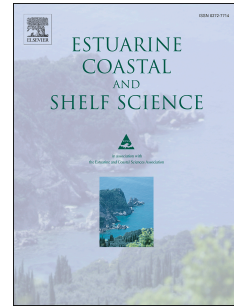


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1 **Comparing the network structure and resilience of two benthic estuarine**
2 **systems following the implementation of nutrient mitigation actions.**

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10 **Key words: Comparative studies, Ecopath with Ecosim, Estuary, Eutrophication, Network analysis.**

11 **Abstract**

12 The structure and resilience of benthic communities in coastal and estuarine ecosystems can be
13 strongly affected by human mediated disturbances, such as nutrient enrichment, often leading to
14 changes in a food webs function. In this study, we used the Ecopath model to examine two case
15 studies where deliberate management actions aimed at reducing nutrient pollution and restoring
16 ecosystems resulted in ecological recovery. Five mass-balanced models were developed to represent
17 pre and post-management changes in the benthic food web properties of the Tamar (1990, 1992,
18 2005) and Eden (1999, 2015) estuarine systems (UK). The network functions of interest were
19 measures related to the cycling of carbon, nutrients and the productivity of the systems. Specific
20 attention was given to the trophic structure and cycling pathways within the two ecosystems. The
21 network attribute of ascendancy was also examined as a proxy for resilience and used to define safe
22 system-level operating boundaries. The results of the resilience metrics ascendancy (A) and its
23 derivatives capacity (C) and overhead (O) indicate that both systems were more resilient and had
24 higher resistance to potential stressors under low nutrient conditions. The less perturbed networks
25 also cycled material more efficiently, according to Finns cycling index (CI), and longer cycling path
26 lengths were indications of less stressed systems. Relative Ascendancy (A/C) also proved useful for
27 comparing estuarine systems of different sizes, suggesting the Tamar and Eden systems network
28 structures have remained within their pre-defined "safe operating zones". Overall, this analysis
29 presents justification that efforts to reduce nutrient inputs into the Tamar and Eden estuaries have
30 had a positive effect on the trophic networks of each system. Moreover, the consensus of the
31 network indicators in both systems suggest ecological network analysis (ENA) to be a suitable
32 methodology to compare the recovery patterns of ecosystems of different sizes and complexity.

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40 1 Introduction

41 There is a growing need to manage ecosystems sustainably so that they can continue to deliver the
42 goods and services on which society depend (Beaumont *et al.*, 2007; Bennett *et al.*, 2015; Costanza
43 *et al.*, 2017). This is particularly the case for coastal marine systems where increasing population
44 pressure, urbanisation and nutrient run-off from the coastal zone has increased the number of large-
45 scale impacts affecting estuarine systems (Dolbeth *et al.*, 2011; Ellis *et al.*, 2015). As a consequence,
46 there is a growing movement towards an integrated 'Ecosystem-based' approach to management,
47 which focuses on how individual actions affect whole ecosystems, rather than considering these
48 impacts in a piecemeal manner (Leslie, 2018). One alternative method to considering the organisms
49 within ecosystems as an aggregate property, is to consider the emergent properties of the whole
50 ecological system rather than of any of its individual components. Exergy, a thermodynamic concept,
51 has been applied in ecology since the 1970's and is defined as the amount of work a system can
52 perform when it is brought to thermodynamic equilibrium with its environment (Jørgensen & Mejer,
53 1977; 1979). Compatibly, ecological network analysis (ENA) can extract comprehensive information
54 on the flow and cycling of matter from mass-balanced flowcharts, including trophic structure and
55 transfer efficiencies, and the organisation or resilience of the food web (Field *et al.*, 1989, Gaedke,
56 1995). Taken together, these methodologies have a long legacy in assessing ecosystem health and in
57 analysing complex interactions within marine ecosystems (Odum, 1953; 1969; 1996; Ulanowicz,
58 1986; 1997; 2012) with several ENA tools now available within a number of easily accessible
59 software packages including NETWRK4 (Ulanowicz & Kay, 1991), WAND (Allesina & Bondavalli,
60 2004), Ecopath with Ecosim (Christensen & Walters, 2004) and R (Laua *et al.*, 2015).

61 Perhaps the most commonly used and emerging example of this type of modelling approach is the
62 Ecopath with Ecosim (EwE) modelling software (Christensen *et al.*, 2005), which has over 400
63 models published to date (Colléter *et al.*, 2015), and is the most applied tool for modelling marine
64 and aquatic ecosystems globally. EwE models have a number of ENA features and can be selected
65 to: identify and quantify major energy flows in an ecosystem, interactions between species, compare
66 coastal ecosystems of different sizes, evaluate the effects of climate induced or anthropogenic
67 variability on ecosystems, explore management policy options. EwE models have also been applied
68 in testing ecosystem theories on eutrophication (Patricio *et al.*, 2006; Baeta *et al.*, 2011; Vasslides *et al.*,
69 2017), resilience, stability and regime shifts (Pérez-España & Arreguín-Sánchez, 2001; Tomczak *et al.*,
70 2013; Arreguín-Sánchez & Ruiz-Barreiro, 2014; Heymans & Tomczak, 2016). Thus, the aim of this
71 paper was to use the Ecopath software with ENA analysis to examine and compare the network
72 system attributes of two temperate UK estuaries, the well-document Tamar Estuary, in south-west
73 England and the smaller less well studied Eden Estuary, in north-east Scotland. Both systems have
74 gone through extensive periods of ecological change over the last thirty years, as a result of a shift
75 towards an agriculture production policy option in the Eden catchment (1999-2015) and a
76 combination of water quality improvement initiatives in the Tamar Estuary (1990-2005), allowing the
77 representation of eutrophic and post-eutrophic states. Therefore, five mass-balanced models were
78 developed using the "Ecopath with Ecosim" software package for the years 1990, 1992 and 2005
79 (Tamar) and 1999 and 2015 (Eden) to assess changes in the benthic food web properties of the
80 Tamar and Eden estuarine systems. Field, laboratory and literature information was used to
81 construct the models. The main study objective was to assess the effects of:

82 (1) a pre-management period of excessive anthropogenic enrichment, which led to excessive
83 production of organic matter in the form of algal blooms and localised hypoxic symptoms (Tamar
84 1990);

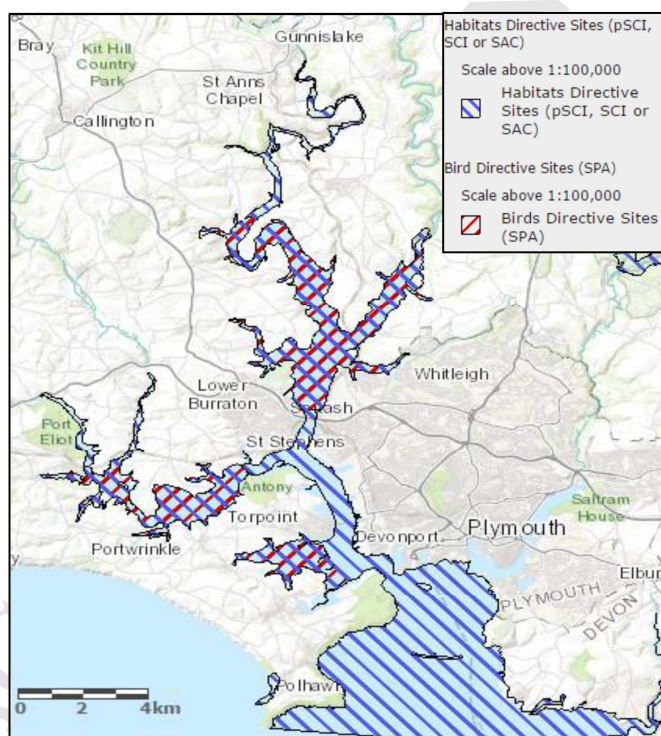
85 (2) a pre-management period with high nutrient levels (Tamar 1992; Eden 1999);

86 (3) a post-management period after the implementation of mitigation measures following long
87 periods of hypereutrophication (Tamar 2005; Eden 2015).

88 2.1 A brief description of the ecosystems

89 Tamar Estuary (50021' N, 004010' W).

90 The Tamar estuary is a medium sized (31 km-long) estuary situated on the border between Cornwall
91 and Devon on the south-west coast of England (Figure 1). The estuary itself comprises a complex of
92 marine inlets (rias) stretching from Gunnislake weir (upper tidal limit) to Plymouth Sound (lower
93 tidal limit) (Money *et al.*, 2011). Together, the Tamar Estuaries Complex (encompassing the River
94 Lynher and St John's Lake in addition to the Tamar–Tavy, and hereafter referred to as the Tamar
95 estuary) and Plymouth Sound, are designated as a Special Area of Conservation (SAC) under the
96 European Union's Habitats Directive (92/43/EEC) and a Special Protected Area (SPA) under the
97 European Commission Directive on the Conservation of Wild Birds (79/409/EEC). The many different
98 habitats within the Tamar estuary, have been studied intensively for more than a century by
99 researchers of the Marine Biological Association (MBA), University of Plymouth (UoP) and Plymouth
100 Marine Laboratories (PML), who have conducted numerous hydrographic, chemical and biological
101 surveys in the Western English Channel, including Plymouth Sound and Tamar estuary (see
102 Southward & Roberts, 1987 for historical perspective). As a result, the Tamar estuary and its
103 surrounding waters is one of the best documented estuarine complexes in the UK and is ideally
104 suited to conducting seascape-scale or systems-based research.



118 **Figure 1:** Map of the Tamar Estuary and Plymouth Sound European Marine Site. © Copyright European
119 Environment Agency (EEA)

120 In common with many British estuaries, from the 1980s to the early 1990s, the Tamar experienced
121 significant nitrogen and phosphorous enrichment due to excessive agricultural run-off due to land
122 use changes in the upper catchment (Knox *et al.*, 1986), while sewage discharges constituted
123 localised chronic contamination and nutrient-associated water quality problems in the lower estuary
124 (Morris *et al.*, 1981; 1986; Readman *et al.*, 1986). As a result during these periods the system was
125 considered eutrophic, with respect to nitrogen under criteria proposed by Dodds *et al.* (1997) (>1.5

126 mg/L⁻¹) and the EU guideline of 9 (µg/L⁻¹) for the protection of course freshwater fish, but not
 127 considered polluted in terms of nitrogen according to criteria under the Nitrates Directive (>5.65
 128 mg/L⁻¹) for official designation as a eutrophic system (Table 1). This culminated during the period of
 129 1990 when low river flows, high water residence times and high nutrient concentrations in the form
 130 of phosphorous compounds, interrupted upstream communication with the upper portion of the
 131 system, resulting in large blooms of benthic microalgae and increased biomass of macroalgae across
 132 the estuary. The resultant conditions included widespread salmonid fish deaths caused by localized
 133 areas of low oxygen conditions (Darbyshire, 1996; Harris, 1988; 1992), in addition to relatively low
 134 pHs and high suspended solids (trapped in the upper estuary following spring tides), leading to
 135 reported changes in biodiversity and functioning of the system. During this period annual reactive
 136 phosphorous concentrations exceeded 100 (µg/L) and the Tamar was officially classed as eutrophic
 137 using interim standards set by the Environment Agency (EA, 1998). Following a recovery period the
 138 following year, in 1992 various management efforts such as the “New South West – Clean Sweep
 139 and Beyond project” and the “Plymouth Urban Diffuse Pollution Project” were put in place to clean
 140 up nutrient related issues across the estuary. As a result, much of the eutrophic symptoms
 141 associated with the early 1990’s had subsided by the early 2000’s. For example average reactable
 142 phosphorus concentrations were shown to decrease from 1990 levels of 110(µg/L⁻¹) to 63(µg/L⁻¹) for
 143 the period of 1992 and to an even lower 47 (µg/L) by 2005 (Mankasingh, 2005).

144 **Table 1:** Summary of annual average concentrations of environmental variables for the Tamar
 145 Estuary (1990-2005).

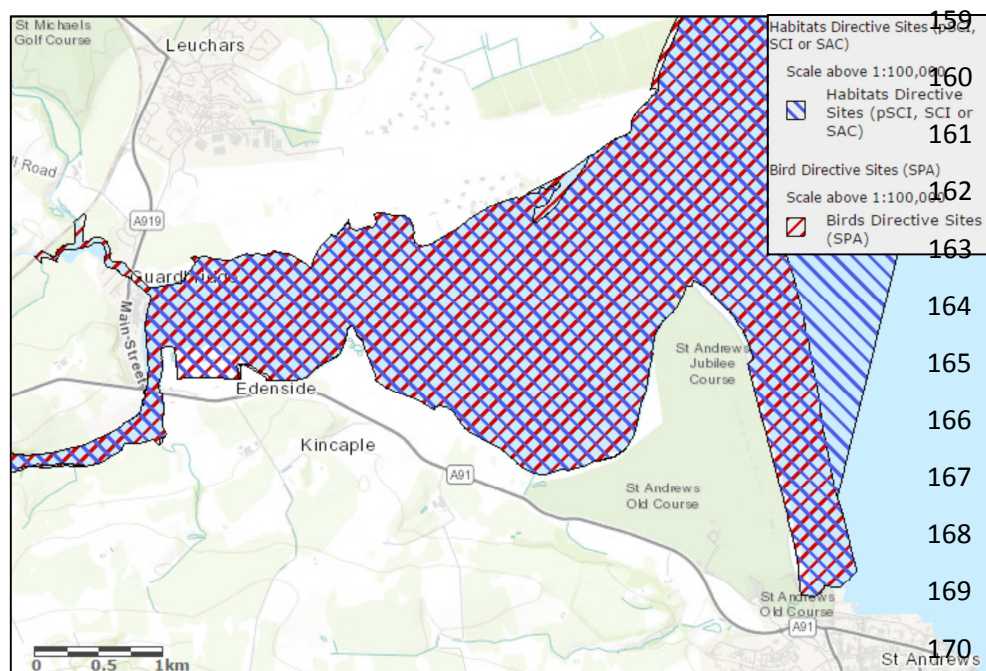
Variable/Year	1990	1992	2005	Source
Ammonium (mg l ⁻¹)	0.07	0.04	0.02	Mankasingh, (2005)
Biochemical oxygen demand (mg l ⁻¹)	2.11	1.52	1.10	Environment Agency
Chlorophyll <i>a</i> (mg l ⁻¹)	29.55	6.98	6.32	Environment Agency
Dissolved oxygen (mg l ⁻¹)	10.00	10.76	10.29	Environment Agency
Filterable reactive phosphorous (µg l ⁻¹)	110	63	47	Mankasingh, (2005)
Nitrate (mg l ⁻¹)	11.65	12.10	12.61	Mankasingh, (2005)
Nitrite (mg l ⁻¹)	0.03	0.02	0.008	Mankasingh, (2005)
pH	6.33	7.70	7.59	Environment Agency
River flow (m ^{-3/s})	3.48	8.65	4.01	The National River Flow Archive (NRFA) Gunnislake gauging station.
Surface salinity (ppt)	17.56	16.30	16.91	Environment Agency
Temperature(°C)	12.10	11.08	11.95	Environment Agency

146

147 **Eden estuary (56022' N, 2050' W)**

148 In comparison with the Tamar, the Eden Estuary is a small (11km-long) shallow bar built or ‘pocket’
 149 estuary, located between the village of Guardbridge and the town of St Andrews on the East coast of
 150 Scotland (Figure 2). Collectively the Eden estuary along with the Firth of Tay Estuary is designated as
 151 a Special Area of Conservation (SAC) under the European Union’s Habitats Directive (92/43/EEC) and
 152 a Special Protection Area (SPA) under the European Commission Directive on the Conservation of
 153 Wild Birds (79/409/EEC). The main channel of the estuary is flanked by relatively wide intertidal
 154 areas (8km²) that plays host to large populations of overwintering waterfowl and wading bird
 155 species. Historically the intertidal mud and sand flats of the estuary have been sampled intensively
 156 by researchers from the University of St Andrews, with many studies undertaken from of the Gatty

157 Marine Laboratory (Bennett & McLeod, 1998) providing a robust baseline from which to draw
 158 comparisons.



171 **Figure 2:** Map of the Eden Estuary European Marine Site. © Copyright European Environment Agency
 172 (EEA).

173 Anthropogenic pressure in the form of increased nutrients from arable and livestock production is
 174 one of the most significant pressures influencing the Eden with high levels of nitrogen compounds
 175 entering the estuary *via* the river Eden (Clelland, 1997). Historically this has led to a number of
 176 ecological problems such as the closure of mussel beds as unfit for human consumption and
 177 widespread fish mortalities (Defew & Paterson, 2009). As a consequence the catchment was
 178 designated as a nitrate vulnerable zone in 2003 (SEERAD, 2003). Nutrient inputs are now in decline
 179 (Table 2) thanks to increased legislation resulting from the Nitrates Directive (NVZ) and Sensitive
 180 Area (UWWTD) designations (Macgregor & Warren, 2015), including an upgrade of the Guardbridge
 181 sewage treatment works in 2008 and the closure of the Guardbridge paper mill and adjacent pig
 182 farm with their associated effluent.

183 **Table 2:** Summary of annual average concentrations of environmental variables for the Eden Estuary
 184 (1999-2015).

Variable /Year	1999	2015	Source
Ammonium (mg l^{-1})	0.091	0.048	Environment Agency
Chlorophyll <i>a</i> (mg l^{-1})	10.56	4.28	Environment Agency
Dissolved oxygen (mg l^{-1})	11.39	10.74	Environment Agency
Filterable reactive phosphorus (mg l^{-1})	0.23	0.098	Environment Agency
Nitrate (mg l^{-1})	7.72	5.82	Environment Agency
Nitrite (mg l^{-1})	0.035	0.015	Environment Agency
pH	7.92	8.11	Environment Agency
River flow (m^3/s)	2.67	2.13	The National River Flow Archive (NRFA) Kemback gauging station.
Temperature ($^{\circ}\text{C}$)	9.45	10.10	Environment Agency

185 **2.2 Materials & Methods**

186 Biomass flow networks ($t/km^2/yr^{-1}$) were constructed for the systems outlined above, using the
 187 “Ecopath with Ecosim” software package (v6.5) for the years 1990, 1992 and 2005 (Tamar) and 1999
 188 and 2015 (Eden) representing eutrophic and post-eutrophic systems. Ecopath trophic models are
 189 mass balance models that create a static snapshot of energy flows and their interactions in an
 190 ecosystem represented by trophically linked biomass ‘pools’ or ecological guilds of species (Pauly *et*
 191 *al.*, 2000). In a model, the energy input and output of all living groups must be balanced. Ecopath
 192 parameterizes models based on two master equations one to describe the production term and one
 193 for the energy balance of each group (Christensen *et al.*, 2005). The first equation divides the
 194 production of each compartment into individual components. This is implemented with the
 195 equation:

196 Production = total fishery catch rate + predation mortality + biomass accumulation + net migration +
 197 other mortality

198 Or, more formally,

$$B_i \times \left(\frac{P}{B}\right)_i - \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}\right) - Y_i - BA_i - E_i = 0 \quad \text{Equation 1}$$

199

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

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

211 Or, more formally,

$$B_i \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \quad \text{Equation 2}$$

212

213 where R_i is the respiration rate, and U_i the unassimilated food rate. Respiration is used in Ecopath,
 214 only for balancing the flows between groups and refers to the assimilated fraction of matter that is
 215 not used in production. Following other estuarine Ecopath models (e.g. Baeta *et al.*, 2011), it is
 216 assumed that autotrophs and detritus based organisms have zero respiration with all nutrients that
 217 leave the compartment being re-utilized. For each compartment unassimilated food (U_i) consists of
 218 food which is egested and flows to the detritus. Following Christensen *et al.* (2000), our models used
 219 a U_i default value of 0.20 for all groups (i.e. 20% of the consumption for all groups).

220 **2.2.1 Sampling methods and data collection**

221 Chlorophyll *a* measures provided by the Environment agency (Table 2) for each catchment were
222 transformed into a proxy for phytoplankton biomass using a conversion factor taken from Anderson
223 & Williams (1998). Quantitative biomass data for the main benthic primary producers
224 (microphytobenthos, macroalgae and other macrophytes) at the estuarine scale were made using
225 the Ecopath model based on case study specific estimates of their production, using data from small
226 scale *in situ* measurements (e.g. Bale *et al.*, 2006) and knowledge of other trophic assemblages.
227 Model biomass estimates were examined and compared with the existing literature to ensure the
228 predations were plausible. For instance, there have been a number of long-term biotope and aerial
229 surveys of saltmarsh and macroalgal extent (Webster *et al.*, 1998; EA., 2000; Widdows *et al.*, 2007;
230 Curtis *et al.*, 2010) on various regions of the Tamar complex. The macroalgal group here is likely to
231 comprise of locally registered species such as *Enteromorpha* and *Ulvae spp.* while the 'other'
232 macrophyte grouping is likely to comprise a wide variety of seagrass and saltmarsh species such as
233 by not limited to: common saltmarsh-grass (*Puccinellia maritime*), common cord-grass (*Spartina*
234 *anglica*), common eelgrass (*Zostera marina*), red fescue (*Festuca rubra*) and sea couch (*Elymus*
235 *pycanthus*).

236 To obtain an approximate value for microphytobenthic biomass and production in the Eden system,
237 contact cores were taken across identical transects of each of the three main zones of the estuary in
238 1999 and 2015 by sampling the top 2 cm of the surface sediment (see Ford & Honeywill, 2002 for full
239 protocols). The presence of macroalgae (biomass t km²) was estimated by a survey of macroalgae
240 within 5m radius of each sampling point (Ford & Honeywill, 2002). Macroalgae were mostly
241 identified to be *Enteromorpha* and *Ulvae spp.* Estimates of 'other' macrophytes in the system were
242 calculated, based on known *in situ* estimates of saltmarsh extent and production (Fife Council, 2008;
243 Maynard, 2003; 2014; Maynard *et al.*, 2011). Common species represented by this grouping were
244 likely to include common saltmarsh-grass (*Puccinellia maritime*), sea clubrush (*Bolboschoenus*
245 *maritimus*) and the eelgrasses (*Zostera augustifolia*), (*Z. noltii*), and (*Z. marina*).

246 In the Tamar system, invertebrate data from three studies allowed some inter-comparisons to be
247 made at the estuarine scale at similar times of the year, using similar sampling methodologies
248 (Watson *et al.*, 1995; SWW Tamar Estuary sublittoral sediment survey 1992 & Sanders, 2008). In the
249 Eden estuary, extensive surveys of invertebrate data were collected in 2015 through identical
250 surveys to those carried out in 1999 by the BIOPTIS programme (Watson *et al.*, 2018). During this
251 campaign three sampling grids were established across three transitional areas of the estuary
252 (Appendix A). Invertebrate densities for both systems were converted to biomasses using case
253 study-specific relationships (e.g., Dashfield & McNeill, 2014 Tamar & Biles *et al.*, 2002 Eden).
254 Invertebrate species that were not naturally present in one of the years or sites or whose roles in the
255 trophic network were unimportant (biomass < 0.01 t/km²) were not taken into account.

256 Data on demersal fish species and epibenthic crustaceans could not be collected at the estuarine
257 level in each system for practical reasons. However, historical fisheries-independent trawl surveys
258 mainly undertaken by Russel (1973), McHugh *et al.* (2011) & Dando (2011) reveal a relative temporal
259 consistency in the overall numbers of flatfish and epibenthic crustaceans in the Tamar estuary
260 between historic (1970 & 1980) and contemporary (2009) trawls. Similar observations into the
261 autecology of the brown shrimp (*Crangon crangon*) by Henderson *et al.* (1987; 1990) and later by
262 Campos *et al.* (2008; 2009; 2012) across several British estuaries including the Tamar suggest a
263 consistency in the population structure and phylogeography of this species over our study period.
264 Therefore, given that the spatial structure of the demersal fish and caridean shrimp assemblage has
265 remained relatively constant, similar biomass values for each of these taxa were used over the time
266 periods. Data on fish populations in the Eden were also unattainable from the literature due to a
267 paucity of fish monitoring surveys within the estuarine complex. Demersal fish biomass estimates
268 were therefore estimated by Ecopath, based on P/B, Q/B and EE. Data on epibenthic crustacean
269 numbers, most specifically the brown shrimp (*Crangon crangon*) were obtained as part of the
270 aforementioned macrobenthic invertebrate data collection.

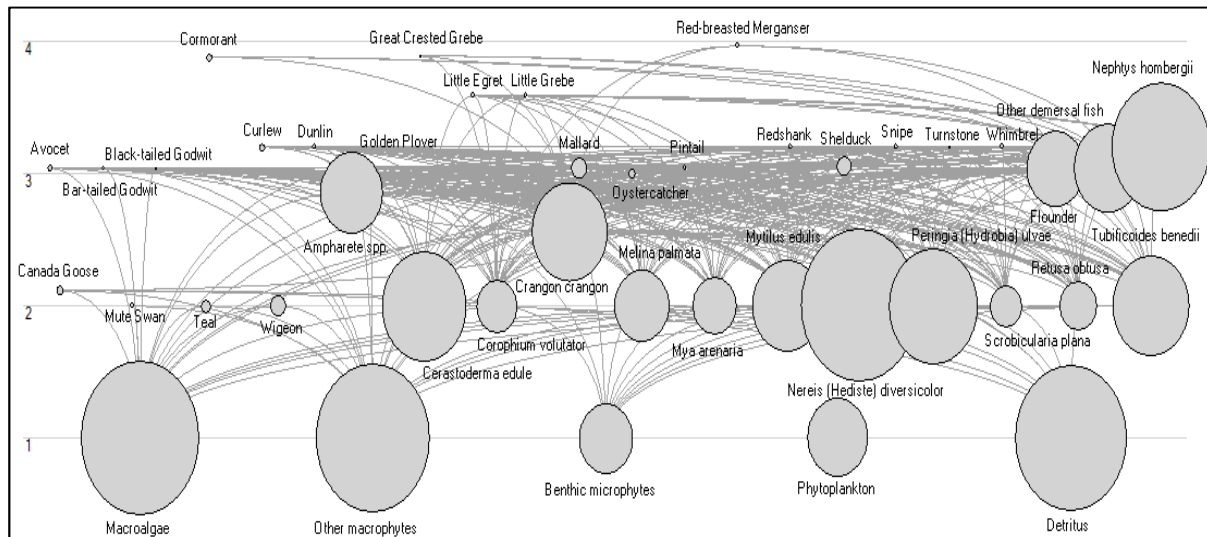
271 Population numbers for waterbirds in both systems were obtained for the period 1990-2015 from
272 the WeBS (Wetland Birds Survey) database (Frost *et al.*, 2016). Bird counts were based on monthly
273 observations across 15 (Tamar) & 5 sectors (Eden) covering the whole of each respective complex.
274 Twenty-three waterbird species were selected from the Tamar system and Eighteen waterbird
275 species from the Eden system (representing >95% of the total bird numbers in each system, with
276 those excluded largely representing seabird species) from a list of local species known to inhabit and
277 feed on the estuary recurrently, to increase the chance of interoperating temporal changes. Prior to
278 analysis counts were converted to biomasses using species specific body weights outlined by Snow &
279 Perrins (1998).

280 **2.2.2 Compartments**

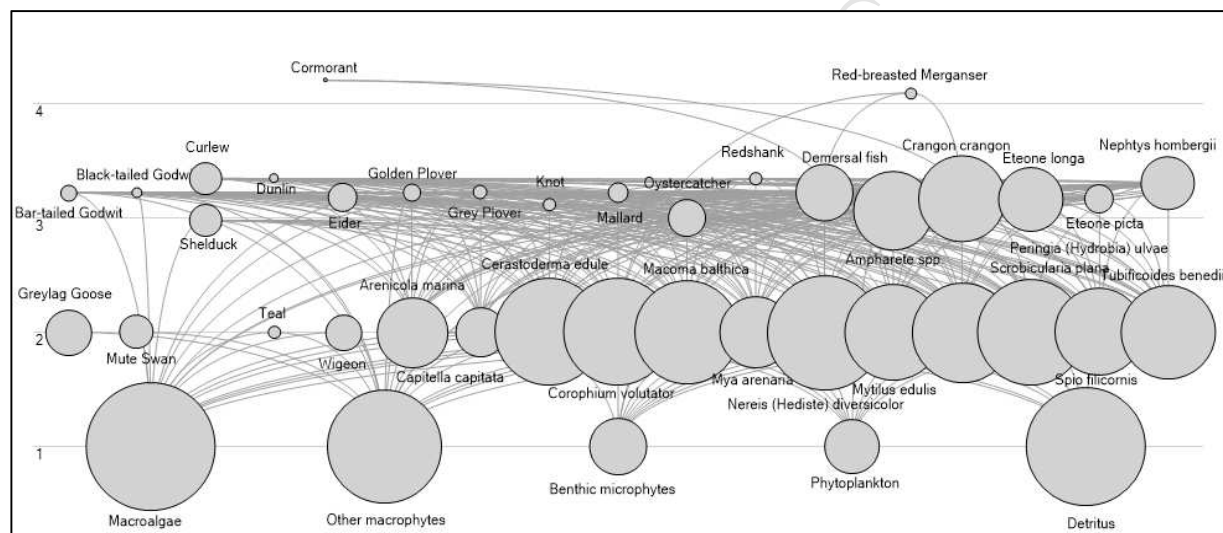
281 Some groups of species were grouped into compartments based on similar ecological niches. The
282 benthic-microalgae group here is primarily composed of freshwater and marine diatoms with no
283 single species dominating the community throughout the year. In the case of the Tamar, demersal
284 fish species were amalgamated into one compartment comprising sole (*Microstomus kitt*), turbot
285 (*Phrynorhombus norvegicus*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). In the
286 Tamar Estuary, the flounder (*Platichthys flesus*) was considered as a separate compartment being
287 the only ray-finned demersal fish to migrate and colonize the upper reaches of the estuary due to its
288 considerable powers of osmoregulation (Hartley, 1940; 1947). In the Eden Estuary, the demersal fish
289 fish identity was assumed to be a combination of all benthic fish species know to occur within the
290 estuary. In all models, invertebrate species belonging to family Ampharetidae were grouped
291 together, with many of these species sharing a functional role. No data were available for bacteria,
292 therefore the benthic bacterial biomass was considered has being part of the detritus compartment,
293 as recommended by Christensen and Pauly (1992a, b).

294 **2.2.3 Ecopath food webs and trophic structure**

295 The final versions of the Tamar (Figure 3) and Eden (Figure 4) food webs comprised 43 and 41 taxa
296 respectively, distributed over four trophic levels



297 **Figure 3** 2D representation of the food web from the Tamar Estuary (1990).



298 **Figure 4** 2D representation of the food web from the Eden Estuary (1999).

299 Whilst phytoplankton and benthic-microalgae are included due to their known importance in
 300 structuring benthic ecosystems, other water column elements (zooplankton, planktivorous fish (e.g.
 301 shad, sand eel) and their consumers (species in the family *Salmonidae*) were not included in this
 302 model and are considered to follow a separate pelagic trophic pathway (Hall & Raffaelli, 1991). This
 303 is due to both planktonic and benthic networks of cycling representing independent domains of
 304 control (Baird & Ulanowicz, 1989), with benthic-microalgae constituting a significant proportion of
 305 benthic estuarine ecosystem functioning. This model instead centres on a detritus based pathway
 306 with particulate organic matter passing through micro-phytobenthos to macro-invertebrates to fish
 307 or birds (e.g. Raffaelli, 2011) and a second pathway is also used from macroalgae to macro-
 308 invertebrates or herbivorous wildfowl (Baird & Milne, 1981). In addition, although the harbour seal
 309 (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) are known to roam freely through the Eden
 310 Estuary (and to a lesser extent the lower Tamar Estuary), they were not included in either modelling
 311 framework due to their diets mainly consisting of planktivorous fish (e.g. sandeels, whiting and
 312 species of the family *Salmonidae*) foraged out with the estuarine area in question. For instance
 313 Sharples *et al.*, (2009), noted in a study of the diet of harbour seals in the Eden and adjacent St.
 314 Andrews Bay to consist of 81 to 94% sandeels in winter and 63% in summer and autumn, with
 315 salmonids making up the remaining prey captured.

316 2.2.4 Production, consumption and diet composition

317 Production/Biomass ratios required for Ecopath were collected from a number of web-based
318 databases (e.g., Fishbase (Froese & Pauly, 2016) and WeBS database (Frost *et al.*, 2016)). For all
319 vertebrate groups this information was readily available from these databases. For avian species,
320 production was calculated as recruitment (R) of young into the adult population in units per
321 individual (tonnes per year; Stenseth, 2002). For the primary producer and invertebrate groups,
322 Brey's (2001) Virtual Handbook on Population Dynamics, version 4 (Brey, 2012) was used to
323 calculate the P/B for all species. The weight-to-energy ratios needed in order to apply the empirical
324 method were also provided by Brey (2001). In the case of combined groups the means of each
325 component parameters, were weighted by the relative biomass of the components. For all
326 heterotrophic compartments, Production/ Consumption ratios were entered into the program in
327 order to estimate the Consumption /Biomass ratio's indirectly. The only exception was in the case of
328 demersal fish species where a holistic predictive model for Consumption/Biomass using asymptotic
329 weight, habitat temperature, a morphological variable and food type as independent variables were
330 calculated using Fishbase

331 Diet matrices were built for each taxa using information from a wide variety of literary sources and
332 summed to unity. Resident invertebrate diet compositions was compiled largely from MBA data
333 holdings including MARLIN and BIOTIC databases while shorebird and flatfish data referenced from
334 the WeBS and Fishbase databases respectively. Complimentary diet information was also gathered
335 from the literature (see Appendix B for all diet references). Initially all species were listed from each
336 taxa along with their percentage contribution to the compartment. Each observed dietary item was
337 then assigned to each individual group of species, with the final percentage of the diet assumed to
338 be proportional to the fraction that its biomass comprised of the total biomass of the functional
339 group.

340 2.2.5 Anthropogenic exports (Yi)

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

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360 2.2.6 Pre-balancing analysis (PREBAL)

361 To add rigor and validity to the models a set of pre-balance diagnostics (PREBAL) outlined by Link
362 (2010) and recommended by Heymans *et al.* (2016) were made to assess any issues with the models
363 structure or quality of the primary input data. First the logarithmic ratios of biomass among various
364 taxa groups were plotted (Appendix C) as they have been repeatedly identified as a major indicator
365 of marine ecosystem functioning (Link, 2005; Mokany *et al.*, 2016). Generally biomass
366 decomposition generally followed a sequential decrease moving across trophic levels. While detrital
367 groups were not used it is noted for context that detrital standing stocks were on the same order of
368 magnitude as primary producer biomass, consistent with systems such as estuaries and benthic
369 orientated food webs that are particularly dependent upon detrital energy. In a second step, the
370 vital rates of all taxa, in the form of Production/Biomass ratio and Consumption/Biomass ratio were
371 plotted (Appendix C) for comparison, as these ratios are reflective of an amalgamation of an entire
372 suite of physiological processes. As with the biomass estimates, there was an acceptable decline in
373 vital rates with increasing trophic level.

374

375 2.2.7 Balancing the models

376 Using the ecological and thermodynamic rules for balancing Ecopath models outlined by Darwall *et al.*,
377 (2010) elements of the diet matrix or the values of the three inputted parameters were adjusted
378 iteratively until all logical constraints were met. This was done starting with the lowest quality data
379 first, preserving the most reliable data. In both the Tamar and Eden case studies, the most reliable
380 data were the biomass and production values, and consequently these values were left largely
381 unchanged. Diet matrices were principally unaltered but differed slightly to reflect the known
382 trophic responses of species to different pressures. In all incidences the balancing parameter
383 changes fell within the ranges of uncertainty associated the development of the 'pedigree'— a
384 routine in Ecopath modelling that quantifies the quality of the input data by assigning confidence
385 intervals based on the origin of the information. The pedigree index P calculated for the Tamar
386 models was 0.481 and 0.593 for the Eden, with the higher latter value reflecting the use of locally
387 collected data and trophic information used to parameterise the models. The various parameters for
388 the balanced Ecopath models of the Tamar and Eden ecosystems are presented in (Appendix D).

389 2.2.8 Summary of system statistics and indices

390 After mass-balancing the models, a number of indices that describe the structure, function and
391 resilience of each system as a whole were calculated using a suite of Ecological Network Analysis
392 (ENA) algorithms incorporated into Ecopath (Christensen *et al.*, 2005). A summary of each index
393 chosen is given in Table 3.

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402 **Table 3 Selected Ecological Network Analysis (ENA) indicators**

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System Indices	Description	Units
Sum of all consumption (ΣC),	ΣC is the sum of all consumption in a system.	$t\ km^{-2}\ yr^{-1}$
Respiratory flows (ΣR)	ΣR is the sum of all respiratory flows in a system.	$t\ km^{-2}\ yr^{-1}$
Flows to detritus (ΣFtD)	ΣFtD 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 (ΣP)	ΣP is the sum of all production flows in a system.	$t\ km^{-2}\ yr^{-1}$
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	$t\ km^{-2}\ yr^{-1}$
Total biomass (excluding detritus) (ΣB)	Total biomass in the system excluding detritus.	$t\ km^{-2}$
Total primary production/total biomass (PP/B),	PP/B, is expected to be a function of the system's maturity (Odum, 1969).	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 (CI)	CI captures the functions of carbon and nutrient cycling in the system using a proxy of (% of total throughput).	% of total throughput
Predatory cycling index (PI)	PI is a slightly modified form of the CI 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 <i>et al.</i> , 1991).	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 (Christensen <i>et al.</i> , 2000).	The SOI is a positive value and is dimensionless.
Ascendency (A)	A represents both the size and organisation of a system (Ulanowicz, 1986, 1997). Ascendency is a measure of a systems stability and a proxy for a systems resilience.	Flowbits or the product of flow (e.g., $t/km^2/year$)
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
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 impacts (Ulanowicz, 1986). Overhead is also defined as the pathway redundancy (Ulanowicz, 1997).	Flowbits or the product of flow

404 3 Results and discussion

405 3.1 Statistics of ecological functioning and network structure

406 To quantify the difference within and between the two systems it was necessary to compare the
407 relative magnitude of change in their various system information indices (Table 4). One clear
408 comparison between the networks is that the Tamar is far more active than the Eden, its total
409 system throughput ($23464 \text{ t km}^{-2} \text{ yr}^{-1}$, 2005, defined as the sum of all flows in the system) is almost
410 25% larger than that of the Eden ($17957 \text{ t km}^{-2} \text{ yr}^{-1}$, 2015). Some of the higher activity in the Tamar
411 can be attributed to its greater size and freshwater inputs than the Eden, but higher nutrient inputs
412 to the Tamar are also likely to enhance its activity. Because total system throughput scales all
413 information indices, the ascendancy and other related variables are uniformly greater for the Tamar.
414 Despite the topological network differences of each system, in both systems, Total biomass
415 (excluding detritus) decreased substantially between the pre and post-management periods. The
416 impact of these changes was reflected by falls in many of the system indices including: consumption,
417 respiratory flows, flows to detritus, and net primary production. There is also evidence that the size
418 (TST) or 'power' of each system decreased greatly between the focal periods. These changes were
419 almost certainly attributed to the direct bottom up-effects of nutrient reductions which altered the
420 abundance of benthic primary producers, with cascading consequences on invertebrate and
421 waterbird species at higher trophic levels. These changes were also responsible for changes in
422 secondary production and a number of higher level systems metrics. The effects are believable, not
423 because of a statistically rigorous experimental design, but because the effect sizes are very large,
424 and the altered biodiversity and ecological functioning are clearly different relative to the post
425 management periods.

426 Associated with TST, the network characteristics of the Tamar and Eden ascendancy (A), capacity (C)
427 and overhead (O), all decreased considerably by the post-management periods. This is consistent
428 with Ulanowicz's (1980;86) interpretation that nutrient perturbed systems can be defined by any
429 increase in system ascendancy that causes a rise in total system throughput (TST), that more than
430 compensates for any fall in the mutual information content (e.g. A, C or O) of the system. In other
431 words, the greater nutrient inputs tend to simulate a systems growth but despite its augmented
432 activity, its organisation or structure is degraded.

433 Relative ascendancy (A/C) was very similar between pre and post-management periods, suggesting
434 that each system was able to accommodate (or resist) the large-scale changes in nutrient loading,
435 primary production, and invertebrate biomass. When only the relative fluxes are concerned, the
436 Tamar Estuary showed a decline of -1.19% in ascendancy (A/C) relative to a larger change of -3.66%
437 in internal A_i/C_i by the 2005 period, indicating a higher dependency of this system on connections
438 to adjacent ecological and physical systems (e.g. the Western English Channel). In contrast, internal
439 relative ascendancy (A_i/C_i) remained relatively similar between the periods (+0.53%) in the Eden
440 system, indicating that this system has maintained its activity without too much dependence on
441 external system connections. As the degree to which environmental change is likely to influence
442 ecosystem resilience will depend on metacommunity structure and connectance (Dunne *et al.*, 2002;
443 Fung *et al.*, 2015), the (A/C) index could therefore be a suitable indicator to compare ecosystems of
444 different sizes (e.g. Mann *et al.*, 1989, Baird *et al.*, 1991).

445

446 **Table 4** Summary of ecological and network statistics/indices for the Tamar and Eden estuarine
 447 systems.

Estuary	Tamar			Eden		Units
	1990	1992	2005	1999	2015	
Sum of all consumption (ΣC)	27416	27790	12254	26122	9386	t km ⁻² yr ⁻¹
Sum of all respiratory flows (ΣR)	16474	16698	7373	15696	5648	t km ⁻² yr ⁻¹
Sum of all flows into detritus (ΣFtD)	60403	6379	2982	5763	2121	t km ⁻² yr ⁻¹
Sum of all production (ΣP)	11508	10863	7156	8560	3860	t km ⁻² yr ⁻¹
Total system throughput (TST)	54675	55592	23464	50526	17957	t km ⁻² yr ⁻¹
Total biomass (excluding detritus) (ΣB)	2680	2617	1703	1926	958	t km ⁻² yr ⁻¹
Total primary production/total biomass (PP/B)	2.320	2.036	2,774	1.74	1.88	-
Total primary production/total respiration (PP/R)	0.367	0.319	0.641	0.21	0.35	-
Ascendency (A)	77715	79561	29844	68252	23523	Flowbits
Capacity (Ca)	256513	273649	127706	294697	84797	Flowbits
Overhead (O)	178798	194088	97862	226445	108320	Flowbits
Relative ascendency (A/C)%	30.02	30.68	31.21	23.16	29.21	%
Internal ascendency (IA)	47448	48099	20390	45641	15763	Flowbits
Internal capacity (IC)	175004	189876	89455	193430	75478	Flowbits
Internal overhead (IO)	127556	141777	69066	147047	59715	Flowbits
Internal relative ascendency (Ai/Ci)%	27.08	26.54	23.42	23.32	23.85	%

448

449 3.2 Cycling structure

450 As making judgment about the trophic status of two entire ecosystems based on a few information
 451 indices may seem precarious to some (Ulanowicz, 2004; Fath *et al.*, 2007), comparisons between the
 452 Tamar and Eden ecosystems were supported by a broader analysis of the two networks. Support for
 453 comparisons were made by considering the trophic structure and cycling pathways contained within
 454 the two ecosystems. Because each trophic pathway is a series of interconnected cycles, stressors
 455 occurring at any point will disrupt flow to higher levels (Voris *et al.*, 1980; Ulanowicz, 1983). We
 456 would expect therefore, that systems with greater resistance to and resilience from nutrient stress
 457 to be more complex, in the sense that they contain longer loops of connections that cycle at lower
 458 frequencies. Conversely, systems under increased nutrient stress would possess fewer such cycles,
 459 due to link disruptions, and each cycle would transfer less medium, particularly to higher trophic
 460 levels (Baird & Ulanowicz, 1993). Indeed this is what the comparison shows: the cycles derived from
 461 the Tamar and Eden systems were deficient both in number and length under high nutrient levels
 462 consistent with hypothesis that systems with longer cycles and low proportions of cycling are
 463 indications of less stressed systems.

464

465 Considering the magnitude of mineral and nutrient cycling within the Tamar system, Finns Index (CI)
 466 increased between both periods by ~10 & 30% respectively (Table 5), while the Predatory cycling
 467 index (PI) increased initially by 0.18% but then decreased by 0.59%. Together these changes point to
 468 a general increase in the detrital cycling process, but a fall in the predatory species contribution to
 469 these processes. Networks of cycled flows for the Tamar show that the total number of cycles in the
 470 system is sixteen, with these cycles distributed to varying degrees though three cycling nexuses
 471 (cycles having the same smallest transfer is called a nexus (Baird *et al.*, 1991)).

472 **Table 5** Cycle distributions of the Tamar and Eden systems

Distribution (%) of cycles per nexus	Tamar			Eden	
	1990	1992	2005	1999	2015
1	16.67	16.67	16.67	10	10
2	50	50	50	40	40
3	33.33	33.33	33.33	30	30
4	0	0	0	20	20
Number of cycles	16	16	16	10	10
Average path length (API)	2.681	2.716	2.945	2.82	2.90
Throughput cycled (including detritus) t km ⁻² yr ⁻¹	1034	1014	984	1395	754
Throughput cycled (excluding detritus) t km ⁻² yr ⁻¹	290	365	449.34	12.52	33.29
Throughput cycled (by detritus) %	72.76	66.06	93.4	99.02	95.52
Predatory cycling index (PI) % of throughput w/o detritus	0.68	0.86	0.27	0.03	0.24
Finn's cycling index (CI) % of total throughput	10.90	20.76	40.54	19.08	40.37

473 The API of associated cycles, and throughput of material cycled (including detritus) was fairly
 474 consistent across the study period (2.6-2.9 and 1034-984 t km⁻² yr⁻¹ respectively), indicating that
 475 flows of cycling were consistently occurring over short and fast loops. The percentage of material
 476 specifically cycled by the detritus compartment was also proportionately high (>72%), with
 477 increasing importance by the 2005 period (>93%).

479 In comparison with the Tamar, the cycling structure of the Eden estuary consisted of a total of ten
 480 cycles, distributed to varying degrees though four cycling nexuses (Table 5). The API of associated
 481 cycles, was fairly consistent between the study periods (2.8-2.9) specifying that flows of cycling were
 482 occurring over short and fast loops. The percentage of material specifically cycled by the detritus
 483 compartment was also proportionately very high (>95%), with around about a 4% shift towards non-
 484 detritus based cycling during the 2015 period. Indices representing the regulating and cycling of
 485 nutrients in a system (CI and PI) also increased during the 2015 period, suggesting greater system
 486 retentiveness and a greater proportion of material cycled across both higher and lower trophic
 487 levels (Odum, 1969). Both estuaries were found to recycle a large proportion of their material
 488 though short-fast cycles, with the majority of matter (e.g. carbon) being retained for approximately
 489 2-3 cycles. The increasingly high CI index indicates both estuaries have a relatively simple cycling
 490 structure with both CI and API of a similar order as other estuaries with a legacy of nutrient
 491 contamination e.g. the Ythan Scotland (Baird & Ulanowicz, 199), with a study by Raffaelli (2011) also
 492 showing a similar increase in the CI index under a period of nutrient reduction.

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496 3.3 A safe operational space

497 In addition to managing stocks and flows, environmental managers often need to know if a
498 particular model projection (or policy option) will push the system being managed into a potentially
499 unsafe state (i.e. whether a system will cross a critical threshold or tipping point). Thus, scientists
500 and managers invested in considering a whole-systems approach may not be interested in the
501 marginal changes of all species (Donohue *et al.*, 2013), but instead whether the system is capable of
502 accommodating potential changes while retaining its capacity to function while remaining within its
503 “safe-operating” space, and hence is resilient (Raffaelli, 2016). While it should be accepted that no
504 single descriptor can fully accommodate the multifaceted nature of ecosystem resilience (Ulanowicz,
505 1992), one possible way to derive system-level measures of resilience, is to adopt a holistic systems
506 approach rather than trying to measure the independent trajectories of several indicators. In
507 particular, Ulanowicz (2011) has argued that the network metric, “ascendency,” has a restricted set
508 of values for real-world ecosystems, where a system lacking ascendency has neither the extent of
509 activity nor the internal organization needed to function sustainably. By contrast, systems that are
510 so tightly constrained and honed to a particular environment appear “brittle” (in the sense of
511 Holling (1986)) are prone to collapse in the face of even minor novel disturbances (Ulanowicz *et al.*,
512 2009). Systems that endure lie somewhere between these extremes, with such networks falling
513 within a “Window of Vitality” (Ulanowicz, 2005). Further, Zorach & Ulanowicz (2003) have
514 demonstrated that such connections within the “Window of Vitality” can be adequately captured
515 using the structural properties of networks. Thus by plotting such variables, scientists and managers
516 can make *a priori* predictions about the preferential loss or reduction of stocks (e.g. species,
517 populations, communities), against the effects on ecosystem functioning in relation to a “safe
518 operating space” (Raffaelli, 2015; 2016). Such an approach also allows trade-offs between different
519 network configurations that support different management and policy options be considered (e.g.
520 under the impacts of different nutrient regimes). In this way different modelling scenarios or
521 management choices can be assessed in a cost effective and canonical way, without the need to
522 disturb natural ecosystems (Dunne & Williams, 2009).

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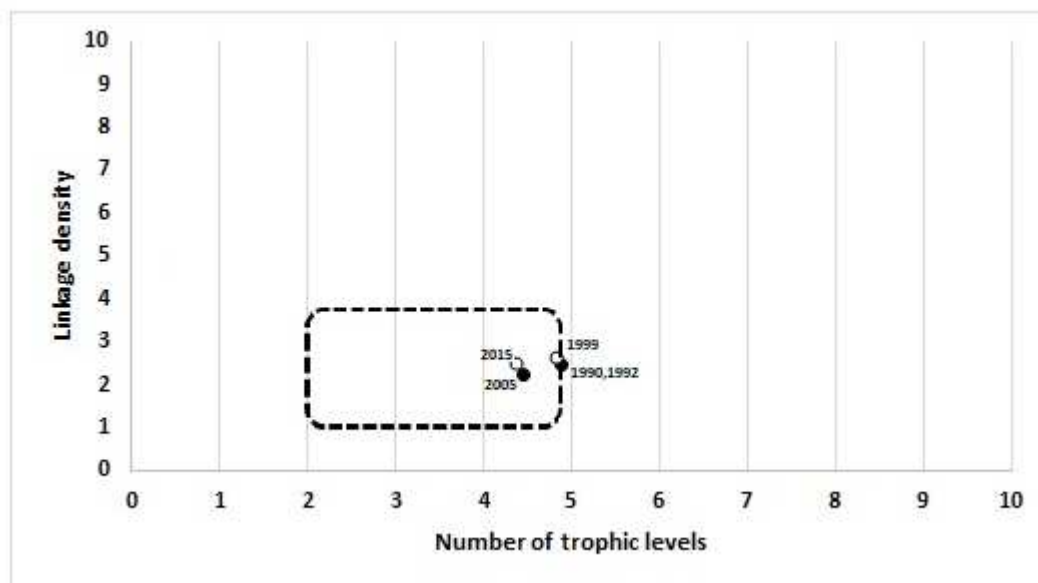
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537 **Figure 5** The “safe operating zone” (delineated by dotted lines) for the Tamar (Black circles) and
 538 Eden (White circles) estuaries defined by ascendancy considerations and captured by two simple
 539 topological properties of food webs: linkage density and number of trophic levels.

540 Encompassing the changes in ascendancy for the Tamar and Eden time periods within Ulanowicz’s
 541 “Window of Vitality” (Figure 5), linkage density and number of trophic levels were shown to be very
 542 different between the pre- and post-management periods. This would locate the post-management
 543 Tamar and Eden periods within the right-hand boundary of the box in Figure 5. In contrast, during
 544 the high nutrient periods in both systems graduated towards the top right area of the perimeter
 545 space, with the Tamar effectively moving close to leaving the defined “safe operating zone”. Under
 546 such circumstances, the results would indicate that the Eden system was able to accommodate
 547 historic large scale effects of changes in nutrient loading over the investigated periods, while the
 548 Tamar was operating in a relatively unsustainable state in the 1990’s and relative to its less disturbed
 549 state in 2005. Implications for the Tamar in its high nutrient state would suggest that some trophic
 550 pathways may have narrowed, leaving the system less resilient with insufficient reserves to resist
 551 future disturbances (Ulanowicz, 2002). Subsequently both systems have moved closer to the
 552 geometric centre of the window ($c = 1.25$ and $n = 3.25$) which represents the best possible
 553 configuration for system sustainability (Ulanowicz *et al.*, 2009).

554 Overall, the system resilience measures used here suggest that large scale shifts in the nutrient
 555 balance of each estuary did not move the systems out of their safe space, which might give grounds
 556 for optimism of traditionally high nutrient systems such as estuaries (Leschine *et al.*, 2003; Elliott &
 557 Whitfield, 2011). Nonetheless, both versions of the Tamar and Eden networks were close to the
 558 “safe” operational boundary during the high nutrient periods and still remain just on the right of the
 559 Ulanowicz’s ascendancy curve, and at the top left corner of his “Window of Vitality”. The question
 560 remains as to whether future stressors acting additively or synergistically with changes in nutrient
 561 loading (e.g. increased river flow or water temperatures) could push the systems out of their safe
 562 space. By plotting the values of the three variables related to Ulanowicz’s (2005) “Window of
 563 Vitality” for many ecosystems under different environmental pressures, it may become possible to
 564 identify a region in perimeter space that characterises a generic healthy and robust ecosystem
 565 (Raffaelli, 2015).

566

567 3.4 Model limitations

568 When interpreting the modelled outputs from this study, several assumptions and limitations of
569 model capability must be considered. Firstly, the development of an Ecopath model strongly
570 depends on the quality of data used to build the model (Christensen & Walters, 2004). In this study,
571 the data for almost all groups (Biomass, P/B, Q/B) were derived from site and time specific raw
572 databases or stock specific assessments providing a solid background for dynamic modelling.
573 However, for groups that play an important role in the Tamar or Eden estuaries food–web but for
574 which no or very little data was available, i.e. certain macrofauna or meiofauna, their omission from
575 the developed ecological networks may have led to an oversimplification in the structure of all food–
576 web components. A specific lack of long term continuous biomass monitoring data in both case
577 study areas, particularly for invertebrates and demersal fish, was also a specific limitation in
578 validating historic trends and improving the validity of future predicted outcomes. Moreover, due to
579 lack of specific knowledge, several functional groups have been aggregated, e.g. demersal fish
580 potentially masking important species interactions (Essington, 2006). Other important factors that
581 this study did not attempt to represent included the variability of future changing climate
582 forcing/environmental or management regimes the adaptive potential of species (e.g. by affecting
583 refuge and breeding space, altering animal behaviour, affecting hydrodynamic transports). While
584 some of these uncertainties could be addressed by further laboratory experiments and *in situ*
585 monitoring of ecosystem conditions, temporal variations in species-specific habitat factors, e.g. a
586 loss of habitat, cannot be addressed in Ecopath but instead needs a spatial model (e.g. the Ecospace
587 component of Ecopath with Ecosim, Christensen & Walters, 2004). We also acknowledge the need to
588 raise the standards of Ecopath models in a management context (Heymans *et al.*, 2011; 2016), with
589 similar standards needed in exploring ecosystem theory (Pocock *et al.*, 2016). Within the last few
590 years, a growing number of diagnostic checks, including the PREBAL checks used in this paper, have
591 been developed to establish best practices in creating and using such models (Mackinson *et al.*,
592 2009; Darwall *et al.*, 2010; Link, 2010; Heymans *et al.*, 2016; Scott *et al.*, 2016). These guidelines take
593 into consideration the underlying thermodynamic and ecological rules available to users,
594 recommend approaches to balance an Ecopath model, and how to evaluate uncertainty. In practice
595 if these practices are upheld, it would allow not only more rigorous and consistent models, but
596 would also aid in the acceptance of Ecopath and other mass balance models within science and
597 management.

598 4 Conclusions

600 The process of constructing the Ecopath models here provides a valuable end product in itself
601 through explicit synthesis of work from many researchers and has allowed a summarising of our
602 current knowledge of the trophic flows, cycling structure and potential safe operational space of two
603 estuaries with ongoing managing challenges associated with eutrophication. The models also help to
604 highlight potential system specific data gaps (e.g. diet compositions, site-specific P/B, Q/B ratios, fish
605 population numbers), that if collected in the future could be used to enhance and improve the
606 knowledge of each system. The results of the mass balanced models show that the trophic structure,
607 ecological functioning and general resilience of both the Tamer and Eden estuaries were affected
608 similarly following distinct restoration events. This adds further evidence that reducing nutrient
609 inputs to estuarine systems is not only beneficial to the biodiversity elements of a system (Howarth
610 *et al.*, 2011), but also has wider positive implications on a wide range of important system properties
611 which may only be revealed at the system level (Raffaelli, 2006). By understanding the recovery
612 trajectory of individual systems and the metrics that can describe such responses, such information
613 can be of direct relevance to many scientific and regulatory frameworks (Duarte *et al.*, 2015), for

614 example the European Water Framework Directive (WFD) in its pursuit to assess benthic integrity
615 and determining good ecological status (GES). In the systems studied here, the shifts in the vast
616 majority of the structural and functional indicators were generally consistent with recovery
617 trajectories described for other UK and European Ecopath studies on nutrient disturbed systems
618 (Patrício & Marques, 2006; Baeta *et al.*, 2011; Raffaelli, 2011; Selleslagh *et al.*, 2012). This supports
619 the usefulness of ENA type approaches for assessing the recovery patterns of temperate transitional
620 benthic systems. As scientists using the “Ecosystem Approach” are increasingly interested in how
621 different impacts or recovery options will simultaneously change the ecological functioning of a
622 system (Bennett, 2015) we also suggest that the comparison of information indices between
623 networks when complemented by the inherent analysis of cycles can comprise a useful quantitative
624 approach for inter-ecosystem comparisons (Wulff & Ulanowicz, 1989). Moreover, while the use of
625 ENA modelling is extremely useful in establishing possible disturbance effects, one difficulty with the
626 use of ecological models might be translating these results to stakeholders in an effective manner,
627 (Fulton, 2011). As such, transforming process based models into simple graphical descriptions of risk
628 may be useful to illustrate the integrity of the networks to future change. As coastal systems are
629 host to a complex array of interactions between multiple stressors (Jackson *et al.*, 2016), a key next
630 step will be to focus on the underlying processes and mechanisms whereby the stressors affecting
631 these ecosystems interact.

632

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