river flow conditions and those applied with the extreme flow alternatives. When variables were applied singly or in combination to baseline flow conditions, the proportion of nutrient and mineral recycling unanimously increased. In contrast, under extreme river flow conditions there was a universal decrease in the preponderance of nutrient cycles in the Eden system under all stressor combinations. Overall regarding the interaction potential of stressors in the Eden, definitive synergistic impacts were apparent in the case of system AMI and Overhead when three stressor combinations were applied i.e. extreme river flow, nutrients (low & high) and temperature. To easily visualise the directional changes in key ecosystem attributes between the two systems a supplementary table is provided below (Table 5.5).

Table 5.5 Direction of impacts on ecosystem attributes in the Tamar and Eden estuaries. Arrows indicate direction of effect relative to the baseline RF simulation with no anthropogenic drivers. RF (River flow), NL (nutrients low), NH (nutrients high). TST (Total system throughput), AMI (Average mutual information), A (Ascendency), O (Overhead) and FCI (Finn’s Cycling Index).

Scenario	Ecosystem attribute	Tamar	Eden
Baseline RF + NL	TST	↑	↓
	AMI	↑	↑
	A	↑	↑
	O	↓	↓
	FCI	↓	↑
Baseline RF + NH	TST	↑	↓
	AMI	↑	↑
	A	↑	↑
	O	↓	↑
	FCI	↓	↑
Baseline +Temp	TST	↑	↓
	AMI	↑	↓
	A	↑	↓
	O	↓	↓
	FCI	↓	↑
Baseline RF + NL + Temp	TST	↑	↓
	AMI	↑	↓
	A	↑	↑
	O	↓	↓
	FCI	↓	↑
Baseline RF + NH + Temp	TST	↑	↓
	AMI	↑	↓
	A	↑	↑
	O	↓	↓
	FCI	↓	↑
Extreme RF	TST	↑	↑
	AMI	↑	↑
	A	↑	↓
	O	↓	↑
	FCI	↓	↓
Extreme RF + NL	TST	↑	↑
	AMI	↑	↑
	A	↑	↓
	O	↓	↑
	FCI	↓	↓
Extreme RF + NH	TST	↑	↑
	AMI	↑	↑
	A	↑	↓
	O	↓	↑
	FCI	↓	↓
Extreme RF Temp	TST	↑	↓
	AMI	↑	↓
	A	↑	↓
	O	↓	↑
	FCI	↓	↓
Extreme RF + NL + Temp	TST	↑	↑
	AMI	↑	↓
	A	↑	↑
	O	↓	↓
	FCI	↓	↓
Extreme RF + NH + Temp	TST	↑	↑
	AMI	↑	↓
	A	↑	↑
	O	↓	↓
	FCI	↓	↓

5.4 Discussion

5.4.1 Drivers and trophic interactions

Variable hydrology of estuaries, as well as climatic drivers (i.e. temperature) may independently affect biophysical factors that influence primary production and population densities, thereby affecting the relative influence of bottom-up and top-down processes in trophic networks (Pörtner & Farrell, 2008; Winemiller *et al.*, 2014). Acting analogously to these factors, anthropogenic influences of introducing or reducing nutrients to ecosystems (bottom-up processes), can also foster complex changes in plant biomass often with widespread damaging consequences for all aquatic ecosystems (Nixon, 1995; Smith *et al.*, 2006; Bricker *et al.*, 2008; Ferreira *et al.*, 2011). However, ecosystems are often not driven entirely by only one control or the other, but by a combination of factors which are likely to act simultaneously and have combined effects (Fitch & Crowe, 2011) which may lead to more severe and unpredictable consequences for coastal ecosystems than individual ones (Breitburg & Riedel, 2005; Crain *et al.*, 2009). Therefore, successful prediction of ecological dynamics within estuarine systems, requires an understanding of causal relationships between hydrology, physicochemical variables, and biotic components (Peterson, 2003; Borja *et al.*, 2008; 2010; Wolanski, & Elliott, 2015).

Based on the model simulations predicted here, it is clear that three common anthropogenic stressors in the coastal environment, river flow, nutrient availability and temperature can combine additively with the potential for interactive effects, and these effects may not be apparent if these stressors are examined in isolation. Interactive effects between increased thermal stress and NH/NL often combined with the influence of extreme river flows were found to be greater (synergistic) when acting on the functional properties of the Tamar (FCI) and the structural (AMI) and resilience (O) properties of the Eden. Contrarily, when the biomass of each system was considered as a whole, the combined impact of stressors (low nutrients + temp Tamar; extreme RF + NH/NL + temperature Eden) in different combinations, produced reduced (antagonistic) effects, increasing overall system biomass. While initially these results may seem counterintuitive, understanding the mechanisms by which each stressor individually drives community or ecosystems response may help to interpret or predict when and where cumulative stressors interact (Folt *et al.*, 1999; Segner *et al.*, 2014). There is now sufficient evidence from small scale studies to suggest that not only are multiple stressor subject to a potential series of higher order interactions (e.g. intensity, timing, duration and spatial extent) but the overall all effects of stressor pairs in similar systems may be disproportionate depending on the effect variables in question and the trophic level under consideration (Nakagawa & Cuthill, 2007; Crain *et al.*, 2008; Griffen *et al.*, 2016). Thus, stressors acting through similar mechanisms may be synergistic (e.g. Russell *et al.*, 2009), while those acting through alternative but dependent pathways may be

antagonistic (e.g. Darling *et al.*, 2010). In this instance, these results are consistent with the interpretation that interaction effects are generally antagonistic at the community or ecosystem level (Crain *et al.*, 2008), resulting from enhanced species interactions within communities that act to dampen and reduce the diffuse impacts caused by multiple stressors (Vinebrooke *et al.*, 2004). However, this study also highlights the need to consider the underlying emergent properties of systems at the community and ecosystem level, as the apparent benefits derived from increased system biomass (or biodiversity), may be concealing a deeper unravelling of food-webs associated with multiple stressor interactions.

Model simulations also predict that the performance and biomass of key consumer groups in both the Tamar and Eden estuary systems are expected to change under such scenarios, but not uniformly. Hence, despite the implementation of mainly negative forcing functions (i.e. that reduce productivity) at the community level many consumer groups in both systems increased in biomass under different stressor combinations. However, these responses were subject to substantial variation between different stressor scenarios within the same system and also showed considerable variation in impact between the same sets of stressors in different systems. For example, benthic invertebrates in the Tamar system increased in biomass under the combined impacts of extreme RF, NL and temperature, but decreased under the same scenario when nutrients were high, in an inverse manner to invertebrates in the Eden system. This high tolerance of the Eden macrofauna to nutrient stress, but not to physical stress has also been recently reported by Kenworthy (2016) who investigated the local environmental context on multiple stressors on Eden benthic assemblages using a series of manipulative field experiments.

While it is encouraging that the results of this long term modelling study correspond to results of more controlled field experiments in the same system, between systems, it is likely that variations in response to different stressors is related to dissimilarities in the way that communities are aggregated (Abarca-Arenas & Ulanowicz, 2002; Pinnegar *et al.*, 2005). This is reflected by the regional differences in community composition and pattern of trophic flows implemented within the relative models (i.e. the relative importance of top-down vs. bottom-up mortality control). As environmental context is likely to modify the influence of biodiversity loss in communities (Geert Hiddink *et al.*, 2009; O'Connor & Crowe, 2005; Boyer *et al.*, 2009; McKie *et al.*, 2009; Crowe *et al.*, 2013), understanding the profile of interaction strengths of individual or multiple stressors on various trophic interactions is likely to be an important factor in determining an ecosystem's future response to climate change (Brown *et al.*, 2013) and one that can only be investigated using a simulated modelling approach such as Ecosim.

Considering the influence of individual and multiple stressors on ecosystem attributes and emergent properties (Figures 5.12 Tamar & 5.13 Eden) two implicit trends were apparent in both systems: 1) an increase of river flow and/or thermal stress (either singularly or in combination) had greatest effects on each systems network characteristics 2) The greatest impacts on each system were when the three stressors were combined. Under the cumulative impact of all three stressors, the ecosystem attributes (A and O) for systems organisation and resilience, indicate that after the fifty year simulated period, each ecosystem was more disturbed, more stressed and experienced greater system flows (TST). The structure related index (AMI), also showed that the internal structures of the food-webs changed from a web-like to a more chain-like structure, where fewer groups were involved in the transfer of energy and flows were constrained thereby channelling energy through a fewer number of specific pathways. Thus, these impacted food-webs are less likely to be buffered against fluctuating environmental conditions (Holling, 1973; Ghedini *et al.*, 2015), with possible reductions in the temporal stability and resilience of key system properties. Synchronously, the recycling index (FCI) showed the benthic components of both ecosystems to conserve less nutrients need more time to recover and channelled more matter directly into detritus.

Furthermore, as the FCI index is considered to be a proxy (see chapter 4 table 4.2) for many of the processes supporting ESs such as carbon sequestration/storage (Beaumont *et al.*, 2014) and the potential for waste/nutrient remediation (Watson *et al.*, 2016), it is also clear that the Tamar and Eden estuaries would suffer serious reductions in the capacity to provide these services under the combined impact of all three stressors. Indeed in the case of the Tamar any addition of stressors was registered to have a negative impact on the cycling capacity of the system, in comparison to the Eden which only exhibited a reduced cycling capacity under the influence of extreme river flows. Overall as changing ecosystem state under the impact of multiple human induced stressors will inevitably have different implications for the provision of a number of marine ESs (Schröter *et al.*, 2005; Mooney *et al.*, 2009; Montoya & Raffaelli, 2010; Scholes, 2016), exploring which stressor pairs deviate from having additive effects may provide insight into when stressor combinations are likely to have the most potent impacts on individual systems (Mothersill *et al.*, 2007; Dunne, 2010; Piggott *et al.*, 2015; Côté *et al.*, 2016).

5.4.2 Management outlook

Although this exercise was not intended to provide guidance regarding the appropriate management responses to anthropogenic or climate change, knowledge of the likelihood of the interactive effects of nutrients and temperature combined with increasing river flows and their potential negative impact of ecosystem properties, illustrates the potential for managing each system under investigation based on the impacts of several stressors. Thus to maintain the specific resilience of each system under the current issues of nutrient pollution, managers and stakeholders need to consider not only the current rates of nutrient loading, but also other interactive effects of human and climatic factors influencing those rates (e.g. Lillebø *et al.*, 2005; Paerl, 2006) . Based on the individual effects of the three stressors measured here, the final year Eden simulations exhibited high specific resilience (based on system overhead and biomass) to all three stressors, in contrast to the Tamar which was more severely impacted under individual stressor combinations.

When considering these results it should be noted that the effects exhibited in this study are only valid when considering the specific combinations of river flow, nutrient availability estimates and temperature within this context. As both the Tamar and Eden estuarine ecosystems are stressed by a broad suite of human activities not addressed here, these too might interact and compound (e.g. Halpern *et al.*, 2008a, b) generating different and unexpected results than those predicted here. This may be particularly true in the Tamar system where disturbance regimes are challenging and uncertain due to the presence of a large array of disturbances (see Chapter 2 section 2.1.4 & 2.4.5), which based on evidence of this study, may be interacting in an antagonistic, synergistic or otherwise unpredictable fashion. In this instance, fruitful understanding and management of such systems may be best achieved by an adaptive research/management framework (e.g. Levin *et al.*, 2009; Atkins *et al.*, 2011) that invests in the general resilience of systems but also in specific resilience until a consensus emerges on what the primary threats to a system are. Ultimately, making decisions about the management of complex systems will involve risks and trade-offs (Rodríguez *et al.*, 2006; Nelson *et al.*, 2009; McShane *et al.*, 2011) with the role of models, such as the ones developed here, to facilitate these hard decisions by making predictions that emphasise the risks and uncertainties involved (Willcock *et al.*, 2016).

From a spatial perspective, although some of the responses to climate change and anthropogenic variables are likely to be generalisable to other similar UK or temperate estuaries, the geographic variation in responses seen here suggest local management efforts might be beneficial, while a more generic adaption strategy might be inefficient or ineffective. While the overall performance and robustness of the ecosystem level indicators generated here are informative on intermediate and long-time scales (Dame & Christian, 2006), such approaches are often difficult to use in annual

assessments as a substantive changes may need to be made to the model parameters as new data become available. Nevertheless, examples of operational use do exist, for example in Europe where the concept of a 'Key run' model (ICES, 2012; 2013) is being used as part of quality assurance procedures for assessing Ecopath and Ecosim models being (or intended to be) used in the provision of advice for management.

The analysis also shows the possibility of a delayed onset of many of the responses to the modelling treatments and the detection of the ecological thresholds of change in each system. While there is little evidence based on the food-web and network indices measured here that either system crossed a fundamental "tipping point", there are clear indications of future increased stress on each system particularly under the combined impact of multiple stressors. As regime shifts have been notoriously difficult to predict because communities often show little to no sign of change before the tipping point is reached (Scheffer *et al.*, 2012; Connell & Ghedini, 2015), it is entirely possible that small changes to the disturbances investigated here may overwhelm the autocatalytic configuration of the systems and hence push them into new and potentially undesirable management states (Côté & Darling, 2010; Möllmann *et al.*, 2011; Parmesan *et al.*, 2013). As the predicted temperature and river flow values used in this study are based on current estimates of climatic change and are therefore conservative and subject to future variation, it is likely that if left unchecked future coastal precipitation and water temperatures will increase at a greater rate than those assumed in this study (Schiermeier, 2010; Lima & Wethey, 2012; Kharin *et al.*, 2013). Such changes are likely to have profound effects on both regional and indeed global future ecosystem health and the flow of ESs, a key challenge for society is now to interact with the marine environment in a sustainable way in order to halt biodiversity loss, promote recovery and prevent abrupt changes in ecosystem structure and functioning (Carpenter *et al.*, 2009; Bellard *et al.*, 2012; Bennett *et al.*, 2015). Understanding the variation in the compounding effects of climate change will be of paramount importance for the prediction of management strategies and the ability to support such adaption measures into policy development and management responses both now and in the future (Halpern 2008a, b: 2009; Chapin *et al.*, 2010; Ban *et al.*, 2010; De Groot *et al.*, 2010; Kenward *et al.*, 2011; Brown *et al.*, 2014; Côté, *et al.*, 2016).

5.4.3 Model assumptions and limitations

As a final point of discussion, improving forecasts of future ecosystem states is one principal goal of climate-change-focused research (Barange *et al.*, 2010; 2016; Stocker *et al.*, 2013; Boersma *et al.*, 2016) and can offer guidance to decision-makers by providing insight into possible futures (Plaganyin & Butterworth, 2004; Fulton *et al.*, 2011; Fulton & Link., 2014; Frost *et al.*, 2016). However, it is also widely accepted that regardless of how much understanding of complex ecosystems we achieve, future ecological predictions will always be laden with significant uncertainties (Cheung *et al.*, 2013;

Knutti & Sedláček., 2013; Guesnet *et al.*, 2015; Elliott *et al.*, 2015; Payne *et al.*, 2015; Clark *et al.*, 2016). Therefore when interpreting the modelled outputs from this study and indeed from all ecosystem models in general, several assumptions and limitations of model capability must be considered.

Firstly, the development of an Ecosim model strongly depends on the quality of data used to build an Ecopath model (Christensen & Walters, 2004) and the accuracy of the Ecosim calibration (Ainsworth & Walters, 2015). The data used to build the current Ecopath baseline models, provides a solid background for dynamic modelling (Chapter 4 section 4.2). In this study for instance, the data for almost all groups (Biomass, P/B, Q/B) were derived from site and time specific raw databases or stock specific assessments. However, for groups that play an important role in the Tamar or Eden estuaries food-web but for which no or very little data was available, i.e. certain macrofauna or meiofauna, their omission from the developed ecological networks may have led to an oversimplification in the structure of all food-web components (Hall *et al.*, 1990). A specific lack of long term continuous biomass monitoring data in both case study areas, particularly for invertebrates and demersal fish, was also a specific limitation in validating historic trends and improving the validity of future predicted outcomes. Moreover, due to lack of specific knowledge, several functional groups have been aggregated, e.g. demersal fish potentially masking important species interactions (Essington, 2007).

As Ecosim is dependent on the mass-balance (equilibrium) assumption of Ecopath, discrepancies such as these may infer the risk of encountering errors in the interpretation of the final Ecosim results, when these are extrapolated far beyond the equilibrium for which Ecopath data are available (Mackinson *et al.*, 1997; Walters *et al.*, 1997). However, using the Monte Carlo routine in Ecosim as a sensitivity analysis (Hill *et al.* 2006) the Ecopath base models used here, were shown to be robust to at least modest (10% SD) variation in input parameter estimates, since each Monte Carlo trial balanced and there was little variation among the ten best trials for each scenario. This indicates that small errors in Ecopath input values would probably not significantly affect Ecosim outcomes.

Although model uncertainty largely concerns model structure, it can also include uncertainties about the values of parameters that determine a model's behaviour (Hill *et al.*, 2007), but are not easily estimated. For instance, due to a lack of specific knowledge, limitations to this specific study may include temporal changes in species diet that might have occurred, alongside the presence of trophic feedbacks and ecological thresholds beyond which anthropogenic effects might act to produce non-linear changes in ecosystem structure and function (Burkett *et al.*, 2005; Van der Putten *et al.*, 2010; Walther, 2010). In this regard important factors that this study did not attempt to represent included the variability of future changing climate forcing/environmental or management regimes the adaptive potential of species and the effects of pathways other than trophic interactions; by which climate

effects might propagate throughout the ecosystem (e.g. by affecting refuge and breeding space, altering animal behaviour, affecting hydrodynamic transports). While some of these uncertainties could be addressed by laboratory experiments and *in situ* monitoring of ecosystem conditions, narrowing the range of error in studies like this one, temporal variations in species-specific habitat factors, e.g. a loss of habitat, cannot be addressed in Ecosim but needs a spatial model (e.g. the Ecospace component of Ecopath with Ecosim, Christensen & Walters, 2004). It should also be noted that the sequence and timing of multiple stressor treatments investigated in this study are based on the assumption that stressors are acting in a simultaneous manner (e.g. Darling & Côté, 2008). While it is acknowledged that stressors may also interact in an asynchronous manner (e.g. Molinos & Donohue, 2011) and that synchrony between stressors does not always lead to the greatest impacts (Molinos & Donohue, 2010), the results present here are still useful and valid in the instances when the particular stressors under investigation co-occur.

Despite the limitations outlined above, the Ecopath with Ecosim modelling routine used here, provides a useful tool, for investigating the complex interactions between all necessary trophic groups and the future consequences of anthropogenically driven changes in two relatively data poor systems. Although a few time series trends were not well emulated, in most instances each regional model reproduced many of the historical time series trends agreeably; as such the models developed here should be viewed as one of the few available approximations of the future state of these ecosystems to date.

5.5 Conclusions

This study revealed that the cumulative nature of localised anthropogenic stressors, including increased river flow and changes in nutrient loading, needs to be analysed in combination with large scale environmental drivers (in this case temperature), ecosystem characteristics and emergent properties as by focusing on one or a subset of properties, key information may be missed and interpretation may be misleading. This encapsulates the holistic approach needed for ecosystem based management (EBM). This study also suggests that multiple anthropogenic stressors can alter the properties of estuarine benthic food webs, with the possibility for stressors to act in an additive, synergistic or antagonistic manner. Overall the effects of increased temperature and river flow were found to be the most pervasive of the three stressors examined, with the greatest impacts in both systems registered when all three stressors combined. Under such circumstances, the simplification in food web structure lead to increased temporal variability of key properties, including an impairment of ecosystem functions (nutrient cycling and carbon cycling) and system resilience (adaptive capacity),

which leaves each system more vulnerable to human- or climate-induced perturbations in the long term (Worm & Duffy, 2003; Folke *et al.*, 2004; Vallina & Le Quéré, 2011).

It is increasingly clear that anthropogenic or climate change impacts cannot be fully estimated without incorporating an understanding of simultaneous changes to the stocks, demands and flows of biodiversity, ecosystem functions and ESs on different spatial and temporal scales (Bellard *et al.*, 2012; Warren *et al.*, 2013). This chapter provides a “standard” setup to aid understanding of a specific a model framework that integrates knowledge of how multiple stressor interactions are likely to impact on elements of biodiversity, ecosystem functioning, ESs and resilience within a common framework, and the results that can potentially emerge. Although there are many provisos regarding the quantitative and qualitative nature of the responses predicted by these model simulations, by taking account of model parameter uncertainty and undertaking specific performance evaluations it is likely the results presented here are robust to assumptions on the additivity of climate effects and on model structure and parameterisation. Hence the modelling approach used here also offers a prospectus for future multiple stressor empirical and modelling research.

While the Ecosim modelling platform used here has a long legacy in the investigation of cumulative impacts, as a strategic tool to explore ecosystem dynamics and to test general management approaches (Colléter *et al.*, 2015), it is also accepted that it may not be suited to all problems (Heymans *et al.*, 2016). As a consequence it should not be the only tool used in the application of EBM and multiple stressor research. Comparing ensemble predictions of ecosystem responses to changes from multiple models, and integrating these frameworks with knowledge of multiple stressor impacts at lower levels of organisation, is likely to be highly instructive, both for the system of interest and in addressing key knowledge gaps in marine ecosystem research (Fulton & Smith, 2004; Hyder *et al.*, 2015; Ianelli *et al.*, 2015). Emerging models exploring the synergistic dual exposure of marine ecosystems to climate change and human activity for example, are likely to play a critical role in highlighting how ecological feedbacks and human behavioural responses can derail adaptive management processes. Such tools will also provide vital advice and evidence to scientists, policymakers and environmental managers aiming to combat multiple stressor impacts in other similar environmental systems and contexts.

Table 5.6 Verification of questions set at the beginning of the chapter Accept ✓ or reject X

Hypotheses	Description	Tamar	Eden
Q1	Would the combination of stressors act to negatively alter the future structure, functioning and/or resilience of the respective food chains? (Tamar/Eden).	✓	✓
Q2	H2: Do different combinations of stressors (river flow, nutrient inputs and thermal stress) act in a non-additive manner? and is there a difference between each system? (Tamar/Eden)	✓	✓

Chapter 6: Holistic modelling approaches for defining sustainable and resilient boundaries in marine systems under the impacts of multiple climate stressors.

Chapter Summary

Having described how an ecological network approach might be suitable to account for some of the complex facets of ecosystem health/status (i.e. structure, function, resilience and the provision of ESs) under the impacts of anthropogenic changes (Chapters 4/5), the aim of this chapter was to explore how the numeric values derived from the Ecopath and Ecosim models could be linked together and further developed with more conceptual and predictive modelling approaches (i.e. Ulanowicz's "Window of Vitality" and Bayesian Belief Networks). This contribution thus aims to show ways of gathering, representing and visualising modelling outputs to enable better decision making based on available knowledge, along with how this type of approach could be applied to support management actions within real-world systems.

6.1 Introduction

Despite the complex nature of real-world systems, environmental managers often desire simplified outputs, before taking the necessary action which may prevent irreversible thresholds and boundaries being crossed, where system characteristics and functions fundamentally change (Rockström *et al.*, 2009; Levin & Möllmann, 2015). As global and natural resources must also be managed sustainably to ensure the continued provision of human well-being, a further quandary for managers and policy makers is deciding between different competing management strategies and policy options for bundles of desired ESs (Rodríguez *et al.*, 2006; Raudsepp-Hearne *et al.*, 2010). Such decisions are often difficult, because the cumulative and complex impacts produced by anthropogenic activities, often vary according to the intensity, number and spatial and temporal scales of the associated pressures. Such changes inevitably come with changing biodiversity and hence the functioning of the system, possibly beyond its normal, safe operating limits (Raffaelli, 2016). Hence as stated by Elliott (2002) "*There is an increasing need to demonstrate, quantify and predict the effects of human activities on these interrelated components in space and time*".

In such complex systems a modelling approach is often advocated to better understand the mechanisms regulating ecological processes (Jansson *et al.*, 2005). Conceptual models for example, can be regarded as diagrams which bring together and summarise information from many research areas and are frequently used in aquatic ecosystems to conduct qualitative ecological risk assessments (ERAs) and more broadly in integrating science and management interactions (Ojeda-Martínez *et al.*, 2009; Kelble *et al.*, 2013; Smith *et al.*, 2016). These models provide a useful focus for scientists and

environmental managers by deconstructing problems and allowing stakeholders to conceptualise and visualise large complex socio-ecological systems using an understanding of smaller-scale social and ecological processes (Mylopoulos, 1992). Such models may range from simple to dauntingly complex diagrams (e.g. horrendograms (Boyes & Elliott, 2014)) and provide the starting point for developing more quantitative and numerical models. While there are numerous examples of conceptual models or “research frameworks” currently circulating in the scientific literature (see Skondras & Karavitis, 2014 and references therein), in recent years, Pressure-State-Response (P-S-R) frameworks (e.g. DPSIR; see Atkins *et al.*, 2011 for the Ecosystem Services and Societal Benefits linked DPSIR approach) have been central to conceptualising marine ecosystem issues. The DPSIR framework for instance provides some structure to the way that complex issues can be conceptualised in a standard way (Patrício *et al.*, 2016). Currently, however, many conceptual models (including P-S-R frameworks) often encounter difficulties when dealing with cumulative impacts, in particular with multiple simultaneous pressures, which more often occur in multi-use and multi-user areas (Wilcock *et al.*, 2016). For example, numerous drivers could interact and cause a solitary pressure, altering the state but causing multiple impacts and responses (Atkins *et al.*, 2011).

While work is now underway to begin to accommodate multidimensional relationships between human activities, pressures and state changes (e.g. Smith *et al.*, 2014), the diverse nature of stressors on marine systems will also require conceptual models to be linked together and further developed towards numerical and predictive models. In particular, an improved understanding of the interactions between drivers, pressures (stressors) and ecosystem state (i.e. in the case of DPSIR the pressure-state change (P-S) linkage) is important to help facilitate consideration of possible risk management responses. Furthermore, even-though there has been a burgeoning interest in initiatives aiming to clarify the links between biodiversity—ecosystem functions—ecosystem services—human well-being, there is still a need for integrating knowledge obtained by various research methods in a manner that is useful for environmental decision makers.

6.2 Model concepts and theory

6.2.1 A systems approach to defining operational bounds of resilience for aquatic ecosystems. Ulanowicz’s “Window of Vitality”

Systems approaches using ecological network analysis have a long history in marine ecology (reviewed in Raffaelli & White, 2013; Raffaelli & Frid, 2010; Jorgensen *et al.*, 2007) and as illustrated in previous chapters of this thesis (Chapters 4 & 5) are well suited to experimentally exploring the consequences of large scale changes in the different elements that provide ESs under the impact of different anthropogenic stressors. However, despite a wealth of literature on relevant theory and concepts such

as resilience, stability, robustness, sustainability and persistence, practical application of this knowledge and understanding to real-world management is still lacking (Raffielli, 2015). Part of the reason for this is that environmental managers of seascapes and landscapes often need to know if a particular model projection (or policy option) that changes several species and ESs within a system will push the system being managed into a potentially unsafe state (i.e. whether any new system state is sustainable). Thus, scientists and managers invested in considering a whole-systems approach may not be interested in the marginal changes of all species (Donohue *et al.*, 2013), but instead whether the system is capable of accommodating potential changes while retaining its capacity to function and provide bundles of desired services while remaining within its “safe-operating” space, and hence is resilient (Raffielli, 2016).

While it should be accepted that no single descriptor can fully accommodate the multifaceted nature of ecosystem resilience (Ulanowicz., 1992), one possible way to derive system-level measures of resilience, is to adopt a holistic systems approach rather than trying to measure the independent trajectories of several indicators. In particular, Ulanowicz (2011) has argued that the network metric, “ascendency,” has a restricted set of values for real-world ecosystems (Figure 6.1) where a system lacking ascendency has neither the extent of activity nor the internal organization needed to function sustainably. By contrast, systems that are so tightly constrained and honed to a particular environment appear “brittle” (in the sense of Holling (1986)) are prone to collapse in the face of even minor novel disturbances (Ulanowicz *et al.*, 2009). Systems that endure – that is, are sustainable – lie somewhere between these extremes, with such networks falling within a “Window of Vitality” (Ulanowicz, 2005).

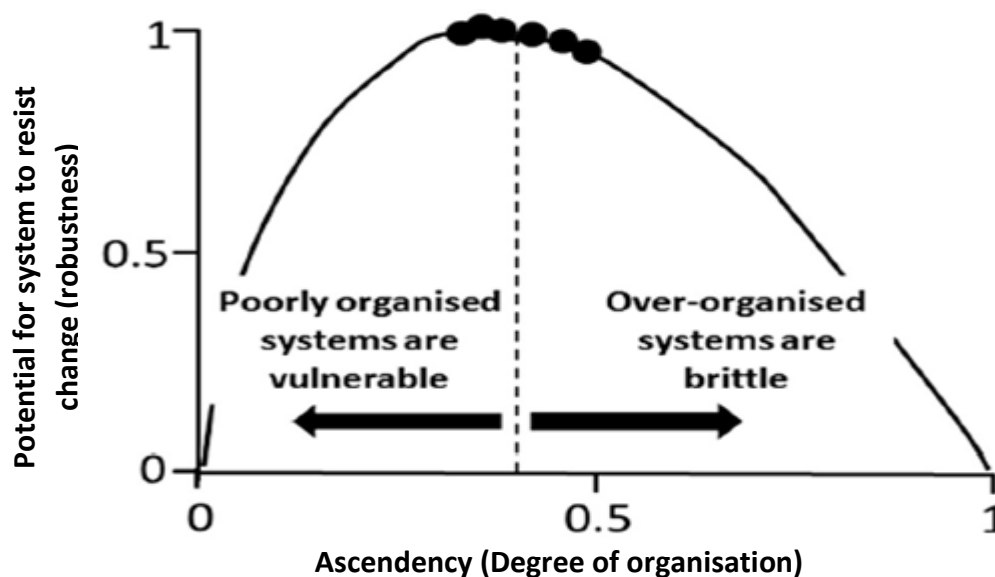


Figure 6.1 Ecological networks are only robust for limited bounds of ascendency. From Raffaelli (2015)

Further, Zorach & Ulanowicz (2003) have demonstrated that such connexions within the “Window of Vitality” can be adequately captured using more easily measured metrics such as the topological properties of networks (Figure 6.2). Thus by plotting such variables, scientists and managers can make *a priori* predictions about the preferential loss or reduction of stocks (e.g. species, populations, communities), against the effects on ecosystem functioning and the ultimate provisioning of ES and benefits in relation to a “safe operating space” (Raffaelli, 2015; 2016). Such an approach also allows trade-offs between different network configurations that support different management and policy options be considered (e.g. under the impacts of different climate stressors). In this way different modelling scenarios or management choices can be assessed in a cost effective and canonical way, without the need to disturb natural ecosystems (Dunne & Williams, 2009).

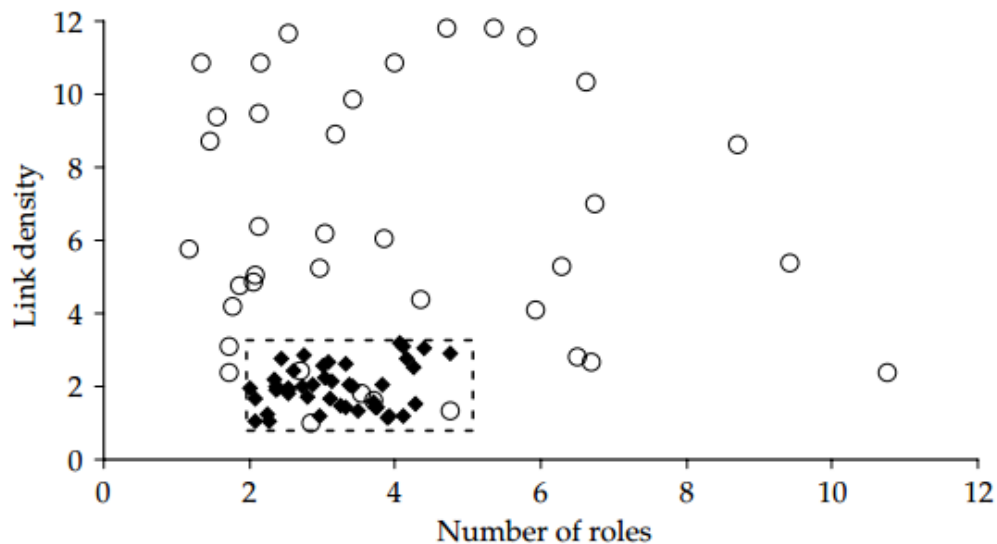


Figure 6.2 The safe operating zone or “Window of Vitality” (delineated by dotted lines) defined by ascendancy considerations for real (diamonds) and random networks (open circles) may be captured by two simple topological properties of food webs: linkage density and number of trophic roles (levels). From Ulanowicz, (2005).

6.2.2 Managing decisions under uncertainty using Bayesian Belief Networks.

While ecological network approaches to whole ecosystem modelling have a long legacy, Bayesian Belief Networks (BBNs; also referred to as Bayesian networks, belief networks, causal nets, causal probabilistic networks, probabilistic cause effect models, and graphical probability networks) are a relatively new modelling approach that are increasingly being applied to marine assessments (Nojavan *et al.*, 2014; McDonald *et al.*, 2015; Uusitalo *et al.*, 2015). BBNs are useful because they offer a pragmatic and scientifically credible approach to modelling complex ecological systems and problems, where substantial uncertainties exist (Smith *et al.*, 2016). They are particularly useful when indicator data are scarce and uncertainty is high, making them prospectively useful tools to investigate the

complex impacts of multiple stressors at large spatial scales. When addressing uncertainty, BBN methods employ assessments of probabilities, with graphically represented casual relationships (or nodes) being used to represent the decision maker risk preferences (McCann, 2006). By representing different potential outcomes of model options with probabilities, they explicitly allow uncertainty and variability to be accommodated in model predictions (Barnard & Boyes, 2013) thus allowing managers to rank management options according to decisions that will most likely lead to desired outcomes. They therefore, show high promise in adaptive management being iterative and especially in being able to mix and use both empirical data and expert knowledge.

Although not valuation methods as such, BBN tools have also gained increasing importance in environmental and socio-ecological modelling research (Schmolke *et al.*, 2010; Carriger & Barron, 2011; Fletcher *et al.*, 2014) by incorporating the findings of assessment and economic valuation exercises to support the decision makers in making trade-offs and choices between resources and their use (Matthies *et al.*, 2007; Bagstad *et al.*, 2013). More recently BBNs have been used in quantitative and qualitative modelling research on ES (Haines-Young, 2011; Landuyt *et al.*, 2013; Poppenborg & Koellner, 2014) and in conceptualising biodiversity—ecosystem functions—ecosystem services—human well-being relationships (Pascual *et al.*, 2016). Notwithstanding their potential, the number of applications of BBNs in marine modelling is still an underutilised area of research (Landuyt *et al.*, 2013), however in future it is expected that they will be used to a greater extent.

6.2.3 Study aim

The two approaches described above were applied, with respect to two aquatic systems (The Tamar and Eden estuaries) which historically have experienced large-scale shifts in its biodiversity and functioning. Here I pose three major questions:

- I. Using the previously constructed Ecopath models of the Tamar and Eden systems (Chapter 4), further network properties were calculated to examine where both systems could be placed with regards to their “safe operational space”, in relation to Ulanowicz’s (2005) “Window of Vitality”.
- II. Using the deterministic Ecosim models and probabilistic future scenarios developed in (Chapter 5), further network properties were calculated to assess how far the system is likely to move from its operational space under the impact of single and multiple stressors (i.e. whether the system exhibits resilience).
- III. Finally the Ecosim models and their associated future scenarios (chapter 5) were used as a basis to develop a single BBN for each system, to highlight the possibility for management trade-offs under the impact of multiple climate stressors.

Details of the two assessment tools used in this analysis, including the dynamic ecosystem models (Ecopath and Ecosim) and BBNs are described below followed by a discussion as to their effectiveness and possibility to be integrated within more holistic research frameworks.

6.3 Modelling approach

6.3.1 Calculating past and future operational boundaries (Ecopath and Ecosim)

Having already calculated the ascendancy and overhead indices necessary to estimate each systems past (Chapter 4 section 4.2 and 4.3) and predicted future positions (Chapter 5 section 5.2 and 5.3) relative to Ulanowicz’s “Window of Vitality” (Ulanowicz, 2005), the subsequent variables linkage density and number of trophic levels were estimated after Zorach & Ulanowicz (2003). Linkage density was calculated for each system period as:

$$LB = b^{OH2} \quad \text{Equation 6.1}$$

Where b is food web connectivity and OH is system overhead. The number of trophic levels in each system also estimated as b^A , where A is ascendancy. The exact dimensions for plotting Ulanowicz’s “Window of Vitality” were taken from Ulanowicz *et al.*, (2007) with points clustering within a rectangle that is bounded roughly in the vertical direction (by $c = 1$ and $c \approx 3.01$ and horizontally by $n = 2$ and $n \approx 4.5-4.9$ where (c) is combinations of link-density and (n) is number of effective trophic roles). A full heuristic description of each boundaries criteria is given by the authors but for context is summarised in Table 6.1.

Table 6.1 The boundary delimiting criteria for Ulanowicz’s “Window of Vitality” from Ulanowicz *et al.* (2007)

Boundary	Description
Lower	$c > 1$ says simply that the networks being considered are all fully connected. Any value $c < 1$ would imply that the graph is separated into non-communicating sub-networks.
Upper	The boundary delimiting maximal link-density, $c \approx 3.01$, is the result of applying the May–Wigner stability hypothesis in its information-theoretic homolog. The precise theoretical value of the boundary, as derived by Ulanowicz, is $c = e^{(3/e)}$.
Left	$n > 2$ for all ecosystem networks, because it is in the very definition of an ecosystem that it encompass complementary processes, such as oxidation/reduction reactions or autotrophy/ heterotrophy interactions.
Right	Only the right boundary remains largely unexplained and is based on the observations that one never encounters trophic pathways greater than 5 in nature.

6.3.2 Bayesian Belief Networks

The choice of creating a Bayesian Belief Network (BBN) for each system in this study was motivated by the graphical representation component that BBN's incorporate (which facilitates bidirectional interactions that can be useful in management and science (Chan *et al.*, 2010) as well as the predictive possibilities that BBN's provide for explicitly handling information uncertainties, particularly when comparing complex and multi-state ecosystems (Henriksen *et al.*, 2007). More specifically the BBN approach proved useful in this particular study, by incorporating and compiling qualitative and quantitative data from long term model simulations, in a way in which uncertainties are made explicit and their influence on the level of risk to environmental values is quantified.

In order to show how the information previously calculated from Ecopath (chapter 4) and Ecosim (chapter 5) could be used in connection with a BBN approach, here I constructed two simplified BBN models which estimate a hypothetical "Benthic Estuarine and Coastal Biodiversity Impact Index". This is a qualitative index representing the negative impact that certain abiotic components (i.e. river-flow, temperature and nutrient loading) have on the biodiversity of an estuarine ecosystem, as well as showing how variations in these abiotic components might impact on a number of ecosystem-based indicators (e.g. structure, resilience, functional processes, capacity to provide ESs) and thus, the overall state and/or health of an ecosystem. The index is represented as a five-point scale rank node which can take one of five values ranging between [0–1] (named as Very Low; Low; Medium; High; Very High) and with an underlying interval of 0.2 between the states. In this context, the final output of the BBN models fulfils the current criteria for indicator selection needed by the Water Framework Directive (WFD) in the pursuit of "Good Ecological (GECS) and chemical (GCS) Status". In particular, since the identification of simple indicators able to assess the health of highly dynamic and complex interactions is difficult (Borja *et al.*, 2010), this analysis has particular relevance to descriptors which focus on marine food webs, which are often accredited to be one of the most challenging to implement (Rombouts *et al.*, 2013). In part this is because the interactions between species in a food web are complex and constantly changing, making it difficult to identify one condition that represents "good" status. Therefore, by considering several emergent properties and energy flows through each investigated food web, this analysis aimed to provide a holistic metric which could be used to provide a broad overview of an ecosystems status integrated across a number of different trophic groups. As it is likely that many pressures will need to be considered in the development of such measures, this analysis also highlights how cumulative effects of multiple activities can be incorporated.

Since one of the hallmarks of best-practice in the development of BBNs, is the iterative development of a conceptual diagram which the aims of the model, variables and sources of information are identified (Daly *et al.*, 2011; Chen & Pollino, 2012; Aguilera *et al.*, 2013), this was the approach taken

here. An example of the conceptual diagram for both the Tamar and Eden estuaries is given in Figure 6.3.

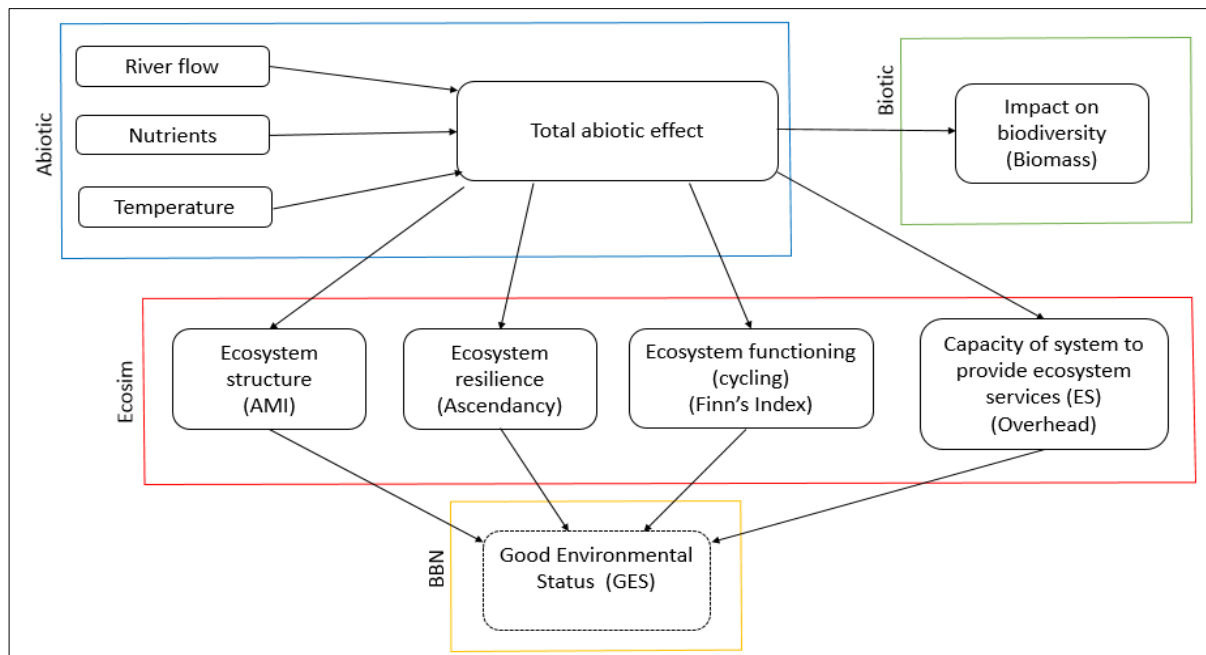


Figure 6.3 Conceptual diagram to illustrate the relationship between food web functioning and anthropogenic stressors as a framework for developing holistic food web indicators of GES.

Following development of the conceptual diagram, BBNs for each system were built by converting the conceptual information into a network of nodes (variables) containing a number of possible outcomes called 'states' using the AgenaRisk software. This software was chosen as it allows the development of hybrid BBNs, which permits the user to specify numeric nodes, which can be continuous or discrete (being the rank node of a particular type of discrete nodes). Hence, even though some of the ecosystem-based indicators derived from Ecosim are naturally attributed to continuous variables for simplicity purposes, they were expressed as discrete nodes (i.e. 0-1) to enable more powerful computations. The network analysis indicators used to examine the status of the two ecosystems as were chosen based on the operational Good Environmental Status (GES) definition proposed by the DEVOTES project (Borja *et al.*, 2015) stated as *"GES is achieved when physicochemical (including contaminants, litter and noise) and hydrographical conditions are maintained at a level where the structuring components of the ecosystem are present and functioning, enabling the system to be resistant (ability to withstand stress) and resilient (ability to recover after a stressor) to harmful effects of human pressures/activities/impacts, where they maintain and provide the ecosystem services that deliver societal benefits in a sustainable way (i.e. that pressures associated with uses cumulatively do not hinder the ecosystem components in order to retain their natural diversity, productivity and dynamic ecological processes, and where recovery is rapid and sustained if a use cases)"*. The reasoning for using this definition, as opposed to the WFD standard definition, was that although implicitly the current WFD framework requires ESs and societal benefits to be delivered (Atkins *et al.*,

2011), the descriptors and their proposed criteria do not mention these aspects (European Commission, 2010). As developing biodiversity assessments able to link GES and ES provision with the sustainable management of detrimental human activities is a desirable attribute for many environmental managers (Borja *et al.*, 2013;2014), the systems indices chosen to represent GES and the capacity for systems to provide ES is given in table 6.2. A more detailed description of each of these indicators is also given in chapter 4 (section 4.3.9).

Table 6.2 Description of the system and network indices used to represent GES and GCS in the Tamar and Eden Bayesian Belief Networks

System and network indices	Description of indices in relation to DEVOTES GES definition	Units
Systems average mutual information (AMI)	Represents how the flows of a system are arranged and measures if the structuring components of the ecosystem are present and functioning.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.
Ascendency (A)	Represents resilience or ability of a system to recover after the harmful effects of human pressures/activities/impacts. For example, ecosystems safely operate within a 'window of vitality' with respect to ascendency (Ulanowicz, 2002, 2005), too low a value and the system tends to disorder, having insufficient cohesiveness; too high a value and the system becomes very vulnerable to stressors.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.
Overhead (O)	Represents the capacity of a system to withstand stress (i.e. resistance). Higher system overheads indicate that a system has a larger amount of energy in reserve (in flowbits) with which it can use to resist stressor impacts (Ulanowicz, 1986). In the present context, system overhead could be viewed as the degree to which capital stocks are able to continue to provide flows of services.	Flowbits or the product of flow (e.g., t/km ² /year) and bits. Here the 'bit' is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.
Finns Index (FCI)	Represents the capacity of the system to provide the functions of carbon and nutrient cycling and quantifies as one of Odum's (1969) 24 properties of system maturity and stress (Christensen 1995).	% of total system throughput cycled.

In AgenaRisk, nodes are linked by arrows (or arcs). Conditionally independent parent nodes within the network are nodes that have no incoming arrows (e.g. river flow, nutrients and temperature in Figure 6.3). Nodes with incoming and outgoing nodes are termed child nodes (e.g. total abiotic effect in Figure 6.3), and nodes with only incoming arrows are output child nodes (e.g. GES in Figure 6.3) (McCann *et al.*, 2006). The causal relationships depicted in Figure 6.3 infer that the probabilities of each state occurring in the independent parent nodes influence the probability of each state occurring in the dependent child nodes (and the subsequent output nodes (Borsuk *et al.*, 2004). However, while it is acknowledged that the conceptual networks and resulting BBNs constructed from Figure 6.3 are a simplified view of the complex reality of real world systems, the aim of joining a deterministic modelling approach with a stochastic methodology is simply to demonstrate the usefulness of representing and modelling the linkages between biodiversity—ecosystem functions—ecosystem services—human well-being and how trade-offs between these variables can be made in a sustainable manner. Therefore, while some of the variables (e.g. biodiversity) were key components in the computation of the ecosystem-based indicators using Ecosim, the subsequent BBNs were developed on the basis of a “divide and conquer” approach. In this manner the complexity of the model is managed by subdividing key variables into objects which are then interlinked (Fenton & Neil, 2013). The complete network thus represents a full joint probability distribution, whereby the underlying theoretical framework (Bayes theorem), ensures that, even though the directed network seems to suggest a unidirectional influence, cause and effect dependencies are mathematically equivalent (Spiegelhalter *et al.*, 1993). As influence can be propagated in both directions in the network, choosing one over the other does not restrict the existing dependencies between factors under consideration (Fenton & Neil, 2013). Furthermore, the modelling algorithm of AgenaRisk efficiently combines dynamic discretisation with robust propagation algorithms on junction trees structures (Neil *et al.*, 2007) which can be used to update the marginal probabilities for each node and allows model construction and testing to be carried out easily. A glossary of the terminology used throughout to describe the BBN models is included in Appendix 6A

Once the conditional structure of the casual links, nodes and states within the model have been determined, the model must learn (or be configured) from Conditional Probability Tables (CPTs) through the input of *a priori* data (Chan *et al.*, 2012). The information on the set of abiotic and biotic factors that needed to be part of each model were obtained from the output values from the ten scenarios used to parameterise and test each systems deterministic and possible future state in Chapter 5. The different scenarios and their changing factors parameterised are outlined in Table 6.3, with full details of the resulting parameters used in the development of the BBN’s detailed in Chapter 5 section 5.3.2, 5.3.3.

Table 6.3 The twelve alternative scenarios and changing factors parameterised and compared by the long-term simulations for the Tamar and Eden estuaries ✓ and X indicate if a factor is included and not included respectively.

Scenarios	Extreme river low	Nutrients high	Nutrients low	Temperature high
Baseline river flow	X	X	X	X
Baseline river flow and nutrients high	X	✓	X	X
Baseline river flow and nutrients low	X	X	✓	X
Baseline river flow and temperature	X	X	X	✓
Baseline river flow and nutrients high and temperature	X	✓	X	✓
Baseline river flow and nutrients low and temperature	X	X	✓	✓
Extreme river flow	✓	X	X	X
Extreme river flow and nutrients high	✓	✓	X	X
Extreme river flow and nutrients low	✓	X	✓	X
Extreme river flow and temperature	✓	X	X	✓
Extreme river flow and nutrients high and temperature	✓	✓	X	✓
Extreme river flow and nutrients low and temperature	✓	X	✓	✓

The resulting BBN models, include 10 nodes: 3 parent nodes (river-flow; nutrients; temperature), 6 child nodes (impact on biodiversity, ecosystem structure; resilience, functioning and capacity to provide ecosystem services) and 1 output child node (GES). Further information on the partitioned expressions used in the nodes to specify their Node Probability Tables (NPT) with explanatory notes for each network node as well as details of the components selected to build the BBN model are included in Appendix 6B. For the purpose of validating each model, each scenario was compared by capturing the effect the evidence had on the model’s output as reflected by the values of the “Good Environmental Status” index.

6.4 Ecopath with Ecosim results and discussion

6.4.1 Operational bounds under different policy options (Ecopath)

In chapter 4, the Tamar and Eden networks were analysed for a range of ecosystem level attributes using the mass-balance software Ecopath. Following large scale changes in biodiversity regimes, as a result of a shift towards a production policy option for agriculture in the Eden catchment (1999-2015) and a combination of multiple water quality improvement initiatives in the Tamar Estuary (1992-2005), ascendancy was very different in the two periods (Table 6.4). Based on Ulanowicz’s (1980;1986) unambiguous, quantitative definition of eutrophication stated in terms of ascendancy theory as “any increase in system ascendancy due to a rise in total system throughput that more than compensates for a concomitant fall in the mutual information of the flow network” both the systems

exhibited augmented periods of enrichment during the 1990's. This was followed by a reduction in ascendancy perimeters to values more typical for less perturbed estuarine systems (Baird & Ulanowicz, 1993).

Table 6.4 Network properties of the Tamar and Eden estuary systems in eutrophic (Tamar 1990; Eden 1999) and post-eutrophic periods (Tamar 1992, 2005; Eden 2015)

Tamar	Ascendancy	Linkage Density	Number of Trophic Levels
1990	75734	2.440	4.879
1992	78565	2.448	4.895
2005	29077	2.232	4.464
Eden	Ascendancy	Linkage Density	Number of Trophic Levels
1999	64431	2.667	4.809
2015	22980	2.504	4.361

Encompassing the changes in ascendancy for the Tamar and Eden time periods within Ulanowicz's "Window of Vitality", linkage density and number of trophic levels were also very different between the pre- and post-management periods (Table 6. 4). This would locate the post-management Tamar and Eden periods within the right-hand boundary of the box in Figure 6.4 and 6.5. In contrast, during the high nutrient periods in both systems graduated towards the top right area of the perimeter space, with the Tamar effectively moving close to leaving the defined "safe operating zone". Under such circumstances it might be surmised that plotting any system too close to any of the four boundaries could be approaching their limits of stability for one reason or another, while those systems most distant from the boundaries are those most likely to remain sustainable (Ulanowicz *et al.*, 2007). Therefore, based on the network measures calculated here, it would indicate that the Eden system was able to accommodate historic large scales effects of changes in nutrient loading, primary production, and invertebrate and bird biomasses over the investigated periods, while the Tamar was operating in a relatively unsustainable state in the 1990's and relative to its less disturbed state in 2005. Implications for the Tamar in its high nutrient state would suggest that some autocatalytic pathways may have narrowed, leaving the system more 'brittle' (see Figure 6.1) with insufficient reserves to persist in the face of novel disturbances (Ulanowicz, 2002). Subsequently both systems have moved closer to the geometric centre of the window ($c = 1.25$ and $n = 3.25$) which represents the best possible configuration for system sustainability (Ulanowicz *et al.*, 2009).

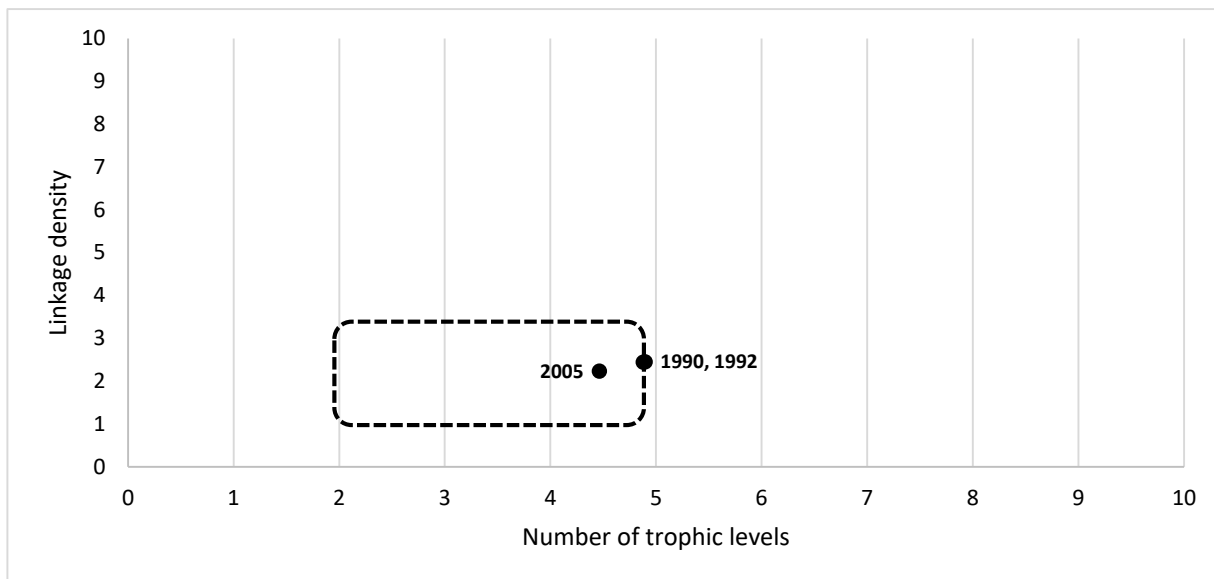


Figure 6.4 The “safe operating zone” for the Tamar Estuary (delineated by dotted lines) defined by ascendancy considerations and captured by two simple topological properties of food webs: linkage density and number of trophic levels.

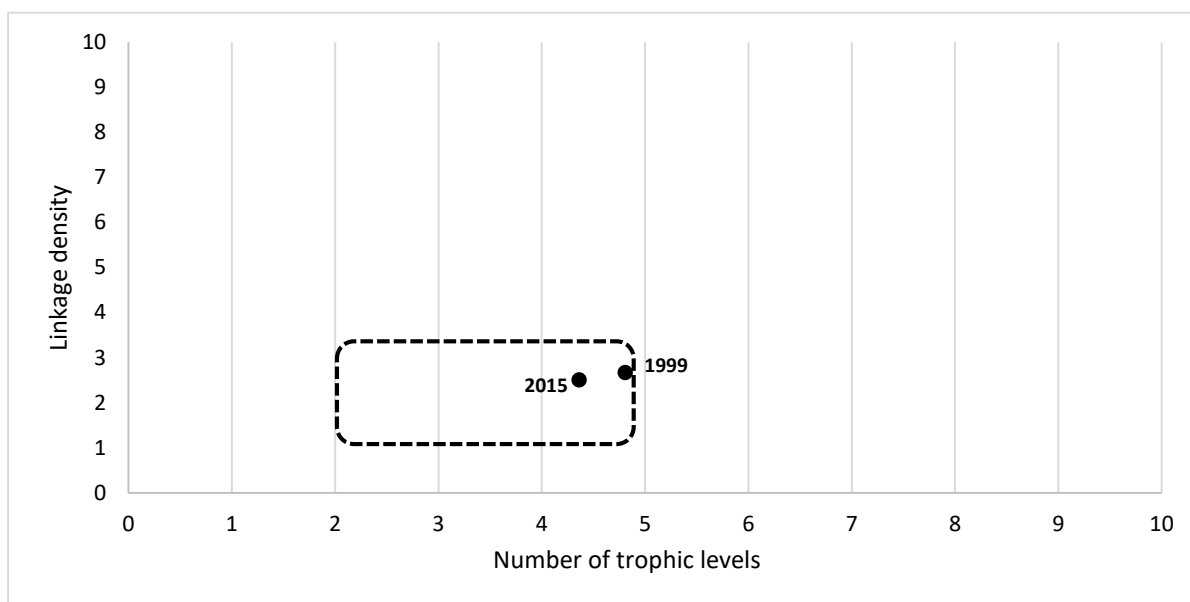


Figure 6.5 The “safe operating zone” for the Eden Estuary (delineated by dotted lines) defined by ascendancy considerations and captured by two simple topological properties of food webs: linkage density and number of trophic levels.

Overall, the system resilience measures used here suggest that large scale shifts in biodiversity did not move the systems out of their safe space *per se*, which might give grounds for optimism of traditionally poorly managed systems such as estuaries (Leschine *et al.*, 2003; Elliott & Whitfield, 2011) and their ability to function. Nonetheless, both versions of the Tamar and Eden networks were precariously close to the “safe” operational boundary during the high nutrient periods and still remain just on the right of the Ulanowicz’s ascendancy curve, and at the top left corner of his “Window of Vitality”. Heretofore, this analysis presents theoretical justification that efforts to reduce nutrient inputs into

the estuaries has had a positive effect on the overall resilience of each system, but also highlights the need to continue to monitor and maintain nutrient inputs at sustainable levels. The question remains as to whether future additional stressors acting orthogonally or synergistically with changes in nutrient loading (e.g. increased river flow or temperatures) could push the systems out of their safe space.

6.4.2 Operational bounds under multiple stressor combinations (Ecosim)

Following the evidence in Chapter 5, that future stressors to the Tamar and Eden catchments will likely alter and erode the resilience, functioning and structure of the associated ecological networks, linkage density and number of trophic levels were subsequently calculated (Table 6.5 & 6.6) to test the theory of how far systems like the Tamar and Eden estuaries can be changed before they slip out of their pre-defined “safe operational space”.

Table 6.5 Future network properties of the Tamar Estuary in 2055. See chapter 5 section 5.2.4 for a full description of the twelve alternative modelling scenarios. RF (River flow), NL (nutrients low) and NH (nutrients high).

Model scenarios	Ascendency	Linkage density	Number of trophic levels
Baseline RF	23169	2.54	4.36
Baseline RF + NL	40763	2.32	4.61
Baseline RF + NH	40351	2.30	4.61
Baseline RF + Temp	41147	2.10	4.61
Baseline RF + NL + Temp	36445	2.20	4.56
Baseline RF + NH + Temp	42392	2.09	4.63
Extreme RF	43631	2.21	4.64
ExtremeRF + NL	43924	2.21	4.64
Extreme RF + NH	43631	2.21	4.64
Extreme RF + Temp	78320	2.06	4.89
Extreme RF + NL + Temp	40162	2.11	4.60
Extreme RF + NH + Temp	40145	2.11	4.60

In the case of the Tamar, the addition of stressors in isolation or in combination all had the same effect of shifting the system towards the centre right area of the “Window of Vitality’s” perimeter space (Figure 6.6), suggesting that any addition of stress is likely to push the system closer to leaving the right hand boundary. This combined with the relatively large increases in ascendency exhibited by all future system states under stress suggest the system will be more “brittle” to novel disturbances (see Figure 6.1), particularly under the observed effects of increasing river flows and temperature. The important point of course from a management perspective is that, despite the observed shift in ecosystem attributes, the system is still operating in a sustainable manner within the prescribed “Window of Vitality”.

Table 6. 6 Future network properties of the Eden Estuary in 2065. See Chapter 5 section 5.2.4 for a full description of the twelve alternative modelling scenarios. RF (River flow), NL (nutrients low) and NH (nutrients high).

Model scenarios	Ascendency	Linkage density	Number of trophic levels
Baseline RF	23911	2.65	4.38
Baseline RF + NL	23264	2.58	4.37
Baseline RF + NH	23246	2.58	4.37
Baseline RF + Temp	23770	3.32	4.38
Baseline RF + NL + Temp	22129	2.44	4.34
Baseline RF + NH + Temp	21884	2.42	4.34
Extreme RF	24319	3.31	4.39
ExtremeRF + NL	25219	2.63	4.40
Extreme RF + NH	24314	2.64	4.39
Extreme RF + Temp	25151	3.31	4.40
Extreme RF + NL + Temp	25219	3.49	4.40
Extreme RF + NH + Temp	25207	3.44	4.40

Contrary to the Tamar, in the Eden system, while number of trophic levels remained similar throughout the scenarios, linkage density varied considerably (Table 6.6). In particular under the effects of extreme variations in river-flow, acting in isolation or concomitantly with nutrients (high and low) and temperature, the Eden configurations moved beyond the upper boundaries of the safe operating zone (Figure 6.7). Under such conditions the Eden system would be aligned with the May–Wigner stability hypothesis (May., 1972) in its information-theoretic homolog (Ulanowicz., 2002) that suggests that large complex systems which are assembled (connected) at random may be expected to be stable up to a certain critical level of connectance, and then, as this increases, to suddenly become unstable. While there is little other evidence of an erosion of system organisation based on the ascendency measures calculated here for the Eden system, it has been compellingly demonstrated in the scientific literature (Scheffer *et al.*, 2009; 2012; Hughes *et al.*, 2013; Dakos *et al.*, 2015; Kelly *et al.*, 2015) that systems can often appear to be within “safe” operating limits before they cross tipping points that are essentially non-reversible (i.e. exhibit hysteresis dynamics).

As such, when combined with the network indices calculated in the previous chapter (5), the analysis presented here can be used to establish just how far systems like the Tamar and Eden can be changed before they slip out of that safe space, and what the system’s dynamics would be when they enter “unsafe” space. This methodology consequently provides a useful guide towards achieving future sustainable communities and identifying the possibility for tipping points in complex ecological systems under the impacts of multiple stressors. While I have adopted a deterministic modelling approach to simulate future ecosystem states, equally this approach could be applied in a continuous

manner (Raffaelli, 2016) whereby the trajectory of the system of interest could be monitored over time with respect to its safe operational bounds and policy interventions applied as necessary.

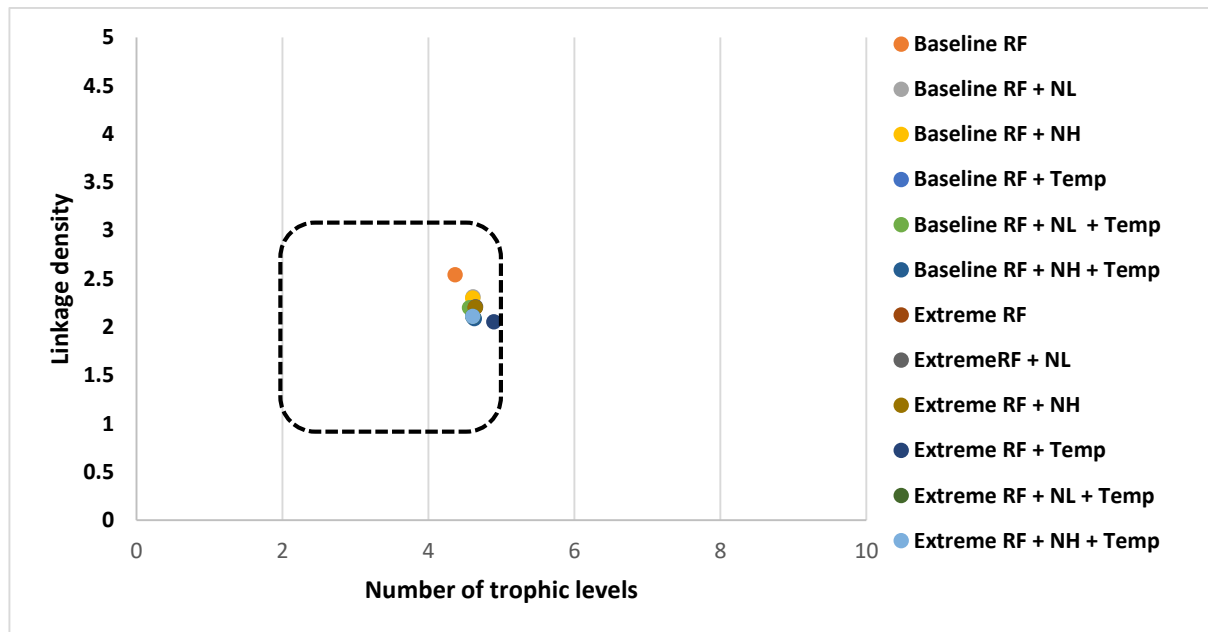


Figure 6.6 The safe operating zone (delineated by dotted lines) defined by ascendancy considerations for the Tamar estuary in the year 2055 under the impact of RF (River flow), NL (nutrients low) and NH (nutrients high).

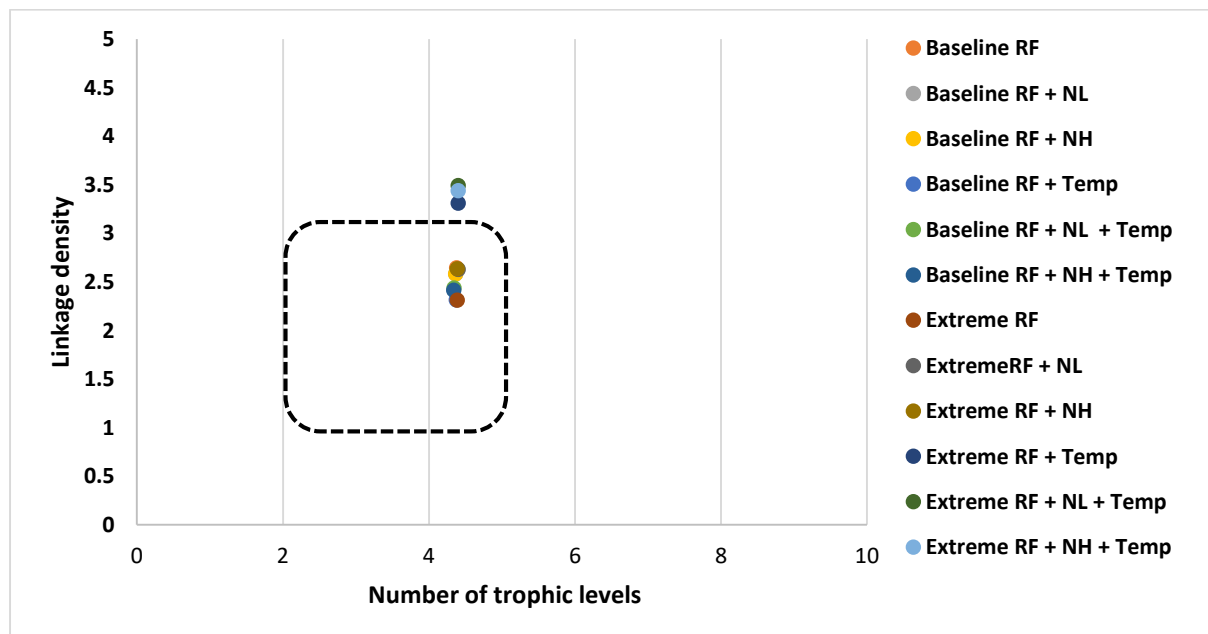


Figure 6.7 The safe operating zone (delineated by dotted lines) defined by ascendancy considerations for the Eden Estuary in the year 2065 under the impact of RF (River flow), NL (nutrients low) and NH (nutrients high).

6.5 Bayesian Belief Network results and discussion.

6.5.1 Predicting the likelihood of Good Environmental Status using Bayesian Belief Network modelling.

While the aforementioned methods provide a useful guide to the general susceptibility of system sustainability under the impact of future climate stressors, understanding the likely probabilities and uncertainties associated with such fundamental shifts in ecosystem state is also of paramount importance. To highlight such eventualities, an example of the “Good Environmental Status” index BBN with its 10 nodes and interactions is shown in Figure 6.8. In order to assess the impact that abiotic components are likely to have on the overall state of the ecosystem, the estimated GES Index was compared between each scenario in each system (Figure 6.9 and 6.10). To achieve this, the evidence for low and high scenarios of river flow, nutrient loading and temperature were propagated through the model and marginal probabilities re-calculated.

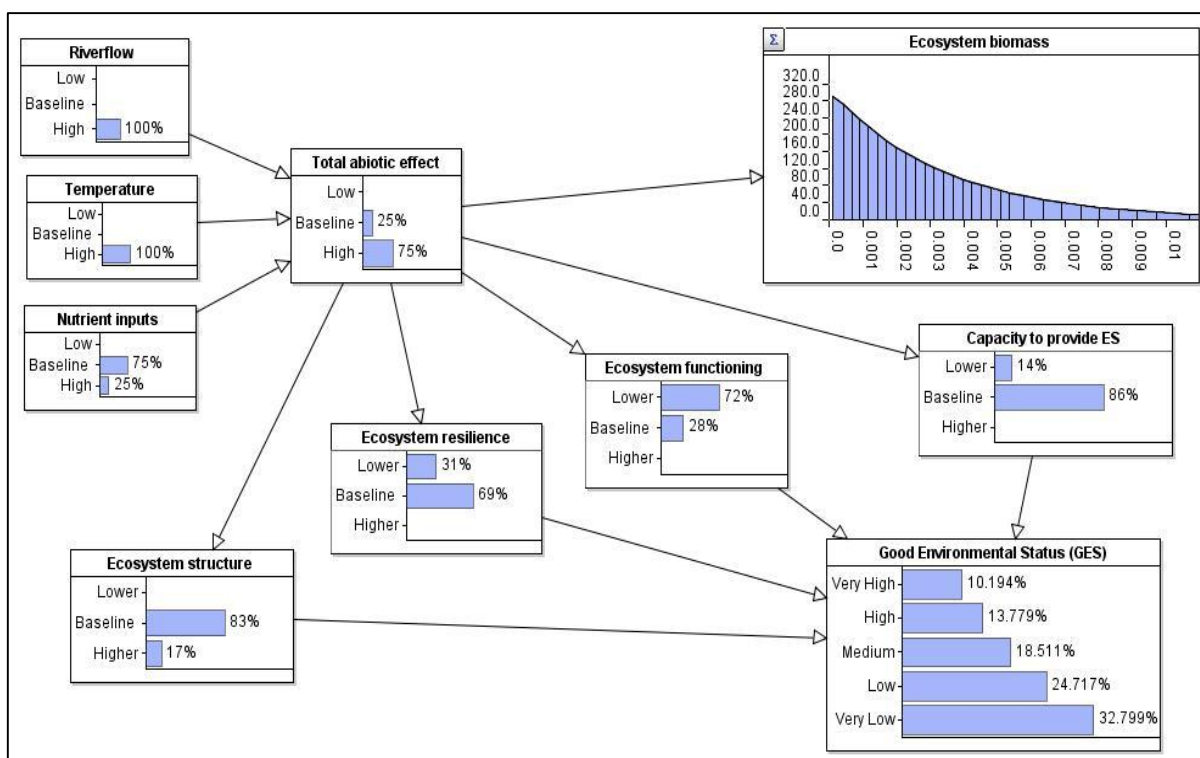


Figure 6.8 Benthic Estuarine and Coastal Biodiversity Impact Index showing the Bayesian Network model’s nodes and links. Tamar 2055 example shown under the impact of high river flow, temperature and nutrients. The index is represented as a five-point scale which can take one of five values ranging between [0–1] (named as Very Low 0.2; Low 0.4; Medium 0.6; High 0.8; Very High 1.0) and represents the probability of achieving GES.

Starting with the Tamar, the results of the GES index (Figure 6.9) showed that under future baseline conditions there was a skewed probability distribution towards the low (22.11%) and very low states (24.64%), with evidence from its BBN suggesting that even in its least impacted state the Tamar would endure significant losses to its resilience, functioning and ability to provide ES. The results also

unambiguously indicated that the addition of further stress to the system (either singly or in combination) would reduce the probability of achieving the high or very high GES states and that the combined effect of all three stressors were the among most significant with only 10.19% (Extreme RF + NH + Temp) and 10.75% (Extreme RF + NL + Temp) of achieving very high status. The greatest impact on the system however, was under the combined impact of baseline river flows, nutrients low and higher water temperatures (9.56% to achieve very high status).

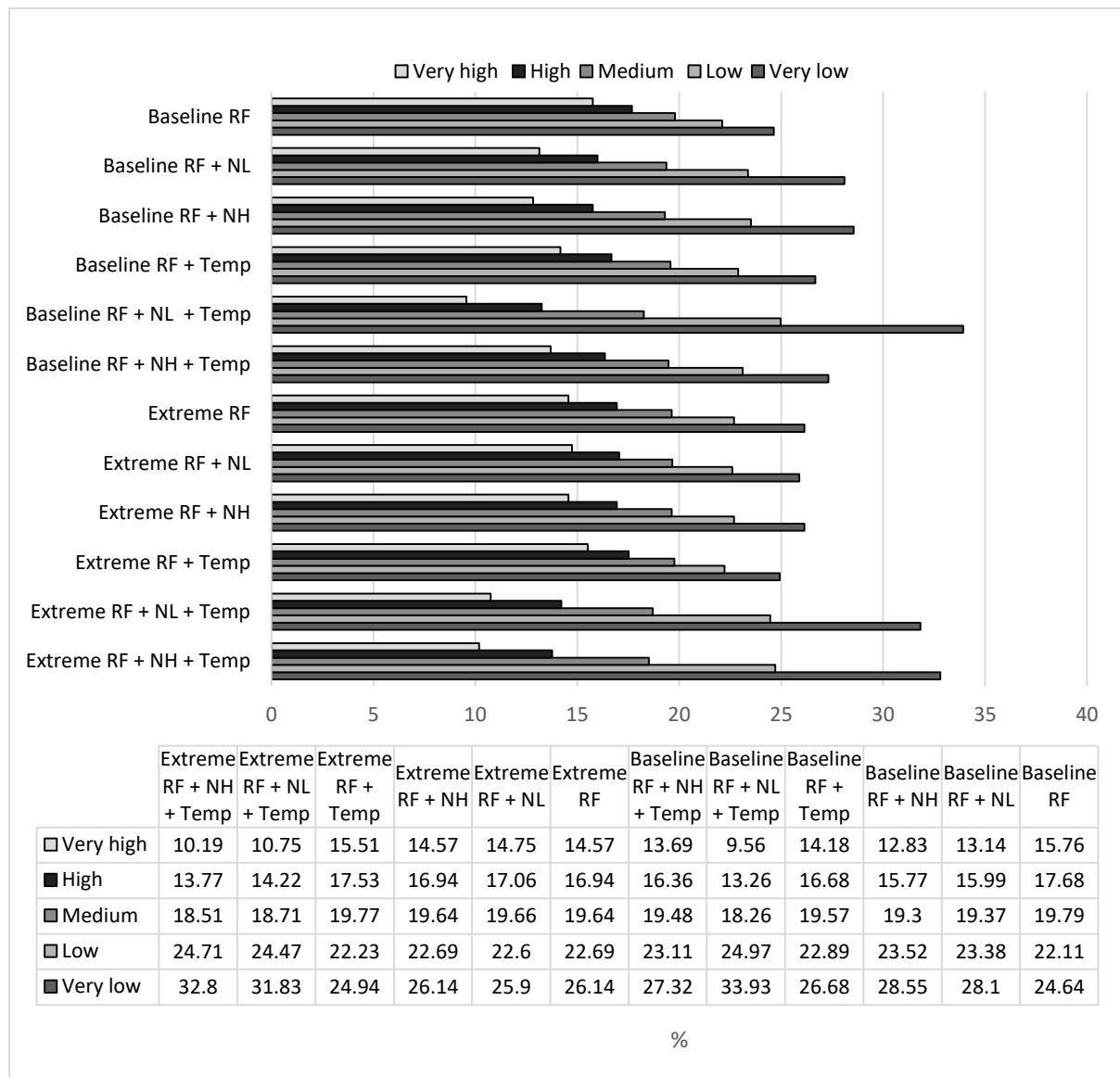


Figure 6.9 Percentage values of the GES index for the Tamar estuary 2055 under each scenario. The index is represented as a five-point scale which can take one of five values ranging between [0–1] (named as Very Low 0.2; Low 0.4; Medium 0.6; High 0.8; Very High 1.0) and represents the probability of achieving GES.

In the case of the Eden BBN, the probabilities of environmental status were initially closer to being evenly distributed across all ecosystem states under baseline conditions (Figure 6.10), with a slight skewed distribution towards the low and very low states. Further additions of the abiotic stressors

nutrient loading and temperature (singly or in combination) generally had little effect on or slightly increased the potential state of the system. The greatest changes in GES were observed when high rates of river flow were introduced and when combined with other variables they had the greatest impact on potential GES. For instance, the probabilities of a very high environmental state were reduced to 13.06 (Extreme RF + NH + Temp) and 13.21 (Extreme RF + NL + Temp), under the impact of all three stressors. A reduction in nutrients (i.e. through the practice of eutrophication management) was deemed to have consistent potential in mitigating some of the impacts caused by other stressors (c.f high nutrients), thus shifting the probability distribution towards the high and very high ecosystem states.

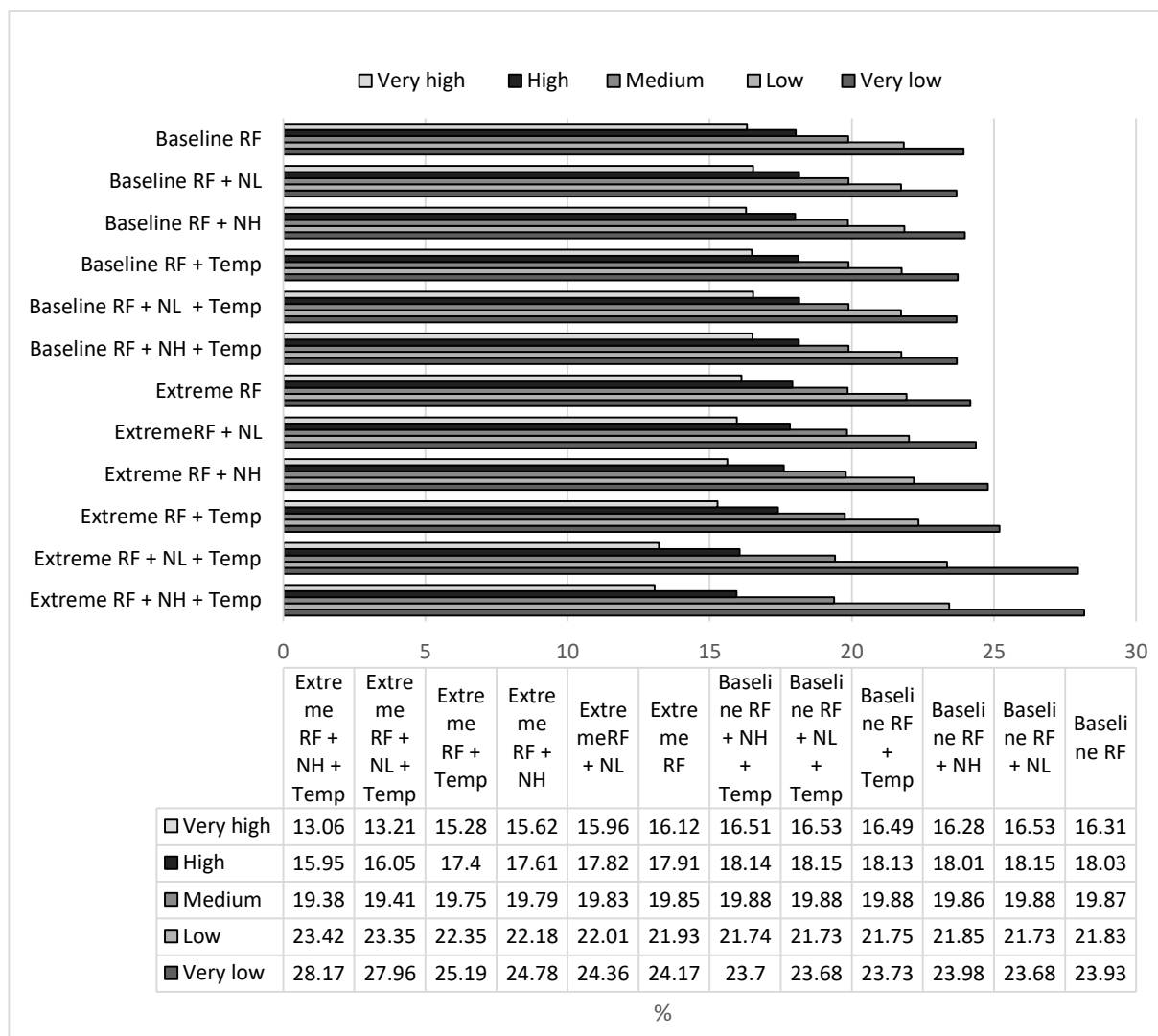


Figure 6.10 Percentage values of the GES index for the Eden estuary 2065 under each scenario. The index is originally represented as a five-point scale which can take one of five values ranging between [0–1] (named as Very Low 0.2; Low 0.4; Medium 0.6; High 0.8; Very High 1.0).

Overall, a central observation from both case studies was that the impact of multiple abiotic stressors was likely to have the greatest impact on achieving high and very high GES, with the combination of extreme river flow, high nutrients and increased temperature being potentially the greatest threat to

the Eden system and the second greatest in the Tamar. As resource management under these states will entail making difficult decisions in the face of interactions among complexity, uncertainty and variability, classical hypothesis testing may provide a poor basis for decision making in this regard because it does not reveal the probabilities and utilities of null and alternative hypotheses given the data (McCann, 2006) - even though this information is what managers frequently want (Ellison, 1996). Consequently, BBNs can contribute to sound decision-making in these catchments by explicitly representing probabilities of ecological responses to natural events, while facilitating management actions and allowing decision makers to examine trade-offs between a desirable outcome (Marcot *et al.*, 2006; Barton *et al.*, 2008). Likewise, given that research on GES and climate change is a rapidly changing area with information becoming available regularly, BBNs are a suitable tool to be used in an adaptive modelling framework (e.g. Nyberg *et al.*, 2006; Henriksen & Barlebo, 2008) because of their ability to update individual causal relations independently (Uusitalo *et al.*, 2007) resulting in better informed decisions.

Another advantage of BBNs in the context of ecosystem sustainability is their explicit treatment of uncertainties (McIntosh *et al.*, 2011). As any measurements made in natural ecosystems under the impact of multiple stressors are likely to be linked with uncertainties, BBNs can overcome these difficulties by incorporating these uncertainties in their probabilistic rule set (Jensen, 1996) and are expressed by the probability distributions in output nodes. It should also be noted that similar representations of uncertainty can be obtained with other modelling techniques such as Monte Carlo simulations (e.g. Ecosim, Chapter 5) but BBNs are generally more efficient (Landuyt *et al.*, 2013) and allow greater transparency for expert evaluation of model outputs generated for different test scenarios or by expert evaluation of the model structure itself (Aguilera *et al.*, 2011).

As mentioned in the introduction to this analysis, as with many pressure–state change models (e.g. DPSIR; Atkins *et al.*, 2011) each of the stages within a BBN conceptual model can be characterised by a series of many-to-many relationships (i.e. relationships between two entities e.g. A and B). Consequently, not only can the causal dependencies or links in BBNs prove useful in enhancing our understanding of the underlying processes/relationships/associations inherent within such frameworks (for example, the DPSIR D-P-S chain links), but they can also be set in the context of the MSFD (or other organisations (WFD) in pursuit of GES) by visualising these links as they relate to an MSFD descriptor. For example Figure 6.8 shows the range of physicochemical state changes that may lead to loss of food web “health” in the sense of MSFD descriptor 4 (D4; food webs) (i.e. effectively those changes that arise due to abrasion of ecosystem level proxies of structure, functioning and resilience) and the consequent range of potential (biological) state changes that may result at the

community or ecosystem level. As most of the currently proposed indicators for Descriptor 4 (D4) typically focus on a one or a subset of food web properties, key information on human impacts on food webs may be missed (O'Gorman *et al.*, 2012). Consequently, this analysis provides a basis for developing criteria directed towards more holistic, integrative and functional indicators (Haines-Young *et al.*, 2012) that as suggested by Rombouts *et al.*, (2013) should consider (1) multiple trophic levels or a whole-system approach (i.e. ecosystem-based indicators), (2) processes and linkages and (3) the dynamics of food webs in relation to specific anthropogenic pressures.

Alongside their potential strengths, an important weakness of the BBNs is their limited capacity to model systems mechanistically and dynamically (Marcot, 2012). In this study this barrier has been overcome somewhat by combining results of a deterministic model to facilitate a fully functional hybrid BBN model. However, the pre-requisite need to define many continuous variables as discrete variables (thus losing information) and the absence of feedback loops (thus losing complexity) is noted to be a critical restriction of BBNs to model complex processes (Nyberg *et al.*, 2006; Castelletti & Soncini-Sessa, 2007; Shenton *et al.*, 2010). While the making of “conceptual models” can assist in the development of BBN structure and the visualisation of the complex production chains required to represent “ES cascades”, it is worth noting that the relationships between biodiversity—ecosystem functions—ecosystem services—human well-being are unlikely to be linear in certain ecosystems (Gascuel *et al.*, 2012). Instead interactions between abiotic and biotic components of ecosystems, will interact in a number of cumulative and complex ways (e.g. many drivers that affect biodiversity may also directly impact ES), potentially jeopardising any modelling predictions of future ecosystem health/state and its subsequent capacity to provide ES and influence human well-being (Bopp *et al.*, 2013). However, as our knowledge of these influences evolves and becomes more reliable, the models such as the ones developed here can be updated as more information becomes available, potentially becoming structured libraries of existing scientific knowledge (e.g. Fernandez *et al.*, 2011; Crossman *et al.*, 2013) enabling the identification of knowledge gaps in ES and multiple stressor research.

The increasing application of BBNs in ES research and adaptive management is a rapidly progressing area in aquatic ecology resulting in new advances in network modelling (McDonald *et al.*, 2015). Growing technological advances in the use of BBNs to evaluate environmental state and by extension ES, include integration with Geographic Information Systems (GIS) and other spatial models. As such, a next logical step would be to integrate the developed BBNs with such methods in order to increase the spatial resolution of the predictive networks (Smith *et al.*, 2007; Haines-Young, 2011; Giretti, *et al.*, 2012; Landuyt *et al.*, 2015). Another important advance and asset of BBN models is the possibility to separately model single GES or ES production processes and to couple several sub-models in one BBN (Haines-Young, 2011). The major benefit of this is the possibility to consider all processes involved

in the biophysical delivery of GES and ES (ecological) and the potential value of the system (socio-economic) separately. Accordingly, BBNs have the potential to be used as a basis for a multidisciplinary modelling framework, whereby the two approaches can be sequentially modelled and the subsequent sub-models combined into one BBN (Dorner *et al.*, 2007). As the context of this study was purely to detail and develop the biophysical linkages available for manipulation with GES, ES and multiple stressor studies, future efforts could and should be made to integrate evidence of costs/benefits of management decisions in order to model the full cascade of ES delivery (Haines-Young & Potschin, 2010). Likewise, modelling multiple sub-processes related to different disciplines and combining them in an integrated whole, is likely to provide a clearer and more transparent picture on how ecosystems can contribute to human well-being, particularly under the impact of future environmental change. Such advances will not only improve the potential adoption of GES and ES models by end users (McIntosh *et al.*, 2011), but will also mean they have more added value as diagnostic tools to enhance system understanding (Young II *et al.*, 2011).

6.6 Conclusions

I used two approaches to estimate how the status of the marine environment can change after additions of three major anthropogenic pressures. The overall aim was to test and visualise outcomes of various modelling tools that could be used for advising planning of the management measures for managing multiple actions and pressures on marine environment. As with other chapters in this thesis, this analysis highlights that coastal and marine ecosystems are under increasing pressure from a number of sources. These sources have interactive effects on the biophysical properties of systems, such that cumulative impacts are typically greater than the sum of individual effects. The same stressors also produce effects on indicators of biodiversity and if left unchecked could potentially lead to systems such as the Tamar and Eden moving beyond their normal, safe operating limits (i.e. their resilience has been compromised and they are no longer sustainable) with serious consequences for all users who rely on the respective systems remaining in a good ecological state (e.g. our ability to draw ecosystem benefits from them).

As a conclusion, both approaches were considered useful in providing structure to understand and communicate the key dynamics and factors driving water quality standard violations in each estuarine system. For instance, sensitivity analysis of ascendancy and its derivatives were found to be useful in identifying the times where a system is most likely to be vulnerable to disturbance. While data on the existing flow networks of the Tamar and Eden ecosystems did not appear sufficient to determine a precise response pattern of specific stressor effects that could be generalisable to other systems, they do however indicate rather clearly those configurations of flows that are not sustainable within

individual systems. From a broader perspective, by plotting the values of the three variables related to Ulanowicz's, (2005) "Window of Vitality" for many ecosystems under different environmental pressures, it may become possible to identify a region in parameter space that characterises a generic healthy and robust ecosystem (Raffaelli, 2015). Also as managers may not be interested in the marginal changes of all species when they manage a system for a desired bundle of ES, this approach can help us understand, not only the extent to which systems may persist in the face of multiple stressors, but can also aid in promoting a range adaptive management strategies (Folke *et al.*, 2002; Leslie & Kinzing, 2008; Ban *et al.*, 2014) at the whole-system level. This may be particularly useful where it is impractical to measure the return times or resistance of individual species with any degree of confidence.

Building on the adopted network approach, the BBN models presented in this chapter also provided a good platform from which to develop an coupled GES-ESs working tool for end-users/stakeholders, with the concept of consequential ES cascades corresponding largely with how BBN's are structured. As an aid to estuarine informed management decisions, the BBNs can be used to make explicit predictions as to potential to achieve GES and the potential trade-offs in ecosystem variables under varying management scenarios (McCann *et al.*, 2006). The BBNs point to the driving forces behind several key stressors to each estuarine system, thereby providing a transparent and fairly simple modelling approach that could be used as a communication tool to interested stakeholders (e.g. Lowe *et al.*, 2014). By manipulating the nutrient loading and climatic conditions, the likelihood of environmental damage to the system can be calculated. Each BBN can also be easily updated as new data are collected, allowing for an adaptive management approach in basin-wide planning.

However, as the ecological side of ES valuation relies a lot on models (Burkhard *et al.*, 2013), many being complex with multiple interactions, linking biophysical models within a BBN framework demands a substantial simplification of the processes with the risk of losing the information on interactions. A further caveat of this analysis, is that the models used in this study did not take into account economic costs or social effects, yet evaluating them is also an important part of successful management (Beaumont *et al.*, 2008; De Groot *et al.*, 2010; Börger *et al.*, 2014; Luisetti *et al.*, 2014). To further improve the models, separate sub-networks could and should be developed that account for the cost/and benefits associated with environmental decision making. Future efforts to address these relationships can be done with the integration of both decision nodes and valuation nodes to model the full cascade of ESs delivery, although implementation of such a model would require a longer dataset to populate conditional probability tables.

As shown by the two different methods utilised here, the concept of ascendancy and other associated network properties has relevance for the management of an ES band for natural resource management. In particular, it provides one way of capturing the non-monetary 'value' of those ecosystem system elements that cannot be easily assessed using traditional monetary valuation methodologies. Both model frameworks also quantified the effects nutrient loading and likely future climate change of the Tamar and Eden systems, and were in agreement with the indicator descriptors from previous chapters (e.g. Chapters 4 & 5). The results also confirm the importance of nutrient input reduction to enhance the possibility of achieving GES. It should be noted however, that like other modelling approaches, network analysis and BBNs should not dictate management decisions (Batchelor & Cain, 1999) but could aid decision-making as components of a larger process of management, research, and monitoring. The responsibility of course remains on the modeller to demonstrate causality and address potential explanatory variables not included in the model. In this regard a common critique of network analysis is the large data requirements for model construction (Raffaelli, 2016). However in reality, the level of data required may be on par with other more empirical mapping approaches (Schägner *et al.*, 2013). Moreover, as network theory and BBNs are founded on a strong scientific theory basis with the capacity to openly code the level of pedigree (or model uncertainty) they can thus convey confidence as to whether those data might apply locally. Hence, given their numerous strengths and opportunities, network and BBN models for quantifying ecosystem scale GES deserve further exploration.

Chapter 7 General Discussion

Chapter Summary

This thesis takes a holistic 'whole ecosystem approach' to investigating the changes an estuary undergoes in response to anthropogenic impacts and climate variability. Embedded within this ethos was a challenge to test and visualise outcomes of various modelling tools and indicators that could be used for advising planning and management of multiple actions and pressures on the marine environment. As efforts to attain “Good Ecological and Chemical Status” (GECS and GCS : Water Framework Directive (WFD)) or “Good Environmental Status” (GES; the Marine Strategy Framework Directive (MSFD)) in the marine realm requires decisions which cannot be done without knowledge of the effects of different anthropogenic impacts (Duarte *et al.*, 2015; Borja,*et al.*, 2016), this study is valuable for looking at whole ecosystems both from a research perspective and in decision making and for quantifying the ecosystem services (ESs) they provide to ensure that society can maintain healthy and resilient natural environments both now and into the future.

As the evaluation of concurrent and alternative management measures is often the first step in cost-effectively assessing the availability and quality of natural resources (i.e. biodiversity) that in turn may provide estimates of ecosystem condition and the goods and services which societies depend (Uusitalo *et al.*, 2016), this study used four different approaches to estimate and visualise how the status of two estuarine systems can change after additions or reductions of anthropogenic stressors. Nutrient loading in the form of nitrogen and phosphorous were identified as a prominent pressure for both the Tamar and Eden estuary systems and was studied using two different assessment approaches, namely multi-metric indices and food web modelling. These approaches were subsequently built upon using deterministic and stochastic modelling techniques to investigate the more topical question of how the impact of multiple stressors such as temperature and increases in river-flow may interact with nutrient loading under alternative management scenarios.

While the indicators and modelling tools used in this study are fundamentally different in approach and often operate at different spatial and temporal scales, they proved a broad overview of how each estuary responds as a dynamic system, capturing many of the physical, biological and chemical processes that are relevant to the scales at which management operates and at which ESs are delivered to society (Kremen *et al.*, 2005; Daily *et al.*, 2009). Developing an understanding of the mechanisms supporting these linkages is an under developed, but much needed area of research. Combined with the stressor–biodiversity–ecosystem process work, this work enabled an assessment of how ecosystem function/service delivery (through various proxies i.e. Chapter 3 bioturbation and Chapter 4/5 Finns cycling index) has varied in the past under historical climate stressor regimes

(Chapters 3, 4), current ecosystem function/service provision (Chapters 3,4), and also a projection of how ecosystem function/services may vary under future climate scenarios (chapters 5/6).

Moreover, the broad nature of working at large spatial scales highlights the potential of re-analysing data sets from earlier research programmes and for generating novel insights at much larger spatial and temporal scales than is generally available from small-scale experimental studies. The breadth of the methodologies used in this study (e.g. aerial photographs and other remote sensing approaches (GIS); predictive modelling; time series analysis; physical habitat measures and resource inventory studies) however, inevitably lead to some loss of resolution and data quality due to time and effort limitations in terms of data collection. Although the uncertainty in all four different approaches is likely to be large due the inherent nature of working at large spatial scales, the models and indicators developed here can still be used to visualise potential directions of change and thus inform about potential consequences and support local planning of management actions.

Additionally as few studies have investigated multiple stressor interactions through modelling analysis in coastal marine systems, the examples in this thesis can be considered among the suite of emerging models exploring the dual exposure of marine ecosystems to climate change and human activity. A summary of the empirical findings from each chapter is given below. Following this, the implications of each chapter are discussed within the broader contexts of their relevance to multiple stressor and biodiversity-ES research, with considerations for how these findings might aid local and wider management efforts and promote future research.

7.1 Summary of main thesis topics

7.1.1 Chapter 3- Review and evaluation of estuarine biotic indices to assess benthic structure and functioning under the influence of differing nutrient regimes in two UK estuaries. (Multi-metric approach)

Most of the structural ecological indicators tested in Chapter 3 (Margalef, Shannon–Wiener, Pielou, Simpson, AMBI) were able to capture useful information about the state of the subtidal macro-benthic community as theoretically expected and behaved consistently with the abundance and biomass trends of the sub-tidal ecological community in both systems. Other structural indicators such as taxonomic based (e.g. taxonomic distinctness and diversity) and the WFD's Infaunal quality Index (IQI) were less effective at tracking the prevalent conditions. As many of the operative indicators form the mainstay of many environmental monitoring programmes, both in the UK and in Europe (e.g. AMBI) these results are encouraging for assessments made in transitional environments , which have been traditionally challenging to monitor (Dauvin, 2007; Elliott & Quintino, 2007; Neto,*et al.*, 2010). Having this knowledge, it becomes theoretically possible to predict in advance the behaviour, and

consequently, the ability of an ecological indicator to measure and detect changes in ecological conditions (Pinto, 2009; Veríssimo *et al.*, 2012). Clearly, differentiating between indicators that may be robust in space and time will be preferable to communicate information to environmental managers (Borja & Dauer, 2008).

It should be taken into consideration however, that environmental context is an extremely important determinant of how marine communities respond to stressors (Dyson *et al.*, 2007; Bulling *et al.*, 2008; Crain *et al.*, 2008; Thrush *et al.*, 2008; Godbold *et al.*, 2011; Donohue., 2013; Kenworthy., 2016). Indeed although many of the indicators indicated significant changes in structure at the level of the whole system, at the level of individual zones the results were far more variable highlighting the fact that shallow-water estuarine systems are highly heterogeneous environments. For example, spatial differences in the Tamar were particularly evident during the high nutrient period of the 90's when the polychaete *Hediste diversicolor* increased exponentially in numbers to become the most numerically important species in the upper reaches of the estuary. Such changes manifested in considerable changes to the functioning of material in the estuary, with the BTA and Bpc indicators proving useful complementary indices, by highlighting broad patterns in trait–environment relationships. When taken together both structural and functional indicators suggest that the structure, functioning and overall resilience of the Tamar macro-benthic communities has increased in the post management period (2005). But, based on the emergence of the oligochaete *Tubificoides benedii*, which is a pioneer in hypoxic and sulfidic environments (Giere *et al.*, 1999), and the high levels of nitrates still prevalent within the catchment, these results support the notion that nitrogen mitigation within the catchment may not have been sufficient and further additional management practices could be required. The study acknowledges however the lack of continuous monitoring data post 2005 as well as the use of continuous long-term data sets in order to understand better the effectiveness of the restoration measure undertaken.

In contrast to the Tamar, quantifying the main pressures presently acting upon the Eden Estuary was considerably easier due to the smaller spatial scale and limited influence of human activities and management measures confounding signals of natural climate variability. Coinciding with the reduction of nutrients entering the estuary, structural and functional indices revealed an increase in benthic ecological quality in both the upper and central regions of the estuary, suggesting that the benthic biodiversity of the estuary as a whole has been positively affected with regards to ecosystem health and the ability to provide ecosystem services associated with the benthic environment such as carbon and organic matter cycling. Although water quality and ecological functioning of the estuary has generally improved as a result of the positive impact that the introduction of NVZ status has had

on water quality (Macgregor & Warren, 2016), the results also highlight that only in the upper estuary has there been significant compositional changes in ecological structure. This is an important consideration, as previous assessments of the macro-benthic structure of the estuary have mainly focused on the central region (e.g. Chocholek, 2013). This specificity seems important from a management perspective, namely when implementing the WFD, with the need to account for different zones inherent natural variability to environmental conditions (Teixeira *et al.*, 2008), all the while exemplifying the need for an ecosystem-based approach to management that considers the entire ecosystem.

As such, comparisons between different methodologies, applications, and evaluation of existing indicators in various countries for different systems is likely to help to improve our knowledge about the suitability of such approaches (Borja *et al.*, 2008; 2009a;2012). As the last few decades have led to a plethora of different indicators being developed for use in monitoring of benthic marine systems, a key focus of future research should be to accomplish sufficient indicator performance comparisons to reach scientific consensus on the preferred indicators approaches for macro-invertebrates (Borja *et al.*, 2009b). Accordingly, the results presented in Chapter 3 may be seen as a case study for other estuarine systems both medium size (Tamar) and small (Eden) with similar characteristics (e.g. low residence times and historic nutrients loading) and suffering from the same environmental problems (risk of eutrophication or increased river flow), where restoration measures may need to be implemented.

As a final point, in Chapter 3 the focus was principally on one component of the estuarine environment, namely the benthic invertebrates. However, research on the relationship between biodiversity and ecosystem functioning is entering a new phase, accepting that biodiversity loss operates at large spatial scales and generally involves reductions and changes in species at different trophic levels simultaneously (Raffaelli, 2006). A key conclusion of this chapter was that future work should be more services-oriented, rather than process-oriented, with a greater recognition on the evaluation of other biological quality elements (especially primary producers such as macrophytes and macroalgae and other keystone species), if effects of estuarine biodiversity change on services and health are to be properly assessed. Therefore the subsequent chapters in this volume, emphasise the role of observational studies and modelling approaches, and their usefulness in understanding multi-trophic biodiversity-ecosystem service relationships at large seascape scales.

7.1.2 Chapter 4: A mass-balance approach to biodiversity–ecosystem service relationships in two estuarine ecosystems under the influence of nutrient reductions. (Thermodynamic analysis)

Chapter 4 showed a number indicators derived from flow analysis and information theory can be used to provide an “instantaneous” profile of each systems development following considerable changes in biodiversity. This has an immediate advantage over the more reductionist approaches (such as those used in chapter 3) by focusing on a systems emergent properties rather than its individual parts, and hence information could be captured using community and ecosystem-scale metrics, without the loss of information commonly associated with scaling from small-scale experimental systems (Raffaelli & Moller, 2000). Perhaps the most pertinent use of these indicators is to quantify the effects of stressors on ecosystems. For example certain characteristic behaviours induce signature changes in information indices – with the process of eutrophication being a vivid example. As a eutrophic system is generally described as one that has received too much of a good thing (the root *eutrphy* being Greek in origin meaning “well-fed”), the negative consequences of enrichment are usually manifested by the loss of important species along with their attendant system functions (Smith *et al.*, 1999; Scheffer *et al.*, 2001). In terms of ascendancy theory, eutrophication can be defined as “*any increase in systems ascendancy due to a rise in total system throughput that more than compensates for a fall in the mutual flow of the network*” (Ulanowicz, 1980;86) or in other words, nutrients tend to simulate a systems growth but despite its augmented activity, its organisation or structure is degraded. For an example of how we might use this theory to detect eutrophication, we can look again at the Tamar and Eden ecosystem networks, which suggest that under the high nutrient conditions systems ascendancy (growth) which is the product of its total throughput (activity or vigour) times its mutual information (structure) all increased respectively. If we then ask if eutrophication has occurred?, the conclusion would simply be that the systems were organically enriched by domestic and agricultural nutrients during these periods, with the prerequisite criteria of a fall in conjugate mutual information required to rightly say that the systems had undergone eutrophication in response to the additions. The results of this study conclude that the Tamar and Eden estuaries have historically been naturally hypernutrified (Boyes & Elliott., 2006), a common feature of estuaries (Tett *et al.*,2007) and were not eutrophic as indicated by the balance of a suite of symptoms of each ecosystems pathology. While it is not likely that the areas will become eutrophic as the organic inputs to the estuary continue to decrease, it is not possible to demonstrate conclusively that the areas will not be sensitive to future change.

Nutrient inputs however, is but one of many anthropogenic changes in these ecosystems and from the example above it may be clear the concept of ascendancy on its own is not broad enough to encapsulate all elements of ecosystem status or health (Costanza, 1992). As managers are likely to desire criteria to measure ecosystem status in broader sense of the maintenance of ecological functions and overall system resilience (Connell & Ghedini, 2015; Oliver *et al.*, 2015a: b), a number of other indices relating to system function (e.g. Finns cycling) and resilience (system overhead) to stressors were calculated to meet these requirements. To quantify the difference within and between the two systems it was necessary to compare the relative magnitude of their various information indices. In doing so questions arise as to the meaningfulness of the magnitude of information indices between different systems. Assuming that the temporal and spatial inhomogeneities are the same in the system under consideration, network indices appear to be quite robust depending on how one deconstructs the system (Ulanowicz & Wulff, 1991). For example if one person ascertains that the system has undergone eutrophication, another investigator working on the same system but with different groupings of taxa or aggregation scheme should still see the same qualitative changes. Of course in the case of this analysis a secondary objective was to compare the current changes in two separate ecosystems. In such a case, valid comparisons can only be made when systems are parsed in a nearly identical fashion (Baird *et al.*, 1991; Christian *et al.*, 2005). This does not mean that those systems in question must contain exactly the same species lists or functional units, but they must be aggregated in to approximately the same number of compartments standing in juxtaposition with each other (Ulanowicz, 1997). Such a comparison is made here between the Tamar and Eden systems containing 42 and 40 compartments respectively. Thus while the topologies of exchanges were similar, but not identical, it was the differences in connections and the relative magnitude of change in each system that makes this type of comparison interesting.

One obvious comparison between the networks is that the Tamar is far more active than the Eden, its total system throughput ($23209 \text{ t km}^{-2} \text{ yr}^{-1}$, defined as the sum of all flows in the system) is almost 30% larger than that of the Eden ($17434 \text{ t km}^{-2} \text{ yr}^{-1}$). Some of the higher activity in the Tamar can be attributed to warmer water temperatures and greater freshwater inputs than the Eden, but higher nutrient inputs to the Tamar are also likely to enhance its activity. Because total system throughput scales all information indices, the ascendancy and other related variables are uniformly greater for the Tamar than the Eden. However of more relevance to comparative analysis are the unscaled information indices themselves. Relative ascendancy (A/C), a dimensionless ratio that excludes the influence of system size for example, suggested that both estuarine systems were highly resistant to negative changes in nutrient loading over the study periods, collaborating with the assumption that the high natural variability within estuaries (Elliott & Quintino, 2007) may have conferred an ability

to withstand stress (in this case anthropogenic). The same index also proved useful in determining the relative dependence of each system to external inputs, with the Tamar Estuary evaluated as having a greater dependence on connecting ecosystems, in comparison to the relatively isolated Eden Estuary. The (A/C) index could therefore be a suitable indicator to compare ecosystems of different sizes (Mann *et al.*, 1989, Baird *et al.*, 1991).

As making judgment about the trophic status of two entire ecosystems based on a few information indices may seem precarious to some (Ulanowicz, 2004; Fath *et al.*, 2007), Chapter 4 also highlighted the need for a corroborative network analysis approach. In this way, the comparisons between the Tamar and Eden ecosystems was buttressed by a broader analysis of the two networks. Support for comparisons was found in the trophic structure and cycling pathways contained within the two ecosystems. Because each trophic pathway is a concatenation, stressors occurring at any point will disrupt flow to higher levels (Voris *et al.*, 1980; Ulanowicz, 1983). We would expect therefore, that systems with greater resistance to and resilience from stressors to be more complex, in the sense that they contain longer loops of connections that cycle at lower frequencies. Conversely, systems under increased stress would possess fewer such cycles, due to sundry disruptions, and each cycle would transfer less medium, particularly to higher trophic levels (Baird *et al.*, 1993). Indeed this is precisely what the comparison shows: the cycles derived from the Tamar and Eden systems were deficient both in number and length under high nutrient levels. Metaphorically the comparison of information indices between networks when complemented by the inherent analysis of cycles has been considered as an exercise in the “comparative anatomy” of ecosystems (Wulff & Ulanowicz, 1989). Together these methodologies comprise a significant quantitative approach to assessing the relative health of ecosystems.

7.1.3 Chapter 5- Modelling the effects of multiple stressors on estuarine benthic food webs: Implications for ecosystem services and resilience. (Predictive model approach)

The preceding analysis has focused exclusively on a single form of stress, however it is becoming increasingly apparent that coastal and marine systems are under increasing pressure from a number of sources (Hoegh-Guldberg & Bruno, 2010; Doney *et al.*, 2012). Due to the multifarious nature of environmental change in these type of environments (Elliott & McLusky, 2002), one of the biggest challenges in environmental science and management is currently how to assess or predict the interactive and cumulative effects of multiple stressors in ecological studies and conservation planning (Breitburg *et al.*, 1998; Sala *et al.*, 2000; Crain *et al.*, 2008; Darling & Côté, 2008; Baird *et al.*, 2016; Chariton *et al.*, 2016). This increased attention to multiple stressors has also been paralleled by an increased focus on the temporal dynamics of environmental stress (Harley & Paine., 2009; Denny & Gaylord., 2010; Thompson *et al.*, 2013). While many studies have been performed on the effects of

multiple stressors (e.g. Hughes & Connell 1999 Benner *et al.*, 2013; Melzner *et al.*, 2013; O'Connor & Donohue, 2013; Alsterberg *et al.*, 2014; Boyd *et al.*, 2015; Feidantsis *et al.*, 2015) many of the current studies that have taken place in benthic coastal systems, focus on the impact of biodiversity-functioning usually at small spatial scales (Atalah & Crowe, 2010; O'Gorman *et al.*, 2012). Further studies are therefore needed to predict how non-tested combinations of multiple stressors interact on marine ecosystems at larger, policy-relevant spatial scales. Furthermore, experimental biologists have traditionally subjected organisms to constant conditions within a given treatment usually based on summaries of environmental measurements such as mean or maximum values of a given stressor. However, environmental parameters fluctuate on multiple timescales, from hours to months to years. These fluctuations are likely to be extremely important for dictating how organisms respond to prevailing conditions and to human-induced environmental change (Vincenzi, 2014).

As systems models can be considered as one of the few means of understanding the potential outcomes of the interactions among multiple stressors at large seascape scales (Fulton *et al.*, 2011; Hyder *et al.*, 2015), in Chapter 5 the previous modelling frameworks developed in Chapter 4 were expanded to investigate the effects of periodic, stochastic, sequential and/or cyclical variations in the future climate and nutrient cycles of the Tamar and Eden estuaries. Three stressors (river flow, nutrient inputs and thermal stress) were investigated due to their known prevalence of impact within the case study systems. Overall, a key finding of the study was the context dependency of the different stressor impacts between the two study areas, with differences in the benthic community structure (Bulling *et al.*, 2010; Fitch & Crowe., 2011) and localised environmental context (Cardinale *et al.*, 2000; Chapman *et al.*, 2005) between the two systems likely contributing to differences in their response to stressors.

In the Tamar, predictive modelling analysis of the network indices TST, AMI, Ascendency, Overhead, and Finns cycling indicated that under the resulting impact of any of the three stressors either singly or in combination, the estuary would suffer losses to its ability to resist future change and would persist with a reduced functional capacity. In contrast to the Tamar, the Eden estuary was determined to be more resistant to nutrient stress but more susceptible to increased river-flows. This has particular relevance for local management planning when taken into consideration with the results of Chapter 3, which suggested an increase in river flow regimes in the catchment is already imminent and has potentially already altered the benthic community structure of the upper estuary. Model simulations also predict that the performance and biomass of key consumer groups in both the Tamar and Eden estuary systems are expected to change under such regimes but not uniformly. Taken together the geographic variation in responses seen here suggest continued local management efforts to monitor nutrient and river flow levels might be worthwhile: alongside a UK climate adaption

strategy within action to cut global emissions and reduce the impacts of global warming, sea level rise, and more severe weather.

Based on the model simulations, it is also clear that the three common anthropogenic stressors in coastal environments: river flow, nutrient availability and temperature, can combine additively with the potential for interactive effects, and these effects may not be apparent if these stressors are examined in isolation. This is of particular importance because to be able to reliably predict the effects of these stressors and, consequently, produce accurate risk assessments to be used in adaptive management, we need to understand interactive effects (Halpern *et al.*, 2008; Van den Brink *et al.*, 2016). In this instance, these results are consistent with the interpretation that interaction effects are generally antagonistic at the community or ecosystem level (Crain *et al.*, 2008; Jackson *et al.*, 2016), resulting from enhanced species interactions within communities that act to dampen and reduce the diffuse impacts caused by multiple stressors (Vinebrooke *et al.*, 2004). However, this study also highlights the need to consider the underlying emergent properties of systems at the community and ecosystem level, as the apparent benefits derived from increased system biomass (or biodiversity), may be concealing a deeper unravelling of food-webs associated with multiple stressor interactions. As there was no evidence from the system indices that a critical tipping point or threshold had been breached in either system, these results demonstrate how resilient estuarine systems can be when subjected to additional stress (see Elliott & Quintino, 2007) and that it may take extreme external pressure to result in a collapse of these naturally stress tolerant and hence resilient ecosystems.

A final key conclusion of this chapter was that predictive modelling studies can only be as good as the data and knowledge it incorporates (Dafforn *et al.*, 2016). Because the interactions among multiple stressors are still only partly understood for aquatic ecosystems (Folt *et al.*, 1999; Piggott *et al.*, 2015a) considerable further research is needed to improve the contribution these system models make to understand interactions among multiple stressors.

7.1.4 Chapter 6- Holistic approaches for defining sustainable and resilient boundaries in marine systems under the impacts of multiple climate stressors. (Decision support tools)

While the use of cause–effect modelling is extremely useful in establishing possible stressor effects, impacts and interactions, i.e. synergistic, antagonistic or additive (Jackson *et al.*, 2016), one difficulty with the use of ecological models might be translating these results to stakeholders in an effective manner, to accurately communicate both the power and the limitations of the tools (Fulton, 2010). As such, transforming conceptual cause–effect models into a quantitative platform using approaches that innately incorporate the dual probabilistic and deterministic nature of ecological structures, using graphical descriptions of risk and example narratives are becoming increasingly used in adaptive

management practices and ecological risk assessments (Ascough *et al.*, 2008; Uusitalo *et al.*, 2015) . On this basis, Chapter 6 provided an example of how conceptual model approaches can be included in the risk assessment of multiple stressors, using the Tamar and Eden estuaries as case study systems. The chapter used two different approaches: an ecological network approach and a Bayesian Belief Network (BBN) to organise the current information on multiple stressor effects in a format that allows the communication of the status of the system for decision-making.

As scientists and using the “Ecosystem Approach” are increasingly interested in how different impacts or policy options will simultaneously change several and if such changes will compromise the resilience of the system being managed (Folke, 2006; Bennett, 2009; Biggs *et al.*, 2012). Therefore, the topological properties of the Tamar and Eden networks were first investigated to illustrate the integrity of the networks to future change. Networks were tested according to how the impact of the predefined stressors used in chapter 5 would push each system beyond its safe operational space (i.e. whether any new system state will be sustainable) in relation to Ulanowicz’s (2005) “Window of Vitality”. In doing so such analysis highlighted how trade-offs between different services and the network configurations (species abundances and their flows) that support them can be more easily explored in relation to a safe operating space using concepts and language more familiar to mainstream ecologists (Raffaelli, 2016).

Empirically, the system resilience measures indicated that even quite large-scale shifts in biodiversity did not move the systems out of their safe space under the impact of high nutrient conditions in the 1990’s. This might reflect the well-adapted capacity of estuarine biota to absorb stress without adverse effects and so the areas may be regarded as resilient to nutrient inputs because of that inherent variability (i.e. Environmental Homeostasis, see Elliott & Quintino., 2007). This may give grounds for optimism for the traditionally poor management of such systems, and their ability to function. However, under the duress of high nutrient conditions both systems were precariously close to their boundaries of sustainability emphasising the need to implement research and monitoring programme to characterise the effects of nutrient inputs, and inform adaptive management strategies. Further analysis also highlighted that additional stress would move both systems closer to crossing their respective boundaries of sustainability, but it was only in the Eden that the combined action of several stressors (high nutrients, increased water temperatures and baseline or extreme rivers flows) shifted the system beyond such boundaries (i.e. its resistance had been compromised).

To provide a second example of how probability analysis can be included in the risk assessment of multiple stressors, a Bayesian Belief Network (BBN) was constructed for both estuaries. The motivation for choosing BBNs was that although BBN’s have been widely used to construct decision

support tools (Marcot *et al.*, 2006; McCann *et al.*, 2006; Newton *et al.*, 2007), they also have much to offer in relation to questions of ES and ecosystem status. For instance if we are to understand how coupled socio-ecological systems operate, we need to disentangle and model the 'production chains' that lead to the output of ES (Haines-Young, 2011). It is suggested that one way to begin this task is to represent these production chains in terms of the 'cascade model' of ES generation and valuation which highlights the links between biophysical aspects/biodiversity and human well-being cascade' (Potschin & Haines-Young, 2011; see also De Groot *et al.*, 2010; Haines-Young & Potschin, 2010). In this chapter, two case studies are therefore presented to explore how BBN's can be used to operationalize different components of the cascade model, and hence promote inter- and trans-disciplinary dialogues in the pursuit of ES delivery and the preservation of GECS and GCS.

The experience of using the BBNs thus helped to make the scenarios developed in chapter 5 operational in the sense that from the projections of multiple stressor impacts, marginal changes in outputs and values associated with different climate scenarios could be represented in such a way that trade-offs, which might need to be considered when exploring alternative scenarios, could be deduced or estimated quantitatively. It was also felt that the modelling exercise had the potential to be developed into more sophisticated yet transparent 'meta-models' that can address some of the complexity surrounding economic impacts on ES. It must be acknowledged that the case studies presented are still a long way from fully representing the structure and dynamics of a real social-ecological system. However, the examples demonstrate that by linking BBN approaches to other tools (in this case a deterministic model), there is some scope for making progress in addressing the spatial and temporal complexities associated with ecosystem assessments.

7.2 Cumulative impacts and interactions associated with multiple stressors

Despite a growing consensus that most marine systems are affected simultaneously by multiple stressors, the prevalence of non-additive, synergistic or antagonistic interaction in marine systems remains unclear due to the inherent difficulties of establishing causality from observational data and a lack of appropriate experimental data (Frid & Crowe, 2015). Notwithstanding these problems, recent meta-analysis techniques are beginning to provide some clues as to multiple stressor interactions. Two of the most widely cited meta-analyses (Crain *et al.*, 2008; Darling & Côté, 2008) for example, suggest that interactions between stressors appear to be very common with evidence of synergistic or antagonistic effects in over three quarters of multiple stressor experiments. In addition while there has been wide acceptance by the scientific community that synergies are a major problem for conservation and management (Paine *et al.*, 1998; Laurance & Useche, 2009), there is also a growing consensus that antagonisms and synergisms occur with roughly equal frequencies (Crain *et al.*, 2008;

Darling & Côté, 2008) and that there has been an overemphasis of synergies in ecological literature (Côté *et al.*, 2016). Alongside this apparent preponderance of ecological synergies, meta-analysis specific to the marine environment (Crain *et al.*, 2008) suggest that our knowledge of cumulative interactions is still biased to some extent, with only a small number of stressor combinations having been investigated to date and that there relatively few studies that have investigated stressor combinations on species richness of other measures of biodiversity (but see Sundbäck *et al.*, 2010; O'Gorman *et al.*, 2012) , particularly at the community and ecosystem level.

To facilitate more ecologically relevant research, there is therefore a distinct need to move away from studying stressors singularly in order to be able to fully understand how future change will impact marine environments (Byrne *et al.*, 2013; Hewitt *et al.*, 2015; Gunderson *et al.*, 2016). For example, the importance of multifactorial analysis in assessing two or more stressors has become increasingly recognised as an important concept (Wernberg *et al.*, 2012). Indeed this study has contributed to understanding the separate footprints of effect of three major stressors in estuaries (nutrient levels, temperature and river flow rates) using long term data. However identifying such interactions before managing them will be challenging at any scale, with a recent study by Halpern *et al.* (2015) estimating that over 95% of marine environments are subject to multiple stressors and another study by Côté *et al.* (2016) suggesting that much of the world's oceans may have more than 10 two-way interactions (which would require at least 16 experimental treatments to quantify) and coastal areas typically having upwards of 100 two-way interactions. The authors also note that these may in fact be underestimates due to the heterogeneity of individual ecosystems that can act influence the physical and chemical characteristics of the ecosystem in question. Due to such complexities, the same authors (Côté *et al.*, 2016) have suggested that identifying generalities about ecosystems, stressors and/or responses may be a more realistic goal than trying to identify the specific outcomes of every possible stressor combination. For instance the results of this study suggest that ecosystem or community-level impacts on biodiversity might be expected to be antagonistic more often than population-level responses if interactions among species act to dampen or diffuse impacts on individual species (e.g. Crain *et al.*, 2008). Unfortunately the results presented here (chapter 5) also indicate that metrics corresponding to community resilience and functioning can also be synergistic in their effect, and thus similar measures can be associated with more than one type of interaction. While a robust pattern of associations might emerge with more data, here a possible explanation for more antagonistic responses by estuarine biota (but not their functions) may corroborate with recent meta-analysis results of freshwater systems by Jackson *et al.* (2016) suggesting that due to the inherent greater environmental variability of smaller aquatic ecosystems, they are likely to foster greater potential for acclimation and co-adaptation to multiple stressors. If true, such trends will likely be good news for

managers interested in protecting assemblages rather than individual species from the effects of multiple stressors.

In the absence of simple generalisations, perhaps the best way to improve our knowledge and predictions of cumulative impacts may be to focus on the underlying processes and mechanisms whereby the stressors affecting the ecosystem interact (Sih *et al.*, 2004; Adams *et al.*, 2005; Crain *et al.*, 2008; Jackson *et al.*, 2016). Laboratory, field and mesocosm experiments are likely to be useful in this regard by giving us an insight into how natural and experimental systems will react to stress. Observational and modelling approaches should not be discounted however, as they are one of few approaches that can integrate physical, chemical, ecological and human-use dynamics in a three-dimensional spatially explicit domain (Fulton *et al.*, 2011) in a manner that is often difficult to mimic or test in a laboratory or field setting (Grieg & Alexander, 2009; Knights *et al.*, 2013). Models as described in chapter 6 can also help test assumptions, evaluate trade-offs in management assessment and account for increasing uncertainty in estimating the cumulative effects of stressors on ecosystems (Duinker *et al.*, 2012). Therefore support for sustainable development of marine systems often requires using primary research, models, and tools (e.g. indicators) in an integrated, adaptive ecosystem-based framework to address cumulative effects (Leslie & McLeod, 2007).

Another point of interest that arises from this study is the current dichotomy that exists between multiple stressor scientific research and conservation practice, with the first typically focused on studying the effects of adding stressors to a system, while the latter is often about understanding the consequences of removing stressors (Clarke-Murray *et al.*, 2014). As the trajectory of change in marine communities under stress alleviation is unlikely to mirror community response under increasing stress, designing and incorporating restoration factors and ecological recovery into experimental and modelling manipulations of single (chapters 3-4) and multiple stressors (chapters 5-6) is likely to be directly useful to inform local adaptive management plans (Borja *et al.*, 2010; Allan *et al.*, 2013).

7.3 The impact of human-induced stressors on marine biodiversity and ecosystem services

Marine and coastal ecosystems provide a wide range of essential benefits to human society, including the provision of food and nutritional resources, a means to remediate waste products, a regulated climate as well as less tangible, but no less important cultural and aesthetic benefits. Despite this, many marine and coastal systems are being degraded to an extent that might reduce their capacity to provide these benefits (Beaumont *et al.*, 2007; Halpern *et al.*, 2008; Barbier *et al.*, 2011). As these benefits are underpinned by ES, characterising the susceptibility of services (and combinations of services) to particular stressors based on knowledge of impacts on biodiversity and functioning is of

increasing importance to the successful management of all marine environments (Daily *et al.*, 2009; Mooney *et al.*, 2009; Bennett, *et al.*, 2015). However, our current understanding of how different anthropogenic and climatic stressors impact on the different parts of the interlinked biodiversity–ecosystem processes/functioning–ecosystem services–ecosystem benefits continuum is still highly fragmented and piecemeal (Austen *et al.*, 2015). For example, initial research on the relationship between marine biodiversity and ES provisioning suggests that ES provision is likely to increase with biodiversity (Balvanera *et al.*, 2006; Worm *et al.*, 2006). Yet, as Chapter 3 of this thesis highlights, such relationships are likely to vary according to the context of the ecosystem being investigated (see also (Bulling *et al.*, 2010; Cardinale *et al.*, 2012) with biodiversity-functioning-service relationships likely to depend on a number of different factors including the role of the species within the ecosystem, the biological structure of the community, compensation dynamics within and between species and local environmental stressor variables.

As many of the aforementioned interactions are likely to occur across multiple trophic levels involving the product of multiple ecosystem processes which are in turn underpinned by a diversity of biodiversity units (interacting networks of species within habitat units) there is also an increasing need to understand the consequences of biodiversity change at larger and longer spatial scales (Raffaelli, 2006; Brose & Hillebrand, 2016) For example, evidence from the literature suggests that large global scale processes such as carbon sequestration and storage are often slow to change (decades to centuries: Duarte *et al.*, 2005; Lo Iacono *et al.*, 2008) and may lag behind the initial shock that initiated the change. In contrast, small processes such as localised algal blooms are often change quickly (months to years: Jaworski, 1981) with little lag. Therefore multifunctional approaches, i.e. that assess the simultaneous performance of multiple ecosystem functions (e.g. as carbon and nutrient cycling), across multiple trophic levels, over a range of time scales, would be beneficial when analysing the effects of multiple stressors on communities and ecosystem functions. While there are a number of approaches that are beginning to address such topics both experimentally (e.g. Alsterberg *et al.*, 2014; Lefcheck *et al.*, 2015) and observationally (e.g. Raffaelli, 2011; Chapter 4 & 5 of this thesis), this is still a poorly researched area and needs further research. In particular, structured research is needed in which the extent and nature of spatial and temporal variations in response to biodiversity loss can be tested (Cumming, 2007; Boyer *et al.*, 2009; Crowe *et al.*, 2012) such that more general predictive frameworks can be developed.

While the links between ES and ecosystem functioning are still not well understood, the links between ES delivery and the stability or resilience of ecosystems are even less so. For instance, frameworks that link ES and human or ecological resilience are still nascent (Carabine *et al.*, 2015). Stability and resilience concepts are however a desirable attribute from an ES perspective, as more stable or

resilient systems are more reliable providers of services and are better able to accommodate the increased stressor impacts sustainably (Kremen, 2005; Mace *et al.*, 2012; Oliver *et al.*, 2015). As a consequence there is increasing evidence that predictive modelling approaches (e.g. Chapter 5) can be used as evidence to support ecosystem-based approaches (e.g. Ecosystem-based Adaptation (EbA) approaches; see Vohland *et al.*, 2012) to managing disaster risk and mitigating disaster impacts and can make a valuable contribution to ecological and human resilience management strategies. Using such models and frameworks, it may be possible to promote the implementation of management activities that conserve biodiversity wherever possible, since this provides an insurance value by underpinning ecosystem resilience and health and the continued provision of ES.

As future climate effects are likely to be uncertain and inevitably confounded by insufficient knowledge about the interdependent and non-linear nature of stressor interactions, it is also likely that any attempt to optimise or manage specific services (or groups thereof) will lead to a reduction or loss in one or more of the other services provided by the ecosystem in question (Rodríguez *et al.*, 2006; Villasante *et al.*, 2016). Trade-offs between ES therefore need to be considered in a coherent manner, where outputs of data and models are available and understandable for all stakeholder groups. While a number of methods can be used to quantify the likely sustainability of communities and systems to continue to provide ES (e.g. the thermodynamic properties of the system chapter 6), the use of monetary (and non-monetary) tools are often seen as a mechanism for enabling trade-offs between different adaptive management scenarios (Daily, 1997; Farber *et al.*, 2002; Costanza *et al.*, 2016). Effective valuation however requires adequate knowledge of key ecological and economic relationships, with economists often requiring very considerable information from natural scientists if they are to conduct valuation exercises (Braat & de Groot, 2012; Börger *et al.*, 2014). This is particularly true if production function approaches are used to estimate the indirect “value” of ES and/or biodiversity (e.g. Chapter 6), since finding robust and generalisable empirical relationships which relate to changes in ecosystem functioning and overall ecosystem health is extremely challenging (Hanley, 2016). Thus while trade-offs will ultimately allow the continued sustainable use of certain ESs (i.e. those most relevant to the stakeholders), addressing multiple stressors for the purpose of biodiversity conservation will in itself automatically support a broad range of ecological interactions and therefore multiple ES provisions (Palumbi *et al.*, 2009). Conserving biodiversity in this manner will also support less tangible (e.g. cultural services) or under researched/valued services (e.g. the service of waste remediation; see Watson *et al.*, 2016) which are often at risk of being underestimated or omitted in policy/management designs.

7.4 Relevance of results for management

Identifying how multiple-human induced stressors interact is important for prioritising management actions, because it can inform which stressors to act on and prioritise when and where actions should be placed to achieve the greatest benefits to biodiversity and society (Borja *et al.*, 2010; Duarte *et al.*, 2013). Implementing strategies based on multiple stressors and ecological interactions in coastal and estuarine systems is however challenging, due to the need to incorporate many local activities and pressures emanating from inside the sea area being managed (endogenic pressures), alongside wider pressures (exogenic pressures), such as global climate (Elliott, 2011). These issues are further compounded by “shifting baselines”, i.e. the gradual change in environmental variables (Duarte *et al.*, 2009) and the management of “unbounded boundaries” given the migration and dispersal abilities of highly-mobile species (Elliott *et al.*, 2015), all of which may confound efforts to predict expected changes on marine biodiversity, ES and the achievement of GES descriptors. Further, given the wide diversity of marine ecosystems, multitude of pressures affecting them and the still poor understanding on linkages between them, there are probably no tools or models available to give all the required answers. Hence, several separate approaches can be used in parallel to give support for management measures.

In this thesis for example, it was shown how four separate approaches (Chapters 3-6 described above) could be used to assess three prominent pressures on the Tamar and Eden estuaries, nutrient loading, river flow and temperature. While each of the approaches was inherently different in approach, with many strengths and weakness (described in detail in each of the relevant chapters), this exercise of running and comparing the four very different methods, serves as a very good starting point for more detailed management support measures based on one or several chosen methods. Moreover as the outcomes of the structural and functional indices approaches gave similar outcomes to the more holistic network models, i.e. they both indicated improved benthic “health” under nutrient reductions, this implies that the basic processes and their direction are well known even if their quantification is different. The deterministic and stochastic modelling processes also highlight the possibilities for predicting measures that can result in trade-offs between different environmental states. Such approaches can therefore be considered as complementary and provide a more complete picture as to the current and future state of each system, including an understanding of the cumulative impacts on each system and the management options available. As this study also used realistic baseline conditions (e.g. the local hydrodynamic conditions at a site in this case river flow were used to set levels of the stressor that are locally relevant) and rates of change in stressor intensity (i.e. temperature change will not occur instantaneously but gradually over longer timescales), effectively simulating the processes of climate change, management or restoration using the ecosystem as the

experimental design. As managers often need advice on how the effects of stressors/management measures propagate beyond their primary target (Uusitalo *et al.*, 2015) an example being how nutrient loading reductions in eutrophied system have consequences beyond phytoplankton biomass to food web structure, the benthos, etc. such results are directly relevant to inform management planning.

Overall a number of key conclusions could be drawn to aid in the specific management of each estuary. In the Tamar initial results suggested that nutrient reductions may have been insufficient thus far and future remedial efforts are needed. As the WFD (i.e. the most significant piece of water legislation in estuaries) does not explicitly consider eutrophication (Andersen *et al.*, 2006), and refers to the word only once in Annex VIII, in the (clearly agricultural) context of nitrates and phosphates, environmental legislation focused on these particular determinants (e.g. Nitrates Directive (91/676/ EEC & Water Framework Directive (2000/60/ EC) will help to prevent further deterioration and protect and enhance the status of the Tamar estuary.

In contrast, in the Eden, increases in river-flow were highlighted to be of greater concern and that there has been a significant improvement in environmental quality of the estuary following nutrient abatement measures. Trophic models of both systems suggest that biodiversity of each system has changed fundamentally over the last few decades and will continue to do so over the next fifty years with the predictive models warning that increased water temperatures in particular could decrease the abundance of many species including many wintering wader and waterbird populations, which are an inherent part of both estuaries. This may reduce the possibility not only of achieving Good ecological and chemical status of each system but specifically in the case of birds Favourable Conservation Status under the EU Birds and Habitats Directives. While most current UK Special Protected Areas (Frost *et al.*, 2016) are likely to continue to support internationally important numbers of wintering waterbirds, even under suggested low impact scenarios, there could be large overall changes to biodiversity.

Results of the predictive models also suggest that stressors may interact in an additive, synergistic or antagonistic manner depending on the component of the food web in question. Given this ambiguity and the potential for other interactions between stressors out with this study, conservation managers should work under the assumption that synergisms, antagonisms and additive effects are equally likely, pending more detailed case study investigations. Furthermore, because managers cannot act directly to alleviate exogenic stressors (e.g. temperature), a focus on reducing endogenic pressures such as nutrient loading will not only reduce the chances of cumulative actions occurring but will also bring some benefits to refuges regardless of the interaction. Equally, while the results from this study emphasise the importance of localised management plans to protect from the effects of multiple

stressors, it also highlights that similar ecosystems may respond similarly to specific effects of non-additive anthropogenic stressors (e.g. nutrient enrichment/reductions) permitting a degree of generalisation and pragmatism in developing management plans for a wide range of marine ecosystems pending an accrual of more detailed ecosystem-specific understanding.

7.5 Future research

This thesis has highlighted that a number of potential developments are needed both within and between science disciplines so as to assess how emerging science and new tools can be applied to study biodiversity-functioning-services relationships and multiple stressors at a large (ecosystem) scales.

In ecology, employing an ecosystem service-led approach may accelerate an understanding about the relationships between biodiversity-ecosystem services, thereby providing a vital evidence base for management. At the same time such research needs to be focused at large scales, those appropriate to the management issues facing marine systems. In particular this thesis follows recommendations by others (e.g. Worm *et al.*, 2006; Caliman *et al.*, 2010) in validating and using data from small-scale experiments to elucidate trends in biodiversity and functioning at larger spatial scales. As observational studies have great potential to add insight, relevance and generality to experimental and field studies but to date have typically been neglected from multiple stressor research, a more integrated framework in which individual studies can be incorporated is needed (Thrush & Lohrer, 2012) and should be a priority in the evolution of BEF and multiple stressor research. Description in the form of such relationships may also lead to better predictions of critical ecosystem thresholds including at what level the use of ecosystem processes, functions and services are compromised.

Accordingly, another important topic that needs much further attention is the interface between understanding ecosystem dynamics and managing human activities to facilitate resilience. Resilience thinking for example is now promoted as a broad socio-ecological approach (Walker & Salt, 2006, 2012; Pisano, 2012) which, in its linkage to environmental management, sustainability and society, mirrors the philosophy of the Ecosystem Approach. The concept of resilience provides a perceptive way of looking at ecosystems, acknowledging processes of change, the importance of diversity and the dangers of thresholds. Without resilience ecosystems can fail to deliver ecosystem services and their benefits to society (Biggs *et al.*, 2012; Oliver *et al.*, 2015; Alexander *et al.*, 2016). Although we know a great deal about ecosystems and how they function, we still have a poor understanding of thresholds and the 'slow variables' that control them (Walker *et al.*, 2012; Hughes *et al.*, 2013). This is potentially a dangerous knowledge gap, and there is need to promote research in this area and to put in place mechanisms to build resilience back into ecosystems. Environmental limits, monitoring

and regulations have a key role to play in building and maintaining resilience (Selkoe *et al.*, 2015; Österblom *et al.*, 2016). We need to review how these elements fit together, identify if any are lacking, and fit them within a broader natural resources framework that allows feedback and adaptive management of natural resources. How the resilience and functioning of species to ecosystems is likely to differ across different types of stressors, that originate from natural and social systems, and their different combinations of course also needs special attention. While this thesis draws attention to the importance that context dependency has on modulating the effects of multiple stressors, an essential goal of ecological risk assessment is to understand the effects of multiple stressors on individuals, populations, and, ultimately, groups of interacting species at different geographical and spatial scales (Bopp *et al.*, 2013; Gunderson *et al.*, 2016).

Traits-based approaches and ecological modelling are designed to integrate physical and biological processes by incorporating the mechanistic linkages of species (Trolle *et al.*, 2012; Edgar *et al.*, 2016). Using such techniques mechanistic linkages between the traits of species and their sensitivity (or vulnerability, which also includes recoverability) towards different stressors could be assessed across clearly defined gradients, in estuaries with varied levels of stressors. For example, with the burgeoning popularity of trophic network descriptors, not just within Ecopath but within the wider scientific community (Goldenberg *et al.*, 2010; Kolaczyk & Csárdi, 2014) it is likely that new comparisons of stressed vs. unstressed systems will emerge to test further the descriptive power of ascendancy and its associated variables. In doing so it will gradually become possible to track quantitatively changes in ecosystem status and to identify unequivocally when and by how much a system has been disturbed. Moreover, the systematic incorporation of functional measurements into ecological studies of multiple stressors (e.g. Piggott *et al.*, 2015b) will allow the development of better ecological assessments that can be applied at a wide range of spatial and temporal scales (Duggan *et al.*, 2015). However, despite the general recognition that functional attributes are important, their measurement is often not included in monitoring programs.

Further analysis should also be conducted to ascertain the nature of the specific interactions between nutrient loading, temperature and river-flow, and the mechanisms for which these stressors affect the study systems. As the current level of each variable was chosen to represent levels to which these systems could realistically be subjected and was based upon current anthropogenic and climatic monitoring data and projections, future studies could investigate a greater range of stressor levels. Future study should likewise analyse other combinations of stressors in these environments with nutrient loading, temperature and river flows being only three of many stressors identified. For instance heavy metal and other persistent contaminants are known to be a significant problem in the Tamar Estuary, with a wealth of literature published on the subject (see Dallas & Jha, 2015 and

references therein), and could easily be incorporated within the current modelling framework using the Ecotracer routine (e.g. Colléter *et al.*, 2015) in Ecopath. Similarly challenges remain in investigating other chronic problems commonly associated with estuarine systems such as hypoxia and geomorphological changes in large scale multiple stressor studies (Ainsworth *et al.*, 2011). Moreover, as benthic communities are well known to respond idiosyncratically to stressors and can adapt over long time scales (Emmerson *et al.*, 2001, Solan *et al.*, 2004; Brose & Hillebrand, 2016), longer or asynchronous application of stressors in this study may have resulted in different alterations of community structure, potentially allowing the identification of critical thresholds of change in these systems. Despite the challenges of integrating more than three stressors in any factorial manner, such results would be highly instructive both in improving our understanding of how stressors interact and would also allow scientists to provide more ecologically useful information to managers of coastal and marine systems where more than two stressors almost always coexist (Crain *et al.*, 2008). Future research efforts should therefore be aimed at determining the specific underlying ecological mechanisms of communities, so as to ascertain the nature of site specificity, in order to build up a generic picture of how combinations of multiple stressors interact, and their consequences to natural communities and systems.

Finally, while ecological knowledge is important to inform accurate estimates of marine ecosystem status, there is increasing pressure on the scientific community to support environmental management decisions with estimates of the economic value of marine ecosystem services (Beaumont *et al.*, 2008; Barbier, 2012; Börger *et al.*, 2014; Tuhkanen *et al.*, 2016). However information on medium to long term environmental change and the subsequent sustainable provision of ecological services is often missing from such valuation studies, limiting their effectiveness. For instance it is the absence of ecological production functions such as those developed in Chapter 4, that is often cited the limiting factor for public policy analysis of nature (Rosenberg & Sandifer, 2009). Comprehensive measurements of gains and losses of ecological proxies (e.g. biodiversity, functions) are therefore needed in appropriate ecological endpoints that will allow economists to capture aspects or features of nature that are most directly important to society. Such endpoints also need to be incorporated within useful decision frameworks (e.g. DPSIR; Atkins *et al.*, 2011) such as those explored in Chapter 6, in which economic assessment and trade-offs can be made. Therefore it is acknowledged that to further improve the models developed here (and indeed systems models in general), separate sub-networks could and should be developed that account for the cost/and benefits associated with environmental decision making. In the interim, this thesis has shown that there is some urgency to define research indicators, models and decision-support tools that can deal

with uncertainty in systems and the need to define the contributions such measures can make to understanding interactions among multiple stressors.

7.6 Concluding remarks

While some of the most pressing issues facing humanity today (e.g. anthropogenic impacts and climate change) are exceedingly complex and highly uncertain, there is an immediate need to account for the cumulative effects of multiple stressor interactions in ecological studies and conservation planning (Lundquist *et al.*, 2016; Neeson *et al.*, 2016; Thrush *et al.*, 2016). Delaying management decisions based on an inadequate understanding of socio-ecological-economic information or linkages, may no longer be considered an option, as even small delays in reducing environmental pressures can result in breaches to environmental thresholds. While the development of indicators and fully coupled hybrid models linking anthropogenic and environmental systems, embedded within research frameworks (e.g. DPSIR) will ultimately enable us to better conceptualise complex socio-ecological systems, in the short-term interactions among stressors will continue to generate unexpected ecological surprises. Pending a general framework for predicting interactions, perhaps the most important priority for conservation planning is to continue to bolster biological resilience as science catches up—and scales up—to the many challenges and uncertainties multiple stressors present in a rapidly changing world.

Main thesis findings

- Outcomes of the structural and functional indices approaches gave similar outcomes to the more holistic network models, implying that management measures to reduce nutrient inputs in both the Tamar (2005) and the Eden (2015) estuaries had indirectly improved benthic “health” and ecosystem functioning (and by proxy ecosystem services) under nutrient reductions.
- The results of this study conclude that the Tamar and Eden estuaries have historically been naturally hypernutrified, a common feature of estuaries and were not eutrophic as indicated by the balance of a suite of symptoms of each ecosystems pathology. While it is not likely that the areas will become eutrophic as the organic inputs to the estuary continue to decrease, it is not possible to demonstrate conclusively that the areas will not be sensitive to future change.
- Despite similarities in the response to nutrient reductions, additional (e.g. temperature and river flow) stressors impacting each site were found to be highly context dependent, varying between and within the geographic locations. Further analysis should therefore be conducted

to ascertain the nature of the specific interactions between nutrient loading, temperature and river-flow, and the mechanisms for which these stressors affect the study systems.

- Considering the influence of multiple stressors on ecosystem attributes and emergent properties two implicit trends were apparent in both systems: 1) an increase of river flow and/or thermal stress (either singularly or in combination) had greatest effects on each systems network characteristics 2) The greatest impacts on each system were when the three stressors were combined.
- This study revealed that the cumulative nature of localised anthropogenic stressors, including increased river flow and changes in nutrient loading, needs to be analysed in combination with large scale environmental drivers (in this case temperature), ecosystem characteristics and emergent properties as by focusing on one or a subset of properties, key information may be missed and interpretation may be misleading. This encapsulates the holistic approach needed for ecosystem based management (EBM). This study also suggests that multiple anthropogenic stressors can alter the properties of estuarine benthic food webs, with the possibility for stressors to act in an additive, synergistic or antagonistic manner.
- The experience of using conceptual models (Ulanowicz's "Window of Vitality & BBNs) helped to represent the projections of multiple stressor impacts, in such a way that trade-offs, which might need to be considered when exploring alternative scenarios, could be deduced or estimated quantitatively. The results of Ulanowicz's, "Window of Vitality suggested that the resilience of both systems would be compromised under the impact of multiple stressors and the Eden system in particular is in danger of crossing an ecological tipping point. Concurrently, results of the BBNs suggested that the probability of achieving "good" environmental status in both system was severely reduced under the combined impact of multiple stressors.

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Appendix 3B Biological matrix ‘taxa by traits’ for the Tamar.

Table 3.33 Matrix ‘taxa by traits’ for the Tamar. The 33 different taxa are fuzzy coded for the 10 different trait categories (see Table 3.2 for the meaning of the labels).

	Maximum Size (cm)			Adult Longevity (Years)			Growth Form			Feeding Method				Environmental Position						
	Very Small	Small (1-2)	Medium-Large	Large (11-Short (<2)	Medium	Long (>5)	Articulate	Bivalved/	Vermiform	Tubicolous	Deposit D	Filter/susp	Opportun	Predator	Hyperben	Epibenthic	Endobenthic			
Ampharete grubei		3				3					3	2	2				3			
Ampharete acutifrons		3				3					3	2	2				3			
Arenicola marina				3			3			3		3					3			
Baltidrilus costata			3		3					3							3			
Capitella capitata			3		3					3			3				3			
Caulerliella killariensis			3			3			3				3				3			
Cerastoderma edule	1			3				3		3				3						
Chaetozone gibber		3			3					3		3					3			
Corophium volutator		3			3			3				2	2				3			
Cossura pygodactyla			3			3				3		3					3			
Cossura longocirrata			3			3				3		3					3			
Cyathura carinata		3			3			3				3					3			
Galathowenia oculata			3			3					3	3	1				3			
Gammarus locusta		3			3			3				3					3			
Hediste (nereis) diversicolor				3	3					3		2	2	2	2		3			
Heterocirrus zetlandicus		3				3				2	2	2	2				3			
Macoma balthica		3				3			3			3	3				3			
Magelona johnstoni			3			3			3			3					3			
Manayunkia aestuarina		3			3						3	1	3				3			
Melina palmata		3			3	2	2				3	3	1				3			
Nephtys hombergii				3		3				3				2	2		3			
Peringia ulvae	3				3				3			3				3				
Phyllodoce maculata			3			3				3				3	3		3			
Polydora cornuta		3			3					3	3	3	3				3			
Pygospio elegans		3			3				3			3					3			
Retusa obtusa		3				3			3						3		3			
Retusa truncatula		3				3			3						3		3			
Scrobicularia plana				3			3			3				3			3			
Spio filicornis			3			3					3	3					3			
Streblospio shrubsolii		3				3				3		3					3			
Tubificoides amplivasatus			3			3				3		3					3			
Tubificoides benedii			3			3				3		3					3			
Tubificoides insularis			3			3				3		3					3			
	Mobility in Sediment			Reproductive Methc Bioturbation Functional Type				Salinity Preference			Ecological Group									
	Fixed Tub	Limited m	Slow free	Free Move	Gonochor	Hermaphr	Surfical	M	BoDiffuso	Upward	Cl	Downward	Regenerat	<5	5-20	>20	Sensitive	Indifferen	Tolerent	Very Toler
Ampharete grubei		3				3					3	3			2	2	3			
Ampharete acutifrons		3				3				3	3				2	2	3			
Arenicola marina		3				3				3					2	2	2			
Baltidrilus costata			3			3			3						2	2				3
Capitella capitata		3				3				3					1	3				3
Caulerliella killariensis		3					3												3	
Cerastoderma edule	3		3			3			3						1	3	3			3
Chaetozone gibber		3				3			3											
Corophium volutator				3	3			3					2	2	2				3	
Cossura pygodactyla			3			3			3						3	3				3
Cossura longocirrata			3			3			3						3	3				3
Cyathura carinata		3				3			3				2	3	3				3	
Galathowenia oculata	3					3			3					3	3	3				
Gammarus locusta			3			3			3						2	3	3			
Hediste (nereis) diversicolor				3	3					3			3	3	2				3	
Heterocirrus zetlandicus		3				3			3					2	2					3
Macoma balthica		3				3			3					3	3				3	
Magelona johnstoni		3				3			3					3	3	3				
Manayunkia aestuarina		3				3			3					1	3			3		
Melina palmata		3				3				3	3			2	2				3	
Nephtys hombergii			3			3			3					3	3			3		
Peringia ulvae		3				3			3					2	2	2				3
Phyllodoce maculata			3						3					3	3	3			3	
Polydora cornuta		3				3				3	3			2	2	2				3
Pygospio elegans		3				3				3	3				2	2				3
Retusa obtusa			3						3						3	3			3	
Retusa truncatula			3						3						3	3			3	
Scrobicularia plana		3				3									3	3				3
Spio filicornis		3								3	3				3	3				3
Streblospio shrubsolii		3				3				3	3				3	3	2			3
Tubificoides amplivasatus			3			3			3						2	2				3
Tubificoides benedii			3			3			3						2	2				3
Tubificoides insularis			3			3			3						2	2				3

Appendix 3C Biological matrix ‘taxa by traits’ for the Eden.

Table 3.33 Matrix ‘taxa by traits’ for the Eden. The 28 different taxa are fuzzy coded for the 10 different trait categories (see Table 3.2 for the meaning of the labels).

	Maximum Size (cm)		Adult Longevity (Years)			Growth Form		Feeding Method				Environmental Position								
	Very Small (<Small (1-2cm)	Medium (3- Large (11-20 cm)	Short (<2)	Medium (2-5)	Long (>5)	Articulate A	Bivalved/Turbin	Vermiform Segment	Tubicolous	Deposit D	Filter/suspension	Opportunistic/Predator P	Hyperbenthic I	Epibenthic EPE	Endobenthic ENB					
<i>Ampharete</i> sp.	3			3					3	2	2				3					
<i>Arenicola marina</i>			3		3			3		3					3					
<i>Bathyporeia sarsi</i>	3			3		3				3					3					
<i>Capitella capitata</i>		3		3					3		3				3					
<i>Cerastoderma edule</i>		3			3			3			3				3					
<i>Lepidochitona cinerea</i>		3			3			3		3			3							
<i>Corophium volutator</i>		3		3			3			2	2				3					
<i>Crangon crangon</i>		3			3		3					3	3		3					
<i>Donax vittatus</i>		3			3			3				3	3		3					
<i>Eteone longa</i>		3		3					3				3		3					
<i>Eteone picta</i>		3		3					3				3		3					
<i>Eurydice pulchra</i>	3			3			3				3				3					
<i>Gammarus locusta</i>		3		3			3			3				3						
<i>Hauistorius arenarius</i>		3								2	2				3					
<i>Macoma balthica</i>		3				3		3		3	3				3					
<i>Mya arenaria</i>			3			3		3			3				3					
<i>Mytilus edulis</i>			3			3			3	3					3					
<i>Nephtys hombergii</i>			3		3				3			2	2		3					
<i>Nereis diversicolor</i>			3	3					3	2	2	2	2		3					
<i>Peringia (Hydrobia) ulvae</i>	3			3				3		3			3							
<i>Retusa obtusa</i>		3						3					3		3					
<i>Scoloplos armiger</i>			3		3					3					3					
<i>Scrobicularia plana</i>		3			3			3			3				3					
<i>Spio filicornis</i>		3		3					3	3					3					
<i>Sthenelais boa</i>		3										3	3		3					
<i>Tellina tenuis</i>		3						3		3	3				3					
<i>Tubificoides benedii</i>		3		3					3	3					3					
	Mobility in Sediment		Reproductive Method			Bioturbation Functional Type			Salinity Preference				Ecological Group							
	Fixed Tubes	Limited movement	Slow free m	Free Movement	FK Gonochoristic	C Hermaphrodite	H Epifauna	Surficial	Modifier	S Bodifusor	B Upward Conveyor	U Downward	(Regenerator)	<5	5-20	>20	Sensitive I	Indifferent II	Tolerant III	Very Tolerant IV
<i>Ampharete</i> sp.	3			3							3	3					2	2		3
<i>Arenicola marina</i>	3				3						3						2	2	2	
<i>Bathyporeia sarsi</i>		3		3						3				2	2	2	3			
<i>Capitella capitata</i>	3			3							3				1	3				3
<i>Cerastoderma edule</i>	3			3						3				1	3	3				3
<i>Lepidochitona cinerea</i>		3			3			3							2	3			3	
<i>Corophium volutator</i>			3	3				3						2	2	2				3
<i>Crangon crangon</i>			3	3				3						1	3	3	3			
<i>Donax vittatus</i>	3			3				3						1	2	2	3			
<i>Eteone longa</i>		3		3						3					2	2				3
<i>Eteone picta</i>		3		3						3					2	2				3
<i>Eurydice pulchra</i>		3		3				3				3	3	3	3		3			
<i>Gammarus locusta</i>		3		3				3							2	3	3			
<i>Hauistorius arenarius</i>		3		3				3					3	3	2	3				
<i>Macoma balthica</i>		3		3				3							3	3				3
<i>Mya arenaria</i>		3		3				3					2	2	2				3	
<i>Mytilus edulis</i>	3			3				3							2	3				3
<i>Nephtys hombergii</i>			3		3					3				3	3				3	
<i>Nereis diversicolor</i>				3	3					3				3	3	2				3
<i>Peringia (Hydrobia) ulvae</i>		3		3				3						2	2	2				3
<i>Retusa obtusa</i>		3		3				3							3	3			3	
<i>Scoloplos armiger</i>		3		3						3					3	3	3			
<i>Scrobicularia plana</i>		3		3										3	3	2				3
<i>Spio filicornis</i>		3		3						3	3				3	3				3
<i>Sthenelais boa</i>		3		3						3					3	3			3	
<i>Tellina tenuis</i>		3		3				3						2	3	3	3			
<i>Tubificoides benedii</i>			3		3					3					2	2				3

Appendix 4A Ecopath references used in the constriction of the “diet matrix” sub-routine.

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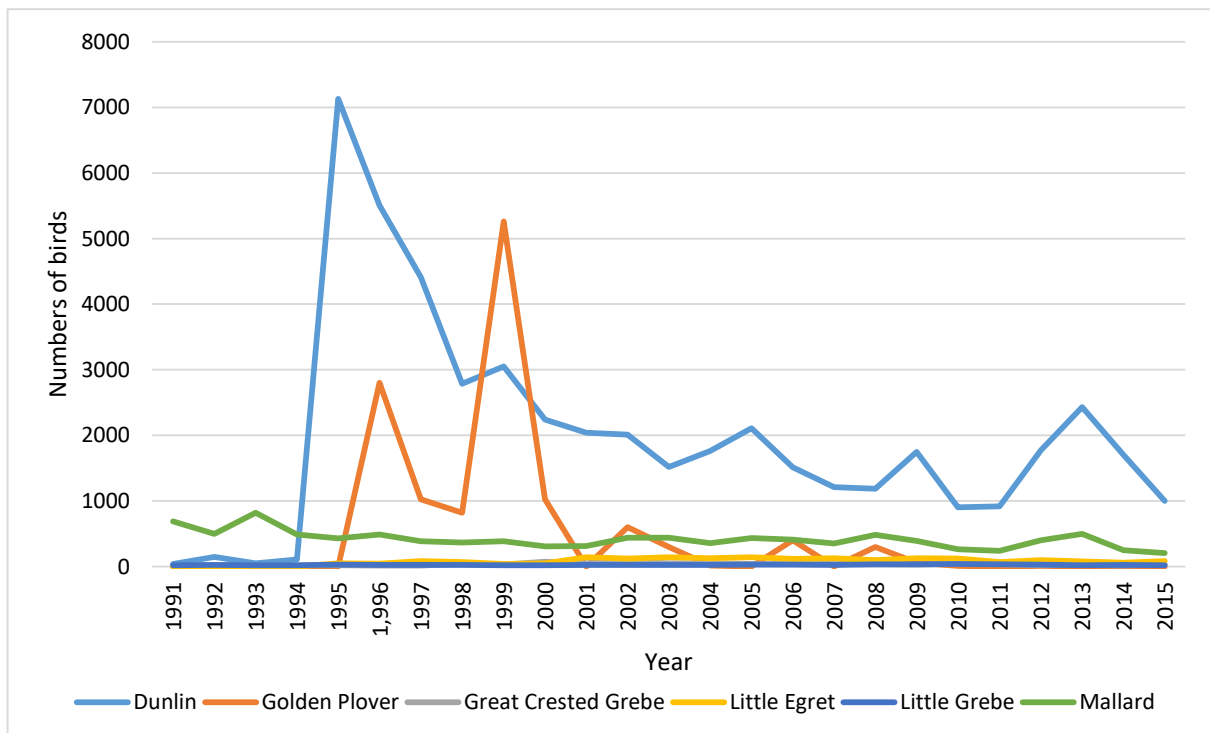
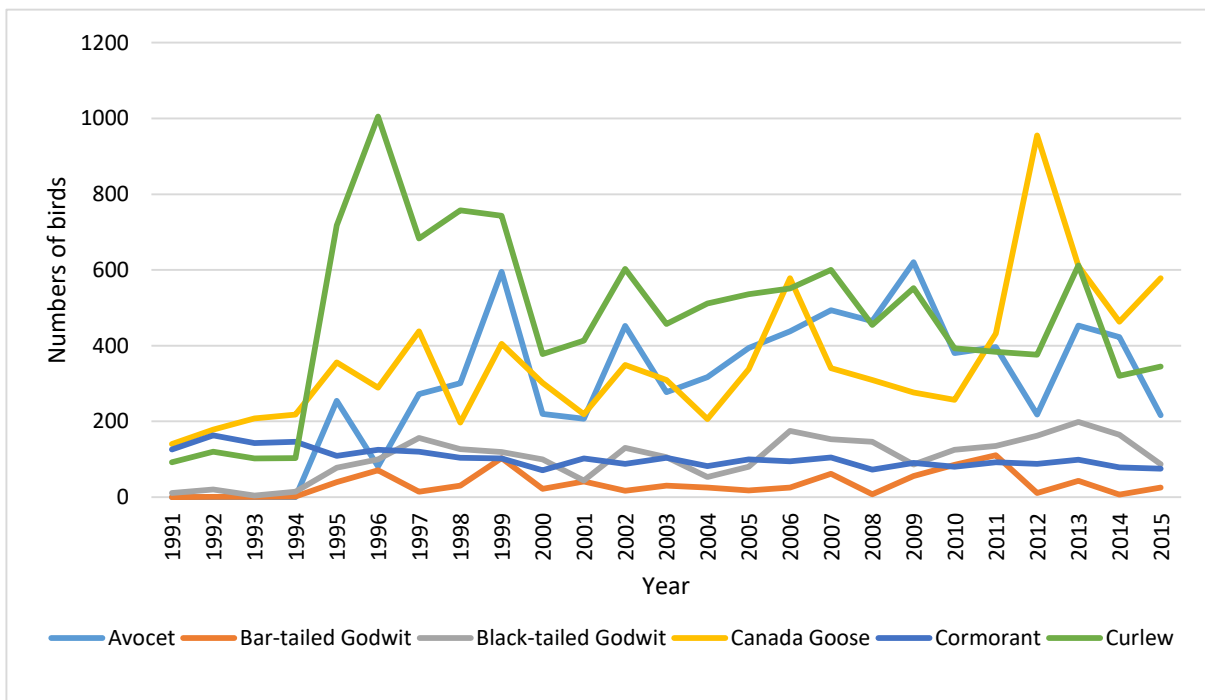
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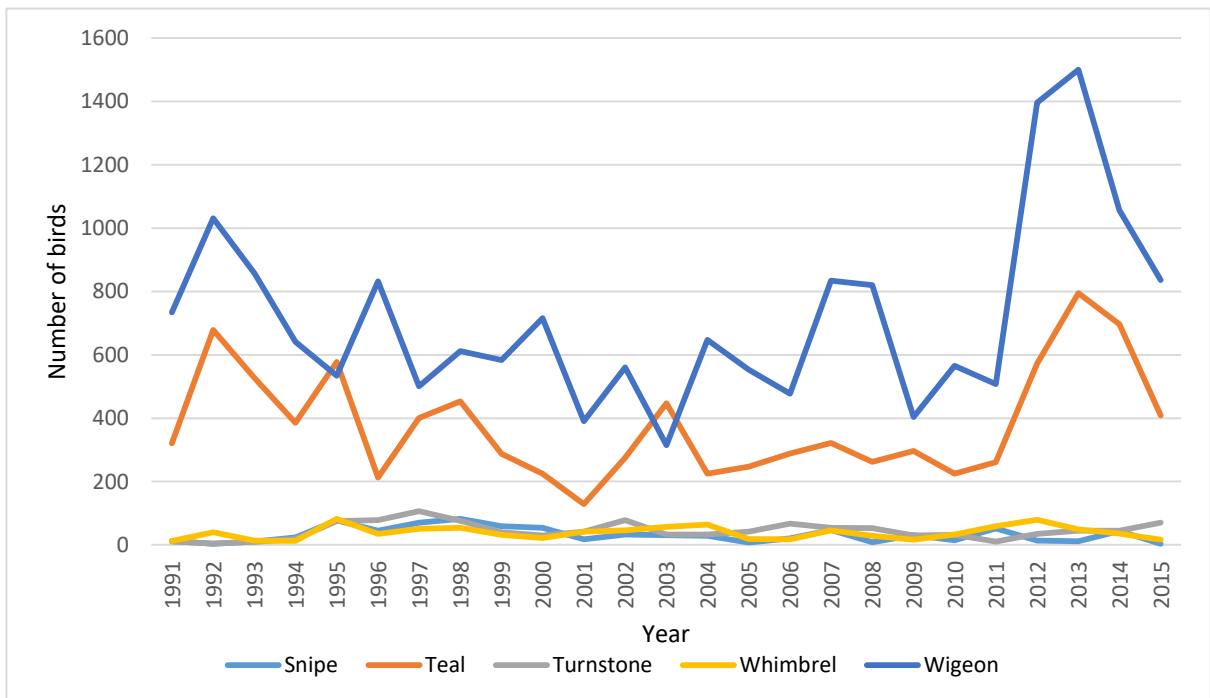
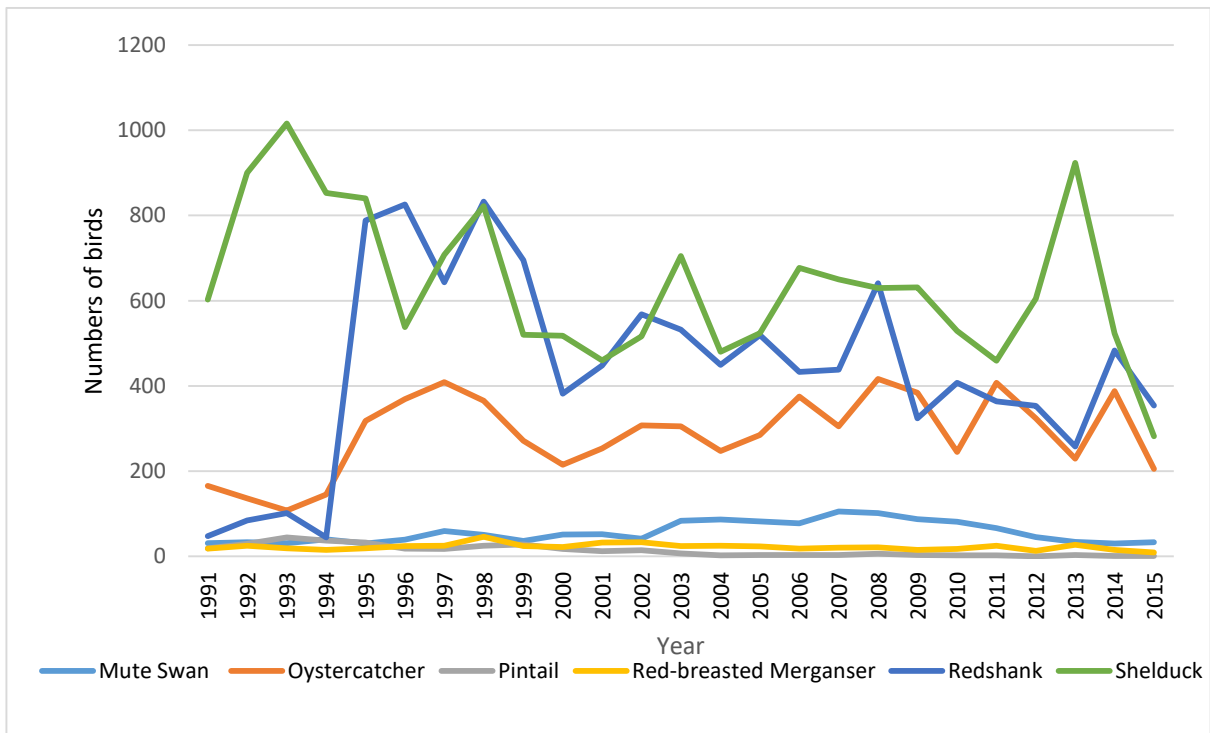
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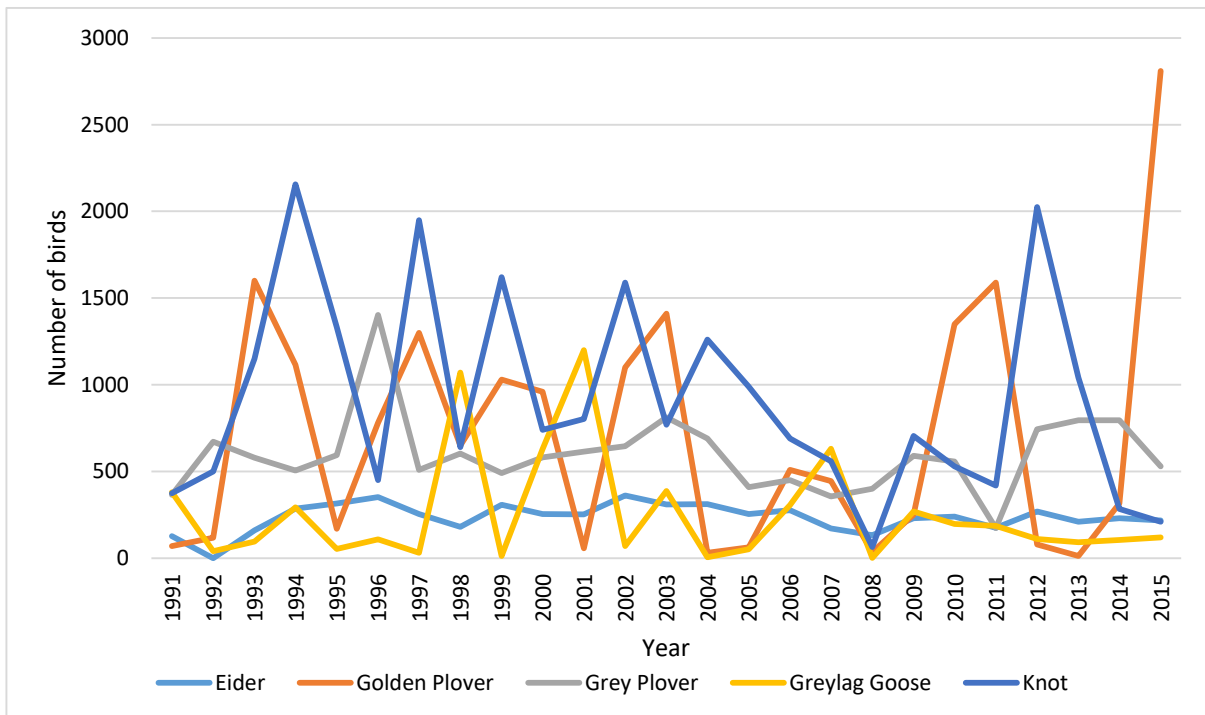
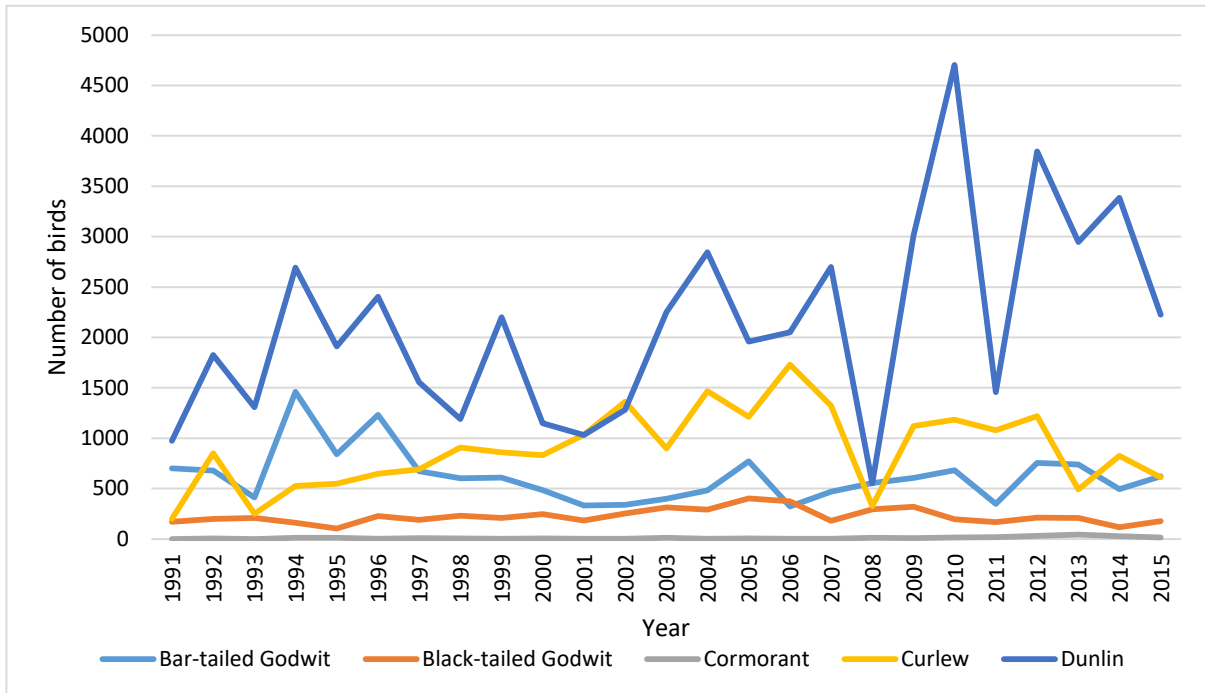
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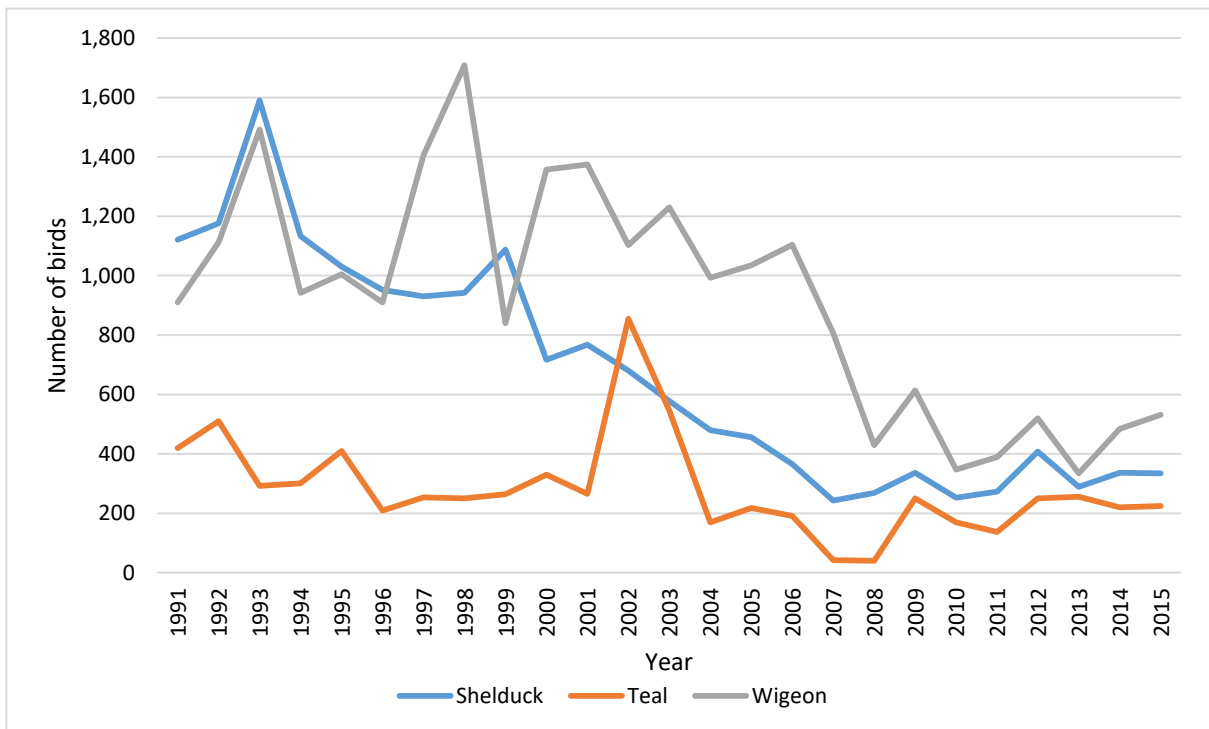
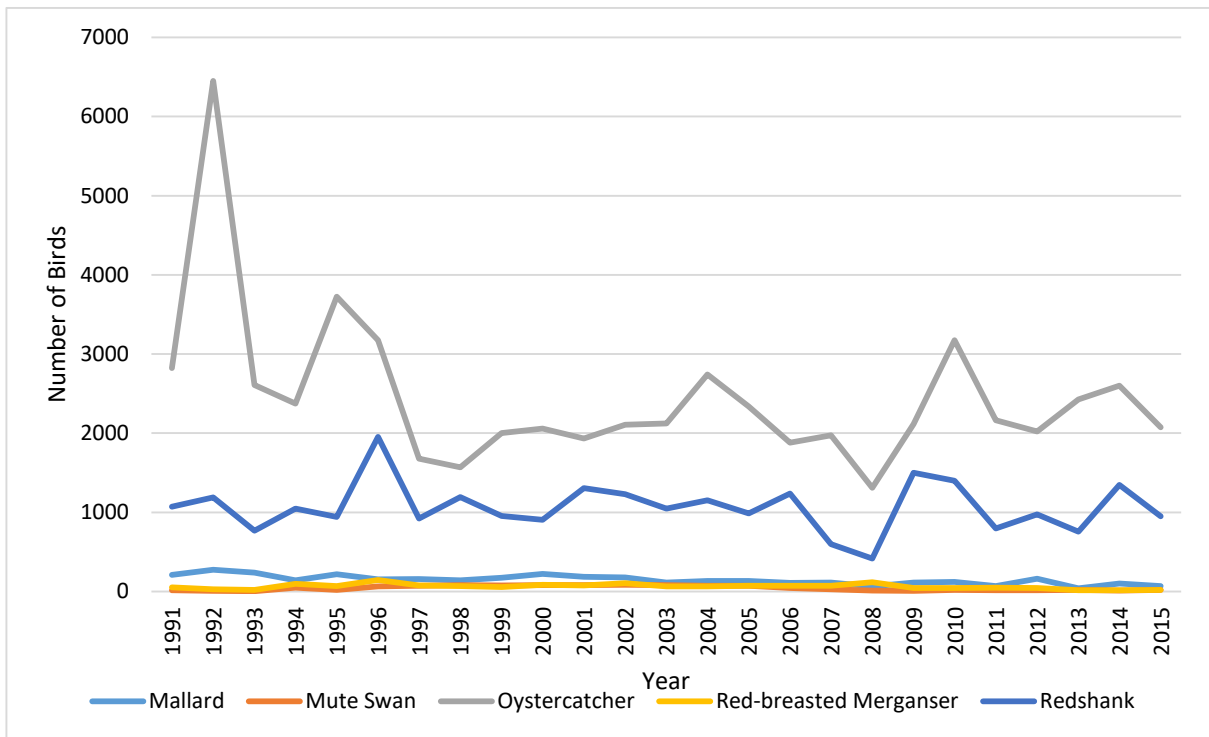
Appendix 4B Bird numbers on the Tamar estuary 1990-2015





Appendix 4C Bird numbers on the Eden estuary 1990-2015





Appendix 6A Glossary table - Bayesian Network (BN) terminology

Glossary table - Bayesian Network (BN) terminology (Note: The following table includes a list of specific terminology commonly used when discussing BBN according to Fenton & Neil., (2013)).

Term	Definition	
Arrows, Arcs (or links)	Represent direct dependencies between the variables (nodes) of the BBN. There is an arc (link) for each dependency identified between any two variables. A directed arc from X to Y, encodes an assumption that there is a direct causal or influential dependence of X on Y; the node X is a “parent” of Y.	
Bayesian Network (BN)	An explicit description of the directed dependencies between a set of variables. The description is in the form of a directed graph and a set of node probability tables (NPTs).	
Directed graph (DG)	Also referred to as the topology or structure of the BBN, consists of a set of nodes and arcs. There must be no cycles in the graph (for example, if there is an arc from X to Y and from Y to Z then there cannot be an arc from Z to X. This avoids circular reasoning in the model.	
Divide and conquer approach	An algorithmic technique to solve a problem, either directly because solving that instance is easy (typically, because the instance is small) or by dividing it into two or more smaller instances.	
Dynamic discretisation	An algorithm designed to estimate and process the continuous distributions linked to the numeric nodes in a BBN. Computing the probability distribution of a numeric node requires a discretisation, which is calculated dynamically (hidden from the model user) with an accuracy that depends on the implementation.	
Idioms	Specific BBN fragments that represent very generic types of uncertain reasoning. The idioms relate to the graphical structure of a BBN and not to the underlying probabilities.	
Idiom types	Cause-consequence	Models the uncertainty of a causal process with observable consequences.
	Definitional/Synthesis	Models the synthesis or combination of many nodes into one node for the purpose of organizing the BBN. Also models the deterministic or uncertain definitions between variables.
	Induction	Models the uncertainty related to inductive reasoning based on populations of similar or exchangeable members.
	Measurement	Models the uncertainty about the accuracy of any measurement
Joint cumulative distribution	If X and Y are discrete random variables, the function given by: $F(x,y)=P(X\leq x, Y\leq y)=\sum_{s\leq x}\sum_{t\leq y}f(s, t)$ for $-\infty < x, y < \infty$ Where $f(s, t)$ is the value of the joint probability distribution of X and Y at (s, t), is the joint cumulative distribution of X and Y. Joint distributions enables reasoning about the relationship between multiple events.	
Junction tree structure	In graph theory, a tree decomposition is a mapping of a graph into a tree that can be used to define the tree-width of the graph and improve the performance when solving certain computational problems.	
Likelihood function	This is the conditional probability function for those variables for which there is data.	
Marginal distribution	If X and Y are discrete random variables and $f(x, y)$ is the value of their joint probability distribution at (x, y), the functions given by: $g(x) = \sum_y f(x, y)$ and $h(y) = \sum_x f(x, y)$ are the marginal distributions of X and Y, respectively. In each case, they are estimated by ‘removing’ either y or x.	
Node	The nodes correspond to the variables specified for the problem that wants to be modelled.	
Node Probability Tables (NPTs)	Each node A has an associated probability table, called the Node Probability Table (NPT) of A. This is the probability distribution of A given	

	the set of parents of A. For a node A without parents (also called root/input node) the NPT of A is simply the probability distribution of A.
Numeric node	A numeric variable is associated to a numeric node. It can be discrete (e.g. counts of the number of humans in a population) or continuous (e.g. amount of rain that falls in an area).
Partitioned expressions	A specific type of expression to specify a NPT in Agenarisk. It allows the modeller to specify the NPT of a node conditioned on the states of the parent node.
Prior distribution	In BBN terminology it is used to describe the prior (initial) distribution for some variables (network nodes). The priors reflect what is known (or not known) about the parameters of interest.
Posterior distribution	This is the distribution for the variables (nodes) after data has been added to the model and an inference has been performed.
Rank node	Any node whose states represent a ranked ordinal scale (Low, Medium and High) is defined as a ranked node.
Uninformed prior	Refers to a prior that contain as little information as possible. Using this distribution the modeller signals nothing is known about parameter to which it is associated.

Appendix 6B Bayesian Network nodes and their explanations.

Node	Term	Definition
River flow	Explanation	Simple, basic ranking of a region's climatologic conditions based on river flow.
	Node type	Ranked (Low, Baseline, High)
	Node Probability Table	Based on chapter 5 scenarios.
	Procedure followed to estimate NPT	The node includes 3 states: Low, Baseline and High. These are ordered according to the impact they have on the ecosystem. Ample literature evidences show mild conditions have the least impact, whilst extreme climatic conditions can be very harmful.
Temperature	Explanation	Simple, basic ranking of a region's climatologic conditions based on temperature.
	Node type	Ranked (Low, Baseline, High)
	Node Probability Table	Based on chapter 5 scenarios.
	Procedure followed to estimate NPT	The node includes 3 states: Low, Baseline and High. These are ordered according to the impact they have on the ecosystem. Ample literature evidences show mild conditions have the least impact, whilst extreme climatic conditions can be very harmful.
Nutrients	Explanation	Simple, basic ranking of a region's climatologic conditions based on Nutrients.
	Node type	Ranked (Low, Baseline, High)
	Node Probability Table	Based on chapter 5 scenarios.
	Procedure followed to estimate NPT	The node includes 3 states: Low, Baseline and High. These are ordered according to the impact they have on the ecosystem. Ample literature evidences show mild conditions have the least impact, whilst extreme climatic conditions can be very harmful.
Total abiotic effect	Explanation	Aggregated function of the effect that the complete set of 'Abiotic components' considered (see above) have on the affected estuarine and coastal ecosystem
	Node type	Ranked (Low, Baseline, High)
	Node Probability Table	Probability of the previously defined abiotic indices

	Procedure followed to estimate NPT	The node includes 3 states: Low, Baseline and High. These are ordered according to the impact they have on the ecosystem. Ample literature evidences show mild conditions have the least impact, whilst extreme climatic conditions can be very harmful.
Ecosystem biomass	Explanation	Rate of the potential loss of benthic ecosystem biomass due to the state of the local estuarine and coastal ecosystem.
	Node type	Integer
	Node Probability Table	Used a partitioned expression (Fenton & Neil, 2013) to specify the node's NPT.
	Procedure followed to estimate NPT	Biomass values estimated by Ecosim.
Ecosystem structure, resilience, functioning and ES provisioning.	Explanation	An estimate of the ecosystem level indicators underlying the estuarine and coastal ecosystem under observation (3 point scale).
	Node type	Ranked (Low, Baseline, High)
	Node Probability Table	Based on chapter 5 scenarios.
	Procedure followed to estimate NPT	Ecosystem indicators were estimated by Ecosim and ranked on their impact relative to the predetermined baseline conditions (Tamar 2005; Eden 2015).
Good Environmental Status (GES)	Explanation	An Index that measures the impact that the 'Abiotic components' have on the intrinsic health of an estuarine and coastal ecosystem.
	Node type	Rank (Very Low, Low, Medium, High, Very High)
	Node Probability Table	Used a partitioned expression (Fenton & Neil, 2013) to specify the node's NPT.
	Procedure followed to estimate NPT	The impact on ecosystem health from the 'Abiotic components', varies from one ecosystem to another according to the ecosystem indicators calculated above. The probability of a less resilient ecosystem to be seriously affected will be higher if the rate of impact of the 'Abiotic components' is above a certain threshold. This is expressed using a boolean expression to set the mean of the distribution function related to this node.



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A conceptual framework for assessing the ecosystem service of waste remediation: In the marine environment

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abstract

In the marine environment, the ecosystem service of Waste Remediation (WR) enables humans to utilise the natural functioning of ecosystems to process and detoxify a large number of waste products and therefore avoid harmful effects on human wellbeing and the environment. Despite its importance, to date the service has been poorly defined in ecosystem service classifications and rarely valued or quantified. This paper therefore addresses a gap in the literature regarding the application of this key, but poorly documented ecosystem service. Here we present a conceptual framework by which the ecosystem service of WR can be identified, placed into context within current ecosystem classifications and assessed. A working definition of WR in the marine context is provided as is an overview of the different waste types entering the marine environment. Processes influencing the provisioning of WR are categorised according to how they influence the input, cycling/detoxification, sequestration/storage and export of wastes, with operational indicators for these processes discussed. Finally a discussion of the wider significance of the service of WR is given, including how we can maximise the benefits received from it. It is noted that many methods used in the assessment, quantification and valuation of the service are currently hampered due to the benefits of the service often not being tangible assets set in the market and/or due to a lack of information surrounding the processes providing the service. Conclusively this review finds WR to be an under researched but critically important ecosystem service and provides a first attempt at providing operational guidance on the long term sustainable use of WR in marine environments.

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1: Introduction

Of the many definitions of Ecosystem Services (ES) Fisher *et al.*, (2009) produced a widely used formulation of “the aspects of ecosystems utilised (actively or passively) to produce human well-being”. This paradigm of ES is an increasingly prevalent concept, but one poorly defined ES is the service of Waste Remediation (WR). In the marine environment, the ES of WR enables humans to utilise the natural functioning of ecosystems to process wastes, potentially without detrimental effect. Without this service humans would either have to process all wastes on land or suffer serious health implications of wastes remaining in a toxic and available state. This would not only impact human wellbeing directly, but would also impact the overall ecological health of marine ecosystems. Whilst preserving the ES of WR is vital in its own right, it is also important for ensuring the provision of a whole host of additional marine ES and benefits that the service provides including: food security, raw materials, recreational amenity, shoreline protection, sequestration of carbon and an equitable environment. The sustainable exploitation of benefits provided by WR depends on our ability to manage waste inputs in relation to the capacity of ecosystems to remediate wastes. This no-damage limit or “capacity for assimilation” is highly variable depending on the ecosystem, waste types, and other pressures on the given environment (Islam & Tanaka., 2004; Nellemann *et al.*, 2008). There is also an added complication that loading limits are dependent on human judgments as to what is an acceptable level of human health risk or structural change to an ecosystem. While it is in society’s interest to ensure that discharges of waste into the ocean are minimal (and in turn reduce the need for the service of WR), in an increasingly human dominated planet there is a growing necessity to utilise and value all aspects of the natural environment to improve health and well-being.

Previously the ES of WR has been defined by the Millennium Ecosystem Assessment (MA) as the service of “Water purification and waste treatment” but as “Water quality regulation” by the UK’s National Ecosystem Assessment classification (NEA); and more recently as “Mediation of waste, toxics and other nuisances” by the Common International Classification of Ecosystem Services (CICES). While many of these classifications are remarkably similar, having been built using the same principles, and are frequently referenced in the literature they are often poorly understood and rarely quantified (Beaumont *et al.*, 2008). It is considered that one of the causes of this is that there are so many classifications available causing confusion and creating an illusion of complexity. More specifically in the case of WR there has also been a lack of application of these sub-classifications in terms of assessing, quantifying and valuing the contribution WR has on the wider marine environment, due to a lack of information surrounding the processes providing the service. This is a fundamental problem for environmental practitioners with the service of WR often being undervalued in policy design and implementation and is therefore at risk of being ignored in future policy decisions.

As a central component to communicating any subject is a readily understandable terminology that is applied consistently, this paper aims to clarify some of the potential confusion surrounding the application of the service of WR and provide a utilitarian guide for academics and policy makers who wish to understand and utilise the ES of WR in the marine environment. Whilst there is always a risk of simply developing another classification, there are obvious benefits of combining the knowledge inherent within different classification systems to develop a more comprehensive understanding of a particular service. This review therefore begins by giving an overview to the different waste types present in the marine environment to ensure consistency of understanding. This is followed by drawing on the current literature and previous analyses of ecosystem services frameworks to provide a coherent definition of WR in the context of marine ecosystems. Following classification, the mechanisms and ecosystem processes involved in the provision of the WR alongside suitable indicators and methods of assessment are then detailed and discussed. Finally a general discussion of the wider significance of the service of WR is given, including how we can maximise the benefits received from it, and possible future research directions for managing it sustainably. Overall as the decision-making context will differ substantially from place to place, issue to issue, and over time, the framework is designed to be sufficiently general to ensure that it can be applied across a wide range of situations, and flexible enough to encourage the user to develop and adjust the classification as required, for example by adding new components if required, and potentially repositioning components within the classification as required. This will result in a situation specific classification of WR that can be developed

according to the purpose of the ecosystem service assessment (Costanza., 2008; Fisher *et al.*, 2009; Johnston & Russell., 2011).

While WR occurs in all marine environments; from estuaries to the continental shelf, pelagic, demersal and deep sea habitats the focus of this paper will be on continental shelf ecosystems and their associated seabeds with the rationale that many of the ecosystem benefits provided directly or indirectly by the service (e.g. clean water, recreational amenity, shoreline protection, fish and shellfish (food)) will be realised by humans on land or in areas surrounding the continental shelf margins (Pauly & Christensen., 1995; Martínez *et al.*, 2007). Equally, there is extensive evidence that specific habitats found in brackish and coastal water habitats (e.g. saltmarshes and mangroves) can provide an important bioremediation function, (Agunbiade *et al.*, 2009; Santos *et al.*, 2011; Mucha *et al.*, 2011; Ockenden *et al.*, 2012; Wu *et al.*, 2014 Ribeiro *et al.*, 2014). While these habitats will not be discussed in detail here (as they are well-referenced elsewhere), the fundamental principles considered in this paper can still be applied to these habitats.

Further, in previous ES classifications there has been a tendency to limit ES to biotic components, with abiotic outputs often receiving less attention or being addressed inconsistently in ES classification systems (Van der Meulen *et al.*, 2016). However abiotic processes such as fluid advection and photochemical transformations play an important role in the provision of WR both in terms of the introduction of wastes into the marine environment but also in their dilution, degradation and dispersal (Bottrel *et al.*, 2014), allowing wastes to remain in the system but at harmless levels (Hinga *et al.*, 2005). This review therefore highlights how to include abiotic flows as an inherent part of an ecosystem services classification with the hope that in doing so, the application of the WR concept can be made more holistic and consistent and will optimize its integration power for practical planning and decision making.

As the marine environment is fundamentally different to that of the terrestrial especially with respect to the physicochemical environment (Carr *et al.*, 2003), there is also an inherent benefit to developing a specific classification for the service of WR in marine systems. Notable differences between the application of the marine, compared with the terrestrial service, would arise from the greater extent and rate of dispersal of water borne compounds (nutrients, organic wastes, contaminants and organisms) as opposed to those in air (Logan., 1985), as well as from expanded scales of connectivity among near-shore communities in the marine environment (Di Lorenzo., 2015). In addition lateral and vertical advective transport (e.g. currents and upwelling) processes also have the effect of augmenting local primary and secondary production at a much greater magnitude in marine than in terrestrial systems (Duggins *et al.*, 1989) allowing natural remediation to occur at much higher rates. As a consequence, it should be noted that some of the waste remediation strategies and frameworks developed and discussed here with regards to the marine realm may not be directly transferable to terrestrial systems.

2. Key Wastes in the Marine Environment

In recent history the sustainable threshold of use of WR has been exceeded by high waste loading rates in many regions (Levin & Möllmann., 2015). In developing countries the impact of contaminated water from inadequate wastewater management is one of the most important factors undermining world health (Corcoran *et al.*, 2010). Incorrectly managed or unmanaged discharges of wastewater have serious implications on biological diversity, ecological integrity and the ongoing capacity of marine ecosystems to deliver the service of WR (Schwarzenbach *et al.*, 2010; Qadir *et al.*, 2010). Within developed countries one of the most important impacts on the provisioning of WR is the enhanced input of nutrients (eutrophication); mainly nitrogen and phosphorus from agricultural sources into rivers, lakes and oceans (Howarth *et al.*, 2011). The impacts of eutrophication is of major global concern as it affects the functioning of marine ecosystems through the exacerbation and rapid growth of eutrophic deoxygenated zones (Diaz & Rosenberg., 2008). These pressures present a global threat to human health and well-being as well as significant challenges for environmental waste management.

The contributing factor for the amount and types of wastes released into the marine environment ultimately depends on the choices or behaviours of governments, organisations, and individuals. Through the implementation of policies and regulation, efficient waste management strategies can promote the

functioning of healthy marine ecosystems (Potts *et al.*, 2014). With the recognition that waste management is highly variable across countries, with waste substances often managed in different ways, by different bodies, there is an increasing need for a holistic approach to ensure environmental protection (Perry *et al.*, 2010). One such approach nominally cited as the ‘Ecosystem Approach’ follows a growing recognition for the need to evaluate ecological functions and the value of the ES they provide as a whole, so that none are overlooked when management decisions are made (Halpern *et al.*, 2008; Mangi *et al.*, 2011). This increased awareness over the past few decades has led to considerable management efforts to reverse the historical approach of dumping wastes, including nutrients, into the oceans (Halpern *et al.*, 2012; Moore *et al.*, 2013b; Jefferson *et al.*, 2014).

However, to enable such holistic waste management strategies, a comprehensive understanding of all sources of waste and how they enter and move through the marine environment is vital. The term waste is often defined as “substances present in the marine environment which would not otherwise be there in the absence of anthropogenic activity and/or is present at a higher level than typical levels” (Hinga *et al.*, 2005). It includes compounds and materials that might otherwise be useful in a different context, such as oil after an oil spill or nutrients once they are no longer at their site of application. In addition, living organisms in the form of pathogens (e.g. bacteria, viruses, fungi) can be included as biological contaminants or “wastes” (Elliott., 2003). The terms ‘pollution’ or ‘pollutant’ are often used interchangeably with the terms waste or contaminant, but is different in being the point at which the levels become damaging in the environment (Chapman., 2007). As such, the term ‘pollution’ and its derivatives are not generally used here as the focus of this ES assessment is to review the processes supporting the service of WR and not the impacts of wastes on the ecosystem.

Humankind produces a large variety of wastes that are introduced into the marine environment either by accident or by design (see Table 1). Although there is no attempt here to systematically assemble and estimate the damage to humans and ecosystems done by past waste releases, a few examples of the types, issues involved, and magnitude of damages of wastes that exceeded ecosystems’ capacity are provided in order to illustrate the importance of managing wastes. Generally, for the purpose of this paper waste types can be divided into three groups:

- 1) Nutrients & organic matter;
- 2) Biological wastes/contaminants
- 3) Persistent contaminants.

A distinction can be made between these three forms of waste in terms of their movement through the marine system and their potential to be broken down by abiotic and biotic processes. The more slowly a waste is cycled or detoxified in the environment (that is the more persistent it is), the greater the chance of it reaching harmful levels in the local or global environment and the greater effects of bioamplification of harmful substances across food chains (Clements., 2000).

For instance, most nutrients and organic matter are normal components of natural ecosystems and will ultimately be completely broken down into their basic components and completely re-cycled by the system (Anderson & Sarmiento., 1994) or can be buried and removed from the normal turnover pathways. Inputs of these wastes often only become detrimental to ecosystem service provision when they reach levels high enough to impair or modify the ability of an ecosystem to function (Woodward *et al.*, 2012). This is often the case in many coastal ecosystems where accelerated flows of anthropogenically-derived organic nutrients, particularly nitrogen and phosphorous compounds from municipal waste and agricultural discharges, provide point and diffuse sources of water quality degradation (Conley *et al.*, 2009; Antón *et al.*, 2011; Sun *et al.*, 2013). Thus the bioavailability of the organic nutrient pool is an important issue in the assessment of this ES if the waste problem in question is a direct result increased nutrients or organic matter for example in the case of eutrophication.

In addition to organic wastes, biological wastes) in the form of harmful bacteria, viruses, fungi and some parasites (e.g. Elliott., 2003; 2011; Olenin *et al.*, 2011) are an increasing problem in marine coastal waters. Many pathogens constitute a pressure emanating from outside a system often as a result of human activities

such as unregulated sewage disposal or dumping of ballast water. Many of these biological wastes entering the marine environment lose viability, under the relatively harsh conditions and may be ingested and utilised for food (therefore being remineralised) by other organisms in the environment without detrimental effects. However under favourable environmental conditions vector-borne pathogens may be maintained at unsustainable levels within hosts or in the environment altering ecosystem functioning and degrading human health.

Many natural and synthetic wastes such as pesticides, fertilizers, petroleum products, metals, plastics, and other manufactured goods, are also becoming ever more prevalent in the marine environment (Fleming *et al.*, 2006; Knott *et al.*, 2009; Naser., 2013) and are a serious threat to environmental health due to their persistence, toxicity and ability to accumulate through food chains (Schwarzenbach et al., 2010). This is largely a consequence of increasing agricultural and industrial processes, either intentionally or as by-products (Halpern *et al.*, 2003) but some compounds, such as petroleum-derived compounds, are also naturally formed and are considered persistent contaminants when added to the ocean in excess such as from oil spills. As many these wastes are persistent against biotic and abiotic degradation processes they are often considered to follow pathways to export and are effectively removed from the immediate environment, although may be partially refined to a less toxic state (Jones & De Voogt., 1999). While metals cannot be degraded to harmless materials, they can be bound organically essentially storing them and rendering them unavailable.

Overall, combined with source, timescales of bioavailability of all wastes should be considered as an important assessment criterion when implementing this service. Wastes are likely to partition into two 'pools': a labile pool, that can be utilised in time frames relevant to water quality processes of interest in the receiving water, and a refractory pool, that is decomposed very slowly and essentially inert for relevant time frames (Wetzel., 1983). While the addition of CO₂ released by fossil fuel burning and other human activities is now realised to have a large impact on basic ocean chemistry (Gattuso & Hansson., 2011; Riebesell & Gattuso., 2015) CO₂ as a waste will not be covered explicitly as part of the service of WR, as CO₂ and its derivatives should be considered under the ES of Carbon Sequestration and Storage, linked to the provision of an equitable climate (e.g. Beaumont *et al.*, 2014; Garrard & Beaumont., 2014).

Table 1 Overview of the major categories of wastes in the marine environment.

Waste category	Character of source	Waste types/examples	Impacts and consequences	Potential for cycling/detoxification/export/sequestration/storage	Timescale to remediation	Relevant management initiatives
Nutrients and organic matter	Point and/or diffuse sources	N, P, Si, Sewage both human and agricultural, Atmospheric deposition.	In excess eutrophication, Harmful algal blooms, Anoxic conditions.	Organic matter can usually be completely broken down into its basic components and in the form of nutrients can be used by the biological components of a system. May also be sequestered and stored in the sediment.	Dependent on the form: Nutrients (minutes to hours) in the presence of acceptable conditions. Organics (hours to days) for readily degradable waste and (months to years) for resistant materials.	Control the release of sewage wastes. Control fertiliser application. Enforcement of emission standards.
Biological wastes/contaminants Pathogens	Point and/or diffuse sources	Herpes virus, Typhoid fever, Dysentery and Cholera	Human health, Mortality, Malnutrition, Loss of viable fisheries.	Endemic and non-endemic pathogens may lose viability in an environment or may be utilised as food for other organisms.	Dependent on lifecycle. Non-endemics typically (hours to days). Endemics may live within or on their host for (hours to years)	Reduction of agricultural inputs to waterways Improving sanitation, hygiene and safe drinking water.
Persistent contaminants Persistent organic pollutants (POPs)	Point and/or diffuse sources	Herbicides, fungicides, insecticides, petroleum products, TBT PCBs, OCPs, HCHs, DDTs, PAHs.	Bioamplification in food chain, Diverse health effects.	Likely to be photodegraded and degraded by microbes and fungi completely destroying the inherent toxicity of the waste. Many have a high affinity to adsorb onto particles and may be stored in the seabed.	Lighter compounds such as hydrocarbons can degrade within (hours to days). Heavier and more persistent compounds are typically (decades to centuries) or indefinitely under anaerobic conditions.	Control of organic chemical runoff from agricultural land, and pesticide misuse. Good industrial manufacturing practices. Monitoring of the global shipping trade. Phase out existing POPs, confine existing sources, and prevent use of new POPs.
Toxic trace metals	Point and/or diffuse sources	Arsenic, cadmium copper, lead, mercury.	Bioamplification in food chain, Metal remobilization, Acute toxicity, Chronic neurotoxicity	Cannot be degraded. May be bound to other material (e.g. Organics). Must be diluted, stored or exported from the environment.	Dependent on environmental setting, such as rates of dilution or precipitation processes. Often (decades to centuries)	Metal neutralization or Removal. Introducing effective nontoxic reagents
Radio-nuclides	Point and/or diffuse sources	³ H, ¹⁴ C, ⁸⁵ Kr, ⁹⁰ Sr, ⁹⁹ Tc, ¹²⁵ Sb, ¹²⁹ I, ¹³⁴ Cs, ¹³⁷ Cs, ⁵⁴ Mn, ⁵⁵ Fe, ¹⁰⁵ Ru, ¹⁰⁶ Ru.	Radioactive exposure both internal and external from the food web and the sediment.	Natural radioactive decay to stable isotopes– some half lives may be very long 14C over 1000 years. May be sequestered to organic material. Likely to be diluted or stored in the seabed.	Half-lives of medical-use radionuclides range from (hours to weeks). Half-lives of radioactive wastes from nuclear reactors range from (decades to millennia).	Containment of radionuclides and monitoring of mitigation processes including natural attenuation.
Plastics	Point and/or diffuse sources	Macroplastics, microplastics, nanoplastics .	Ingestion or phagocytic uptake. Leaching or dissociation of toxic contaminants from the plastics.	Will degrade under the influence of many abiotic processes including: photo, thermal, oxidative and hydrolytic degradation pathways. This is often followed by remineralisation by microbes.	Degradation generally classified according to the process causing it. Plastics exposed to a range of environmental degradation mechanisms (years to centuries) while those buried or in anaerobic conditions can last indefinitely.	Quantifying the input of plastics to the marine environment. Management actions to reduce terrestrial and shipping inputs.
Emerging and novel wastes	Point and/or diffuse sources	Nanoparticles, flame retardants, oestrogens, pharmaceuticals, endocrine disruptors.	Largely unknown. May interfere in the normal functioning of organisms .	Ecosystems may be very ineffective At detoxifying novel chemicals. Many are resistant to abiotic and biodegradation processes.	Half-lives are still unquantified for many of the emerging wastes. Some of the better studied compounds e.g. pharmaceuticals are thought to have short half-lives (days to years).	Active monitoring and stringent regulation on novel chemicals discharged in wastewater, agriculture and industry.

3: Defining the Ecosystem Service Waste Remediation in the Marine Environment.

The Millennium Ecosystem Assessment (MA) is the most widely accepted ES classification for assessing the benefits derived from marine ecosystems. The MA, (2005) classification system has been criticised because it confuses services (means) and benefits (ends) (Boyd & Banzhaf., 2007; Wallace., 2008) and supporting services with ecosystem functions (TEEB., 2010); which in economic terms may lead to double counting of services. To overcome this there are now a multitude of more precise ES classifications, including; The Economics of Ecosystems and Biodiversity classification (TEEB., 2010), the UK's National Ecosystem Assessment classification (NEA., 2011); The Common International Classification of Ecosystem Services (CICES., 2013); Fisher *et al.*, (2009); Haines-Young & Potschin., (2010); Atkins *et al.*, (2011); Beaumont *et al.*, (2007;2008). Despite these extensive theoretical developments, the practical application of these ES classifications remains limited (Daily *et al.*, 2009; Naidoo *et al.*, 2008). This section aims to clarify some of the potential confusion and provide a guide to the future application of the ecosystem service of WR in the marine environment.

With regards to terminology and in line with the MA and NEA frameworks, the ES of WR is classified here as a regulating service. Further, building on the classifications of the service outlined in the MA, TEEB, NEA, CICES and the outline of the service in Beaumont *et al.*, (2007) “the removal of pollutants through storage, burial and recycling”, the service of “Waste Remediation” is defined here as:

“The removal of waste products from a given environment by ecosystem processes that act to reduce concentrations of wastes by the mechanisms of cycling/detoxification, sequestration/storage and export”

The mechanisms responsible for removing or degrading waste through an associated suite of ecosystem processes are outlined as follows:

1. **Cycling/Detoxification:** *Processes that act to change wastes into harmless or less toxic compounds.*
2. **Sequestration (storage):** *Processes that sequester waste in the environment in such a way that they are not biologically available and do not exhibit toxicity. Essentially stored sequestration may be reversible if conditions are altered, with the wastes returned to harmful forms.*
3. **Export:** *Processes that transport waste from a given bounded system, including atmospheric, benthic and lateral export.*

Each set of ecosystem processes are fundamental transformations which occur in the natural environment driven by physical and chemical reactions, both biotic and abiotic, which may include surface, solute or cellular processes (Paterson *et al.*, 2012; De Groot *et al.*, 2010). Many of these processes occur at very small scales but cumulatively combine to produce a transfer of energy or material often recognised as ecosystem functioning and resulting in the flow of ES (Paterson *et al.*, 2011). In terms of WR, humans can utilise these biophysical processes to remediate wastes which otherwise would need to be treated or stored in order to avoid health implications. There is however the consideration that the definition outlined may be context dependent (Langenheder., 2010); with different processes becoming services depending on environmental and management conditions. For example, some export processes may also concentrate wastes into localised ‘hot spots’ of relatively high waste concentrations potentially acting as an ecosystem disservice in the affected area.

As a consequence, WR also warrants more detailed investigation as human activities and wider global changes have, and continue to, significantly impact all marine ecosystems (Harley, *et al.*, 2006; Hoegh-Guldberg & Bruno., 2010) In turn, these impacts affect the capacity of the marine environment to remediate our wastes. To understand how the WR service will be affected by these continuing impacts it is necessary to understand the mechanisms and processes supporting the provision of this service. Understanding these processes will also enable the sustainable utilisation and management of this service, and also maximise benefit received from it.

4: Identifying Processes and Indicators to Measure the Ecosystem Service of Waste Remediation

While many managers strive for instantaneous information to enable mitigation of harmful wastes entering the marine environment, measurements at high levels of organisation (e.g. community and ecosystem levels) are often slow to obtain and difficult to interpret. This difficulty is attributed to a lack of knowledge with respect to specific elements of the ecosystem structure and processes (Börger et al., 2014). Therefore, to understand the potential WR capacity of an ecosystem, and how to sustainably manage this ES, it is essential to understand the processes which support its provision including identifying indicators that can be used to measure these processes. To aid this, we discuss the ecosystem processes influencing the provisioning of WR and finish with a short discussion of different quantitative indicators of this service with suggestions for their measurement.

Each of the compartments outlined in the waste pathways (Figure 1) describe the transport and fate of a given waste in a marine environment and are provided by a group of associated ecosystem processes (Table 2) which may amplify or reduce concentrations of substances entering a marine environment. This list is not exhaustive, but was derived during an interdisciplinary expert workshop (UKOA project, <http://www.oceanacidification.org.uk>) by combining the processes listed in other ecosystem service classifications (e.g. MA, NEA, TEEB, CICES) regarding the service of WR. Alongside are suggested practical guidelines for selecting indicators relevant to the service of WR derived from Hattam *et al.*, (2015). As viewing the ecosystem as a series of steps allows discussion to focus on individual compartments of the specific system in question and how each compartment, rather than individual processes can be regulated, each of the steps involved in the remediation of wastes is discussed in more detail below.

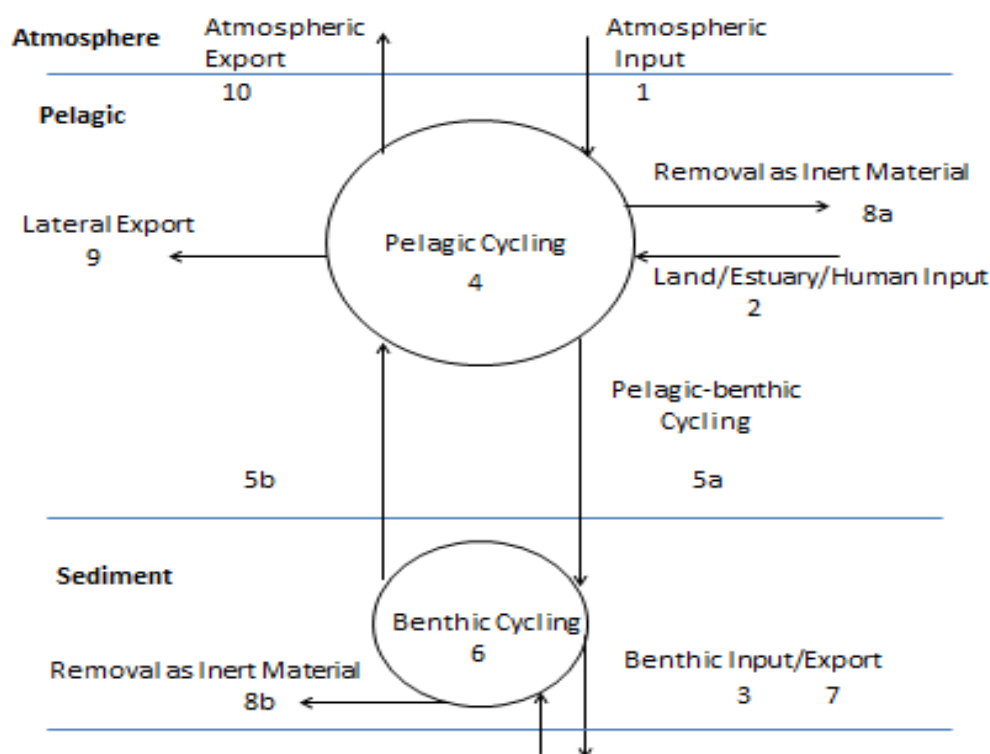


Figure 1: The processes and flows potentially involved in the transport and fate of a given waste in a marine environment grouped broadly into 3 categories: **Inputs** (steps 1 Atmospheric, 2 Land/Estuary/Human, and 3 Benthic); **Cycling/Detoxification** (steps 4 Pelagic, 5a,b Pelagic-benthic 6 Benthic); **Sequestration/Storage and Exports** (steps 7 Benthic, 8 Removal from system as inert materials, 9, Lateral export and 10 Atmospheric export.).

Table 2: Ecosystem processes & Indicators relevant to the processing of wastes in the marine system ✓ = relevant to a particular numbered step in **Figure 2**

Categories of ecosystem processes	Examples of ecosystem processes	Inputs		Cycling/ detoxification		Exports & sequestration (storage)			Description of the processes	Indicators of processes and their measurement (adapted from Hattam <i>et al.</i> , (2015))	
		1	2	3	4	5a, b	6	7			8a & b
Abiotic transformation	Photochemical, hydrolytic, oxidative and thermal degeneration, radioactive decay, redox reactions.				✓	✓	✓	✓	✓	Abiotic processes in the environment that chemically alter wastes. Often leads to a structural change that may not reduce the toxicity of a waste, but it may be a first step toward detoxification and act as a catalyst for many other processes.	Absolute levels of waste in the water column or sediments.
Abiotic Transport	Advection, aerosol formation, chemical partitioning, dilution, dispersion, dry deposition, mixing, precipitation from solution, tidal currents, volatilization, water residence time, wind, wave action, wet deposition.	✓	✓	✓	✓	✓	✓	✓	✓	How chemicals are moved by abiotic processes in the environment and thus affect the fate and reduce the concentration of the substances in the environment.	Diffusivity and advection flux determined, for example, from hydrodynamic modelling.
Biogeochemical cycling	Biomass production, diagenesis, remineralisation.			✓	✓	✓	✓	✓		The overall cycling of chemicals through the ocean as modified by chemical, physical, and biological processes.	Degradation and mineralization rates measured as microbial metabolism, concentrations of organic matter over time and space or chemical analysis for contaminants.
Biotic transports	Migration, propagule dispersal, bioamplification (food chain transfer).					✓			✓	Movements of wastes in the ocean by the: uptake of organisms, settling of organic materials and food chain transfers.	Production and biomass at different trophic levels.
Biotic transformation	Bioaccumulation (living), biodilution, biosorption (non living), dehalogenation.				✓	✓		✓		Processes by which organisms, take up the waste substance, transform it and thereby reduce the concentration of the waste substance in the organism and or in the surrounding area.	Body biomass of toxicants.
Biotic habitat modification	Bioturbation biodeposition, bioirrigation.			✓		✓		✓	✓	All transport processes carried out by organisms that directly or indirectly affect sediment matrices. These process a pivotal role in the delivering of the service through the storage and degradation of organic matter, mediating the exchange of gases to the atmosphere, storing, degrading and transforming materials, as well mediating the water and habitat quality.	Bioturbation measures such as: burrow extent, turnover and stability per unit time, sediment accumulation and deposition.

4.1 Ecosystem Processes Responsible for Inputs of Wastes into the Marine Environment (Steps 1-3)

4.1.1 Step 1 Atmospheric Input

On a global scale marine ecosystems contribute to air quality by removing waste products from the atmosphere via atmospheric exchanges (O'Driscoll *et al.*, 2013). This exchange of gases and volatile organic compounds across the sea surface interface (**step 1**) represents an important pathway in transport of volatile wastes into the marine ecosystem and is controlled by abiotic physicochemical transport processes (Wurl & Obbard., 2004). These interactions are complex with the direction of exchange – water to air or vice versa – relative to the concentrations of the compounds in each phase and their relative solubility or volatility. In the case of persistent chemicals, nutrients and organic wastes such as POP's (Moore *et al.*, 2013a), the main pathway through which they reach the marine environment is via 3 major processes : 1. Dry deposition of particle-bound pollutants, 2. Diffusive gas exchange between the atmosphere and surface ocean, 3. Wet deposition (rain) (Gioia *et al.*, 2011).

4.1.2 Step 2 Land/Estuary/Human Input

Due to their proximity to human development, estuarine environments act to convey terrestrially derived wastes onto the continental shelf (**step 2**). Waste inputs derived from terrestrial urban wastewater, agricultural and industrial activities are the major contributors for the majority of the nutrient, pathogen and xenobiotic compounds entering the marine environment (Mason., 2012). This is amplified by natural abiotic transport processes such as leaching and lateral advection often in the form of storms acting as a locus of input for transient wastes into the marine environment (Dagg *et al.*, 2004; Mckee *et al.*, 2004). For example, a number of studies have shown how the high unidirectional flow of estuarine systems drives the movement of plastic debris into the oceans (Browne *et al.*, 2010; Andrad., 2011; Cole *et al.*, 2011; Ballent *et al.*, 2012).

4.1.3 Step 3 Benthic Input

Once in the environment the ultimate fate of many non-buoyant wastes is deposition to the ocean sediments (**step 7**) as mediated by various water column transport processes. Benthic inputs are therefore largely a consequence of the materials previously accumulated or deposited in the sediments. However due to the dynamic nature of these environments it is inevitable that eventually many persistent wastes will be re-circulated back into the environment and become “new” sources of waste (**step 3**) (Perelo., 2010). Sediments may be disturbed by a number of abiotic processes such as across sediment water flows, wave action, tidal currents (e.g. from floods and storms) leading to the re-suspension of contaminants across a range of spatial and temporal scales (Schiedek *et al.*, 2007). In addition, burrowing fauna can significantly influence the stability, mixing, burial and re-suspension of particles and solutes at the sediment-water interface, through the processes of bioturbation and bioirrigation (Richter., 1936; Rhoads., 1974; Volkenborn *et al.*, 2007). These processes modify the ability of the sediment to act as sinks of contaminants and therefore their upward redistribution into the environment (Gilbertson *et al.*, 2012, Mayor *et al.*, 2013). POPs and metals for example are groups of contaminants known to desorb into a dissolved phase from sediments and again enter into the environmental cycle (Garcia-Flor *et al.*, 2009). Consequently, sediments may not be final sinks of persistent contaminants, depending on the presence and activity of burrowing fauna and physics, and on the presence of other interacting stressors like ocean acidification and hypoxia, that can exacerbate contaminant leaching from sediment bonds and their bioavailability (Roberts *et al.*, 2013, Atkinson., 2007).

4.2 Ecosystem Processes Responsible for Cycling & Detoxification of Wastes in the Marine Environment (Steps 4-6)

4.2.1 Step 4 Pelagic Cycling & Detoxification

Under natural conditions organic wastes entering the pelagic pathway (**step 4**) are often completely degraded at this stage to harmless compounds by biogeochemical cycling processes such as remineralisation by marine microbes and accumulation into biomass (Cunliffe *et al.*, 2011) preventing harmful symptoms such as eutrophication. In coastal shelf-sea environments liable nutrients and high-nutrient content organics are more likely to be rapidly turned over and cycled than in open ocean systems (Proctor *et al.*, 2003), lending to different remediation strategies depending on the environmental context. For more persistent contaminants

abiotic transformation processes that occur at the ocean-atmosphere interface such as photochemical, hydrolytic and thermal degeneration reactions act to change the structure and reduce the toxicity of a waste. For many complex wastes such as crude oil, POPs and plastics these processes may be the first step towards remineralisation (Guitart *et al.*, 2010) and complete detoxification. Rates of detoxification by abiotic transformations may vary widely between contaminants even those with similar structural compositions.

4.2.2 Step 5 a, b Pelagic –Benthic Cycling & Detoxification

Many of the same biogeochemical cycling and detoxification processes that occur in the upper surface layers also occur in the underlying water column (**step 5 a&b**) but to a much lesser extent. For waste compounds not completely degraded at the surface, bacterial activity along with phytoplankton, zooplankton and fish (Echeveste *et al.*, 2010; Szlinder-Richert *et al.*, 2009) provide much of cycling connectivity between the pelagic and benthic compartments facilitating further decomposition of available wastes on route to the sediment.

4.2.3 Step 6 Benthic Cycling & Detoxification

Once wastes enter the benthic pathway (**step 6**), bacterial cycling of wastes is facilitated by biogeochemical and physical processes in the sediment (e.g. diagenetic alterations, particle mixing, compaction, redox state reactions). Specifically the process of reductive dehalogenation is an important biodegradation process undertaken by anaerobic microbes and is responsible for making numerous xenobiotic compounds less toxic and more readily degradable (Payne *et al.*, 2011). Combined with hydrolytic degradation, dehalogenation is the most likely degradation pathway followed by remineralisation for many contaminants entering the benthic pathway (Mohn & Tiedje., 1992). In addition, increased rates of transport of particulates and solutes mediated by burrowing fauna through bioturbation and bioirrigation enhance the depth and complexity of redox transition zones (Queiros *et al.*, 2011, Pischedda *et al.*, 2008) promoting remediation. This affects not only the bioavailability of contaminants through changes in the chemical speciation of sediment bound metals (Teal *et al.*, 2009) but also their position in the sediment (Reibsel *et al.*, 1996). Ultimately this creates a juxtaposition of different biogeochemical niches for bacteria (Bertrics *et al.*, 2009), including those necessary for the degradation wastes (Cuny *et al.*, 2007).

4.3 Ecosystem Processes Responsible for the Sequestration (Storage) & Export of Waste in the Marine Environment

4.3.1 Step 7 Benthic Sequestration (Storage) & Export

One particularly important process is that influences the sequestration, storage and export of many persistent aquatic wastes is that of sediment partitioning and scavenging. Often described by the general concentration mechanism known as “solvent switching” (Macdonald *et al.*, 2002) - whereby low-solubility chemicals and metals in the dissolved phase, adsorb to organic particles and/or organisms such as phytoplankton before being removed (or scavenged) from surface waters and delivered to the sediments by sinking particles and vertical animal migration (Fowler & Knauer., 1986; Suedel *et al.*, 1994). In this way both organic matter and persistent contaminants can be sequestered, stored and then exported to the sediments (**step 7**). Once in the sediment, vertically oriented burrowing fauna can then act to convey organic matter and by association contaminants down into the sediments by the processes of bioturbation and bioirrigation (Shull & Yasuda., 2001; Kristensen *et al.*, 2011) where they may be indefinitely stored (Ciutat *et al.*, 2003). Whilst this process may not directly reduce the toxicity of a waste, essentially the waste material has been utilised in such a manner that the input of waste is no longer evident in the immediate environment. Aquatic sediments may therefore be among the media with highest concentrations of wastes and depending on the persistence of the waste, the sediments may remain contaminated even if the inputs are stopped.

4.3.2 Step 8a, b Removal from System as Inert Materials

Some waste materials may be sequestered in the environment in such a way that they are not biologically available and do not exhibit toxicity (**step 8a, b**). The sequestration of certain metals in marine sediments by acid volatile sulphides is one such an example. These metals are bound into a mineral form that is not biologically available and as long as there are sufficient sulphides to bind all the metals, no toxicity is

exhibited (Di Toro *et al.*, 1992). Toxic compounds may also be taken up directly by organisms and held within biological tissue. In natural systems a variety of organisms are known to accumulate and bind contaminants which might include industrial and agricultural wastes (Vijayaraghavan & Yung, 2008; Hung *et al.*, 2014). Biosorption and bioaccumulation are physiochemical processes, which involve interactions and concentration of toxic xenobiotic contaminants in the biomass, of either living (bioaccumulation) or non-living (biosorption) matter (Gad., 2009). Both these processes play an important role in natural storage and export of wastes in the marine environment and occur in virtually all biological wastewater treatment processes and in all bioremediation technologies (Rehman *et al.*, 2006; Kan *et al.*, 2013).

4.3.3 Step 9 Lateral Export

Hydrological connections (**step 9**) provide important export pathways for many persistent and non-degradable wastes such as metals, which can be transported horizontally to other bio-geophysical compartments and in the long term ‘off-shelf’ and effectively removed from the immediate ecosystem. Reduction of waste concentrations in a single body of water is best understood as a result of two abiotic transport processes: dispersion (dilution by mixing into larger volumes of water) and advection (water moving downstream). Both of these processes reduce the concentration of the waste at its point of entry in the ecosystem and facilitate the lateral export of wastes between bio-geophysical compartments. Wastes removed by currents or diluted into larger bodies of water may in turn support other services such as the regulation of pathogens and the reduction of contaminants in seafood (Keeley *et al.*, 2013). Fast flowing or dynamic ecosystems will increase the rate of waste dilution and mobilisation from sources (Johnson *et al.*, 2009) while slow flowing systems will likely lead to areas of relatively high waste concentrations. However this capacity for waste transfer is finite and under the influence of high waste-loading rates the intrinsic capacity of the ecosystem may be overwhelmed such that wastes build up locally or even across whole regions.

4.3.4 Step 10 Atmospheric Export

For more volatile contaminants atmospheric export is an important export pathway from the water column (**step 10**). Some chemicals such as POPs and hydrocarbons present as dissolved gases in the surface ocean can build up to supersaturated concentrations in surface waters and can be lost to the atmosphere by the process of negative dry deposition (McVeety & Hites., 1988; Palm *et al.*, 2004). In the case of petroleum compounds, most of the volatile fractions evaporate into the atmosphere shortly after they have been released into the environment. While atmospheric and lateral exports are fundamental processes in the provisioning of the service many wastes that are inputted into the entire ocean and atmosphere of the planet have reached concentrations above acceptable levels, thus reducing the ability of organisms to detoxify them.

4.4 Developing Quantitative Indicators of WR

Regardless of the source, the management of waste inputs and the processes driving them is an important function of human societies and is essential to understand all potential sources of wastes if we are to safeguard human well-being into the future. However with such a complex array of factors influencing the fate of a waste, it is not a simple matter to predict the persistence of a waste in the wider environment. Under the guidelines provided by Hattam *et al.*, (2015), evidence and success of the service in action may be observed directly from physiochemical observations such as environmental degradation and mineralisation rates measured as bacteria metabolism, concentrations of organic matter over time and space, chemical analysis for contaminants or by diffusivity and advection flux (see Table 2).

In the absence of physiochemical data, specific responses by living organisms can act as indicators or biomarkers in response to exposure to waste, acting as retrospective and predictive signals of change within an environment (Au., 2004). Biomarkers can be general or specific, reflecting the general stress or relative environmental disturbance of a system and may indicate capacity for waste assimilation if waste inputs are known. Further by using different bio-monitoring indices, effects can be measured at different levels of biological organisation, from the molecular to the ecosystem level. For example microbes, algae, mussels, oysters and other sensitive benthic species are often used as sentinel organisms in bio-monitoring and ecosystem modelling studies (e.g. Schubert *et al.*, 2013; Keeley *et al.*, 2013). Success of many cycling and

detoxification processes can be suggested by the presence of resilient and healthy communities indicated for example by: biodiversity levels or numbers of sensitive species. However how to use these indicators to demonstrate avoided change, such as the avoided impacts of a waste incident, still remains a challenge. Therefore, future development of indicators within the context of assessing WR is a greatly needed research area. Evaluating what waste compounds are present (**steps 1-3**), their possible rate of degradation (**steps 4-6**) and the likelihood of persistence in the environment (**steps 7-10**) is an important element of this ES assessment and when combined with biological monitoring data will enable the development of qualitative indicators of the service of WR that can be compared over time and space to denote change in the system.

5. Discussion

In summary, the service of WR is of critical importance on many levels, providing an important function for human societies and is essential in the promotion of human well-being. The WR service provided by the marine environment is a pure public good in terms of its use for the disposal and eventual remediation of waste. This has direct implications for the waste management of companies and other businesses that derive benefits from the service at the local level. At the same time, that same use may have implications for the user community with interests in recreation and tourism at the local and regional level, and in the conservation of marine biodiversity at the local through to the global level, depending on the particular site characteristics. Deciding on a safe or acceptable level of utilising the service is not usually a simple matter, as is clear from the complex set of processes and the wide array of possible waste types described in this paper. It is recognised, however, that to successfully manage the service of WR it is essential to include all abiotic processes alongside biotic processes when applying this ES classification in a policy or decision-making context.

Insufficient regulatory management often leads to human health impairment, economic loss, or ecosystem degradation with excessive use in certain areas meaning further use of this service is not possible. This has resulted in many ecosystem functions that act to provide the service of WR being overwhelmed locally and globally well beyond levels that can be sustained under current demands, much less future ones (Hooper *et al.*, 2012). A lack of capacity to manage the service of WR not only compromises the ability of the marine environment to process our waste but also causes a loss of an array of benefits that we often take for granted.

The future sustainable utilization of WR will depend on our ability to understand the properties of possible wastes interacting within marine ecosystems combined with the mechanisms and processes supporting the provision of this service (as outlined in Section 4). By understanding these processes, and the interlinkages between them, we will begin to understand how this service is provided and how we can enable the management of this service, maximise benefit received from it, and furthermore, help us consider the vulnerability of this service to over-exploitation and broader impacts. The previous discussion defines WR to be primarily a result of those processes involved in cycling/detoxifying, sequestering/storing and exporting waste and as such it is these processes we should seek to influence if we wish to maximise the removal of waste from a system.

Understanding of the relative permanence of storage and timescale for waste degradation is essential when determining the benefit of the service of WR. Most notable are wastes that cannot be detoxified, safely stored or cycled and any input will result in a continual decline in environmental quality (often without notice until it affects human health), and therefore provision of this ES. Given sufficient time, a change in water column conditions may bring about the release of stored wastes back to the environment. Therefore the premise of storage of contaminants in biomaterials and sediment is often a short term environmental solution to the problem of toxic wastes. Specifically in the case of non-degradable compounds such as metals, these wastes will continue to persist in the environment unless physically exported out of that system by natural or human means. As such, an important consideration in terms of the “point of entry” versus the location of the environment is most likely to lead to efficient sequestration and storage of all waste types. One such growing international example of humans maximising the service is through the use of marine waste bioextraction (Kim *et al.*, 2014). In USA, Sweden and other European countries the commercial practice of farming organisms that cycle, detoxify and store waste products and then harvesting (exporting) marine organisms

out of the system is being considered as a cost effective solution to mitigate excess waste and compliment traditional wastewater treatment programs.

It is noteworthy however, that some management efforts may also negatively affect the ongoing provision of WR itself. Using the same example as above, the same organisms that are introduced to provide the service of WR may also act as an ecosystem 'disservice' decreasing human wellbeing by translocating nutrients into the sediment, which facilitates the runaway growth of nuisance benthic algae, and the occurrence of other organisms that may not be involved in the bioremediation of other wastes. Similarly many detoxification and export processes may actually produce more toxic forms of a waste or may export wastes from one area to another more sensitive area with a lesser capacity to remediate that particular waste. Thus the overexploitation of this service can have a negative feedback effect on its provision, as well as on other ecosystem services and should be considered when designing suitable management strategies.

Despite the uncertainties surrounding the application of this service, deferring waste management actions until the problem becomes excessive is not an effective management approach. The costs of trying to reverse damages to waste-degraded ecosystems or remove persistent contaminants from the environment, if possible at all, can be extremely large and burdensome on society (Hinga *et al.*, 2005). Management decisions regarding the service need to be made in the context of the precautionary principle elaborated by US Commission on Ocean Policy., (2004) that is, relying on the best information available to reduce potential risks and the need to discharge wastes into the environment while at the same time promoting human wellbeing.

In this regard, policy makers and environmental regulators have become increasingly interested in the costs and benefits of meeting water quality standards. This follows a growing recognition of the need to evaluate ecological functions and the value of the ES's they provide so that they are not overlooked when management decisions are made (Daw *et al.*, 2015). However, while the service of WR provides a variety of benefits and supports a number of other ES's, there has minimal research undertaken on the valuation of this service. For example, WR was excluded from analysis in the marine economic analysis section of the NEA (Bateman *et al.*, 2011) as, - although its importance was noted - there was insufficient long-term monitoring data of ecosystem processes to support its inclusion. It was also noted as important in Costanza *et al.* (1998) and Beaumont *et al.* (2008) but excluded from valuation in both marine and coastal ecosystems due to insufficient information. Further, in studies that do evaluate the service, there is often a significant risk of underestimating the value of the service whereby processes that support the service such as nutrient cycling, can be overlooked or considered to be 'free' and therefore not considered within management strategies (Braat & de Groot., 2012). Conversely there is also the risk that the service may be overvalued for example when the waste processing capacity of WR is valued (by a replacement cost method), in addition to the benefits of clean water (by a health and/or recreational use metric) in a process often referred to a 'double counting' (d'Arge *et al.*, 1997; Fisher *et al.*, 2009; Fu *et al.*, 2011). This lack of a cohesive strategy for valuation may be in part because the benefits of waste processing capacity are not often tangible benefits set in the market and/or due to a lack of perfect information surrounding the processes providing the service. This is a fundamental problem for environmental practitioners with the service of WR often being undervalued in policy design and implementation and is therefore at risk of being ignored in future policy decisions. As a consequence, it seems clear that future research is needed to disentangle the complexity of valuing the service of WR, particularly in light of its socio-economic importance under increased anthropogenic pressures such as increased nutrient loading and global warming. While this task was outwith the remit of this study, it is hoped that the framework provided here will provided a useful basis for more focused work aiming to understand the direct possible human application of utilising the waste processing capacity of the environment to avoid negative impacts on human wellbeing.

6. Conclusions

From a global perspective the service of WR and many of its associated benefits are compromised not only by the unsustainable use of this service, but also through increasing large scale environmental fluctuations such as climate change (Schiedek *et al.*, 2007). While it is difficult to predict on a global scale the effects of climate change on the service of WR it is likely that many ecosystem processes will be altered both in the

capacity of the environment to remediate waste products and the susceptibility of organisms to differing waste conditions (Broszeit *et al.*, 2016). For instance changes in large scale water exchange mechanisms, which periodically “flush and clean” continental shelf areas, are likely to be altered being either up-regulated (increasing the turnover of waste material) or down regulated (decreasing the turnover of waste) altering the ability of locations to assimilate wastes (Di Lorenzo., 2015). As a consequence some systems with may allow conditions that continue to process wastes in a non-chronic manner, possibly as a result of greater levels biodiversity and therefore ecosystem resilience (the ability to recover from short-term perturbations), in contrast to other systems where organisms living near their physiological limits may inherit a reduced ability to provide the service into the future. A realistic generalisation is that unless effective waste management efforts can keep pace with the development of nations and the large scale implications of environmental change it is likely that in many regions high waste loading rates will overwhelm the remediation capabilities of systems to the detriment of human health, economic loss, biodiversity and ecosystem functioning. While it is desirable to ensure that discharges of waste into the ocean are as low as can possibly be managed, it should also be our intention to safeguard the many organisms that provide a constellation of other ES's. Making suitable and informed judgments as to the intrinsic capacity of marine and coastal environments to remediate our wastes will help achieve this.

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