Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy

Abigail McQuatters-Gollop[1*], Angus Atkinson[2**], Anaïs Aubert[3], Jacob Bedford[1], Mike Best[4], Eileen Bresnan[5], Kathryn Cook[5,6], Michelle Devlin[7], Richard Gowen[8], David G. Johns[9], Margarita Machairopoulou[5], April McKinney[10], Adam Mellor[10], Clare Ostle[9], Cordula Scherer[8,11], and Paul Tett[8]

[1]Center for Marine and Conservation Policy Research, Plymouth University, Drake Circus, Plymouth, UK PL4 8AA
[2]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, UK PL1 3DH
[3]National Museum of Natural History, CRESCO, 38 Rue du Port Blanc, F-35800 Dinard, France
4Environment Agency, Kingfisher House, Orton Goldhay, Peterborough, UK PE25ZR
[5]Marine Scotland Science, 375 Victoria Road, Aberdeen, UK AB11 9DB
[6]National Oceanography Centre, European Way, Southampton, UK SO14 3ZH
[7]Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, UK NR33 0HT
[8]Scottish Association for Marine Science (SAMS), Oban, Scotland, UK PA37 1QA
[9]The Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, UK PL1 2PB
[10]Agri-Food & Biosciences Institute, 18a Newforge Lane, Belfast, UK BT9 5PX
[11]Trinity College Dublin, School of Histories and Humanities, Centre for Environmental Humanities, Dublin 2, Ireland

*Corresponding author: Abigail.McQuatters-Gollop@plymouth.ac.uk
**Co-authors are listed in alphabetical order

Abstract

Plankton are sensitive indicators of change and, at the base of marine food webs, they underpin important ecosystem services such as carbon sequestration and fisheries production. In the UK and the Northeast Atlantic region, change in plankton functional groups, or ‘lifeforms’, constructed based on biological traits, is the formally accepted policy indicator used to assess Good Environmental Status (GES) for pelagic habitats under the Marine Strategy Framework Directive (MSFD: 2008/56/EC). To identify changes in UK pelagic habitats, plankton lifeforms, were used from diverse UK data sets collected by different methods, including plankton sampling by nets, water bottles, integrating tube samplers, and the Continuous Plankton Recorder. A Plankton Index approach was used to identify change in plankton lifeforms. This is the first time that the pelagic plankton community has been assessed on a UK-wide scale and forms the foundation of the UK’s 2020 MSFD Assessment for pelagic habitat biodiversity and food webs. This approach revealed that some of the plankton lifeforms used in the assessment displayed spatially-variable changes during the past decade. Assessing plankton community change using a common indicator at the UK scale for the first time is a significant step towards evaluating GES for European seas. Determining GES for pelagic habitats, however, is a challenging process, with additional work required to interpret the assessment results and to identify causation of the changes observed.

Key words

Functional groups, ecosystem approach, Marine Strategy Framework Directive, Good Environmental Status, plankton traits

1.1 Introduction

The Ecosystem Approach (EA; Secretariat of the Convention on Biological Diversity, 2004) and Ecosystem-Based Management (EBM; Katsanevakis et al., 2011) are high-level strategies that are increasingly influencing management of marine systems for sustainability and social equity. The European Union’s Marine Strategy Framework Directive (MSFD; 2008/56/EC) is a large-scale example of this holistic style of management. The MSFD requires European seas to achieve Good Environmental Status (GES). An integral part of assessing GES and ensuring that it is maintained is the establishment of environmental targets and indicators of ecosystem state (Claussen et al., 2011). The Directive is a complex, adaptive, and ambitious policy, whose scientific and operational implementation will evolve and adapt throughout its lifetime. Like all Member States, the United Kingdom (UK) is required to assess the state of pelagic habitat biodiversity in its national waters, and to contribute to the MSFD regional-scale assessment, led by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) in the Northeast Atlantic.

The MSFD requires the monitoring of community-level plankton indicators in support of environmental targets for criteria in its biodiversity and food web descriptors (Table 1; European Commission, 2010; European Commission, 2017). Plankton are the foundation of most pelagic and benthic food webs, supporting a range of key ecosystem functions including carbon sequestration and energy flow to higher trophic levels, including species of commercial importance to humans, such as fish (Falkowski et al., 2004). They have also been described as “beacons of climate change” due to their short lifespans, temperature-dependent physiology, and high potential for dispersal (Hays et al., 2005; Richardson, 2008). Furthermore, because most plankton species are not heavily exploited commercially, change in plankton abundances is a direct response to environmental pressures. Because the time-series coverage of plankton in the North Atlantic and fringing shelf seas is exemplary in its spatial and temporal extent (see O'Brien et al., 2017), plankton time-series provide an opportunity to tease apart the prevailing footprint of climate change on ecosystems from other pressures, for example, nutrient loading and fishing. Accordingly, plankton time-series are increasingly used to inform marine policy and management (McQuatters-Gollop et al., 2015; McQuatters-Gollop et al., 2017), as well as for fundamental understanding of marine food webs (Beaugrand and Kirby, 2018).

The UK has defined its MSFD target for the pelagic habitat to achieve ‘Good Environmental Status’ as *the plankton community is not significantly adversely influenced by direct anthropogenic pressures* at the scale of the two MSFD sub-regions that include UK seas. These two sub-regions are the Greater North Sea (OSPAR region II) and the Celtic Seas (OSPAR region III). Detecting changes in planktonic communities, and then attributing them either to climate change or to directly manageable human pressures, such as fishing or nutrient enrichment, is not a trivial task. There are two reasons for this. The first relates to sample collection and analysis. Although multiple plankton time-series exist in Europe (O'Brien et al., 2017), differences in sampling methods, levels of taxonomic identification, and methods of taxa enumeration, even within Member States (see for example Eloire et al., 2010; Richardson et al., 2006; Whyte et al., 2017; Widdicombe et al., 2010) limit the direct comparability of the data, and utilising these different time-series to deliver assessments at the MSFD sub-region level represents a significant technical challenge.

The second reason concerns the dynamic nature of the plankton. Species of plankton are adapted to the ecohydrodynamic conditions of the water bodies within which they live. As a consequence, the ‘patchwork’ of different hydrodynamic regimes found in north western European waters (van Leeuwen et al., 2016), gives rise to spatial variation in the abundance and diversity of plankton and the species that contribute to the plankton at the spatial scale of MSFD reporting regions and/or sub-regional scales (Gowen et al., 1998; Pingree et al., 1978). Furthermore, the inherently variable environment experienced by the plankton, coupled with the short generation time of some taxa (e.g. ≤ day) influences the abundance of individual species and hence the composition of the plankton over a range of temporal scales.

Plankton indicators have been developed and utilised under previous European environmental directives such as the Urban Waste Water Treatment Directive (91/271/EEC) and the Water Framework Directive (2000/60/EC). While these have explored aspects of diversity and community structure as part of indicator development, the Directives focus on nutrient enrichment and eutrophication (Devlin et al., 2009; Gowen et al., 2008) and have not been used in biodiversity assessments, and also do not consider zooplankton. Plankton biodiversity indicators can be constructed from data at varying taxonomic scales, with each option possessing benefits and compromises (McQuatters-Gollop et al., 2017). Single plankton species have long been used as indicators (Beaugrand, 2005) but tend to focus on specific questions, e.g. the abundance of *Calanus finmarchicus* as an assessment of the amount of food available for cod larvae. Furthermore, single species indicators do not assess the diversity of the whole plankton community. There is also the problem that there are no individual species of plankton that can be used to represent the state of the plankton as a whole. In contrast, diversity indices, composed of abundances of all species in a region, attempt to capture the diversity of the plankton community. Diversity indices, however, were developed based on ecological principles relevant to terrestrial ecology. Such indices are difficult to construct with plankton data based on light microscopy due to difficulties of identification and cryptic speciation (species that look the same under a microscope) within the plankton community (Appeltans et al., 2012), and are highly influenced by sampling effort (Stoetaert and Heip, 1990) and the identification of rare species (Lindeque et al., 2013). Finally, Tett et al. (2013, and references cited therein) point out that most meta-studies failed to find relationships between standard species diversity measures and ecosystem functions that are consistent across ecosystems and concluded that functional-group diversity is the key component of ecosystem structure.

Multiple characteristics of the plankton are required to assess the status of the plankton community. One such approach (Tett et al., 2008; Tett et al., 2013) uses a more theoretically-based approach to ‘package’ the available information by grouping species into lifeforms, or functional groups, analogous to the guilds of species used by benthic ecologists (Bremner et al., 2004; Bremner et al., 2003). A lifeform is a group of species (not necessarily taxonomically related) that carry out the same important functional role in the marine ecosystem. For example, diatoms as a group of species have a functional role related to silicon cycling. Metrics based on functional traits are more closely linked to ecosystem structure and functioning than those based on single species or number of species (Litchman et al., 2007; Mouillot et al., 2013; Stuart-Smith et al., 2013; Villéger et al., 2008). Indicators based on a functional group approach have been shown to provide a useful means of describing plankton community structure and biodiversity (Estrada et al., 2004; Gallego et al., 2012; Garmendia et al., 2012; Mouillot et al., 2006) and have been used to assess community response to pressures such as nutrient enrichment (Gowen et al., 2015; Tett et al., 2008) and climate change (Beaugrand, 2005). Indicators based on plankton lifeforms address the above challenges and can be used to examine change in plankton communities based on multiple datasets with different taxonomic resolutions (Gowen et al., 2015; Tett et al., 2008). Plankton lifeform indicators have thus been developed to inform the biodiversity and food webs MSFD Descriptors (Table 1).

Table 1: MSFD Descriptors for determining GES, relevant to the pelagic habitat. *Quoted text in italics.*

Descriptor (Annex I of the MSFD)	
Relevant criteria (European Commission, 2010, part B)	Relevant criteria (European Commission, 2017, Annex)
1. **Biodiversity** *Biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions.*	
At the habitat level, assessment includes habitat distribution and extent, plus *1.6. Habitat condition* including condition and relative abundance of *the typical species and communities*, and *1.7. Ecosystem structure – composition and relative proportions of ecosystem components (habitats and species)*	*D1C6 the condition of* each broad *habitat type, including its biotic and abiotic structure and its functions (e.g. its typical species condition and their relative abundance, absence of particularly sensitive or fragile species, providing a key function, size structure of species) is not adversely affected due to anthropogenic pressures.*
4. **Food webs** *All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.*	
This descriptor concerns important functional aspects such as energy flows and the structure of food webs (size and abundance) and the criteria include: *4.3 Abundance/distribution of key trophic groups/species – Abundance trends of functionally important selected groups/species.*	The relevant 'trophic guilds' are phytoplankton and zooplankton (ICES, 2015); the criteria are: *D4C1 The diversity (species composition and their relative abundance) of the trophic guild is not adversely affected due to anthropogenic pressures.* *D4C2 The balance of total abundance between the trophic guilds is not adversely affected due to anthropogenic pressures.* *DC43 The size distribution of individuals across the trophic guild is not adversely affected due to anthropogenic pressures.*

This paper describes a preliminary and novel assessment of changes in the plankton communities found in UK waters via the OSPAR common plankton lifeform indicator (PH1/FW5: Changes in Phytoplankton and Zooplankton Communities). This it is the first time that the plankton found in UK waters have been examined at a regional scale using a consistent method applied to a diverse suite of datasets. This assessment represents an important step towards determining GES for pelagic habitats and will contribute to the UK's formal 2020 assessment for the MSFD. We explore the initial results and some of the challenges that remain and outline the additional requirements to determine whether UK pelagic habitats are in GES.

2.1 Methods

2.1.1 Addressing spatial variability of UK pelagic habitats

UK waters are ecologically and physically heterogeneous and cannot be considered as one uniform system even within individual MSFD sub-regions (van Leeuwen et al., 2015; van Leeuwen et al., 2016). Furthermore, plankton taxa are adapted to live in different hydrodynamic conditions (Margalef, 1978), so that plankton community composition, distribution, and dynamics are closely linked to environmental conditions (de Vargas et al., 2015; Jones et al., 1984; Williams et al., 1994). Using density stratification, an important large-scale physical feature in shallow shelf seas, UK waters were spatially partitioned into six “ecohydrodynamic” (EHD) regimes (Figure 1) (van Leeuwen et al., 2015). The main EHD zone types, based on a 50-year modelled hindcast of water-column structure, are:

- Permanently mixed throughout the year
- Permanently stratified throughout the year
- Regions of freshwater influence (ROFIs)
- Seasonally thermally stratified (for approximately half the year, including summer)
- Intermittently stratified
- Indeterminate regions (inconsistently alternate between the above).

UK EHD zones were divided into North Sea and Celtic Sea zones for this analysis in order to align with the OSPAR Greater North Sea (OSPAR Region II) and Celtic Seas (OSPAR Region III) sub-regions. A more highly resolved EHD model exists for the North Sea than the Celtic Seas (van Leeuwen et al., 2015; van Leeuwen et al., 2016), and therefore the zoning might be less reliable in the case of the Celtic Seas and western English Channel.

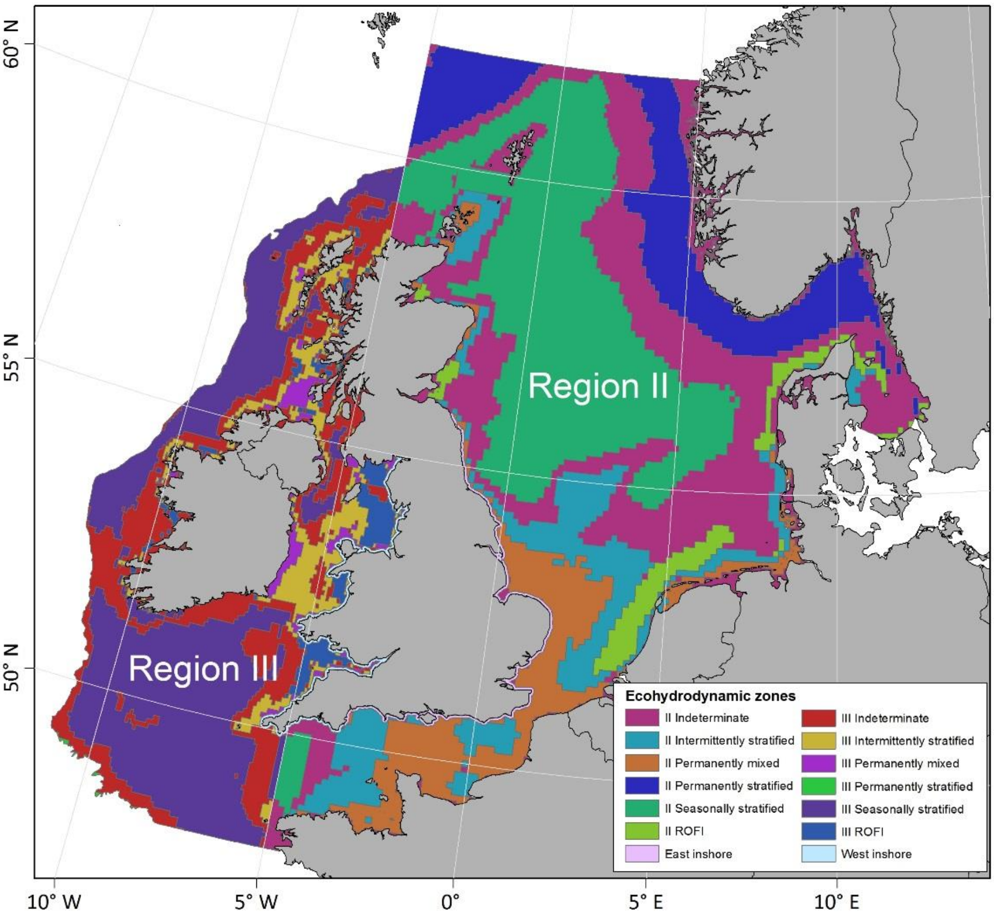


Figure 1: Map of ecohydrodynamic (EHD) zones in the Greater North Sea (OSPAR Region II) and Celtic Seas (OSPAR Region III), coloured by EHD type and region number. EHD zones were constructed based on key simulated water column features, which are important to plankton community structure and dynamics. The main EHD zone types, based on water-column structure, are 1) Permanently mixed throughout the year, 2) Permanently stratified throughout the year, 3) Regions of freshwater influence (ROFIs), 4) Seasonally thermally stratified (for about half the year, including summer), 5) Intermittently stratified and 6) Indeterminate regions (inconsistently alternate between the above levels of stratification). East and west inshore (>1 nm from shore) regions are also shown here, although they were not identified from simulations.

As there is no coastal EHD type, the very near-coast (< 1nm from shore) regions have been divided into east and west coastal inshore EHD zones. The hydrodynamic model Figure 1 indicates an `indeterminate' type in the inshore waters of the Scottish highlands and islands. However, observations (e.g. Inall and Gillibrand, 2010; Wood et al., 1973) show that salinity-stratification and associated density-driven circulation are common here. For this reason a fjordic system EHD type was used for sea lochs on the west coast of Scotland.

The UK plankton monitoring programme (Figure 2) consists of coastal, fixed-point sampling stations including PML L4 (Atkinson et al., 2015), CEFAS SmartBuoys (Weston et al., 2008), Environment Agency (EA) Water Framework Directive (WFD) monitoring stations (UKTAG, 2014), Scottish Environmental Protection Agency WFD monitoring stations, Agri-Food and Biosciences Institute monitoring stations (Gowen and Stewart, 2005), the Firth of Lorne Observatory (Tett, 1973; Tett and Wallis, 1978; Whyte et al., 2017), the Scottish Coastal Observatory (Bresnan et al., 2016), and the offshore Continuous Plankton Recorder (CPR) survey (Richardson, 2008) (see Figure 2). These various sources of data provide complementary information, with the CPR data illustrating regional and long-term change and the fixed-point stations providing detailed information at higher time and depth resolution at a local scale. EHD zones provide a spatial framework by which to use these two types of data together. CPR data and EA coastal sampling network were thus aggregated at the EHD zone scale, allowing comparability between CPR and fixed-point results in the same EHD zone. Because EHDs are constructed based on the dominant hydrodynamic features of the water column, this approach also enables data from one part of an EHD zone to be used for the whole of that EHD zone (Scherer et al., 2014). In other words, features of the plankton community at a fixed-point station in a particular EHD zone are assumed to be representative of the plankton community throughout that EHD zone.

2.1.2 Plankton lifeform construction

The UK plankton monitoring programme consists of surveys from a variety of government agencies and research organisations. They employ sampling techniques ranging from collections at fixed (buoys or moorings) time-series stations using nets, tubes integrating the top 10m of the water column, and water bottles to the Continuous Plankton Recorder survey, a large scale plankton monitoring programme which uses ships of opportunity (Figure 2) (Bean et al., 2017). All these surveys contribute towards a large quantity of UK plankton data, however, variation in sampling methods, levels of taxonomic identification, and methods of taxa enumeration provide a challenge to UK-level assessments.

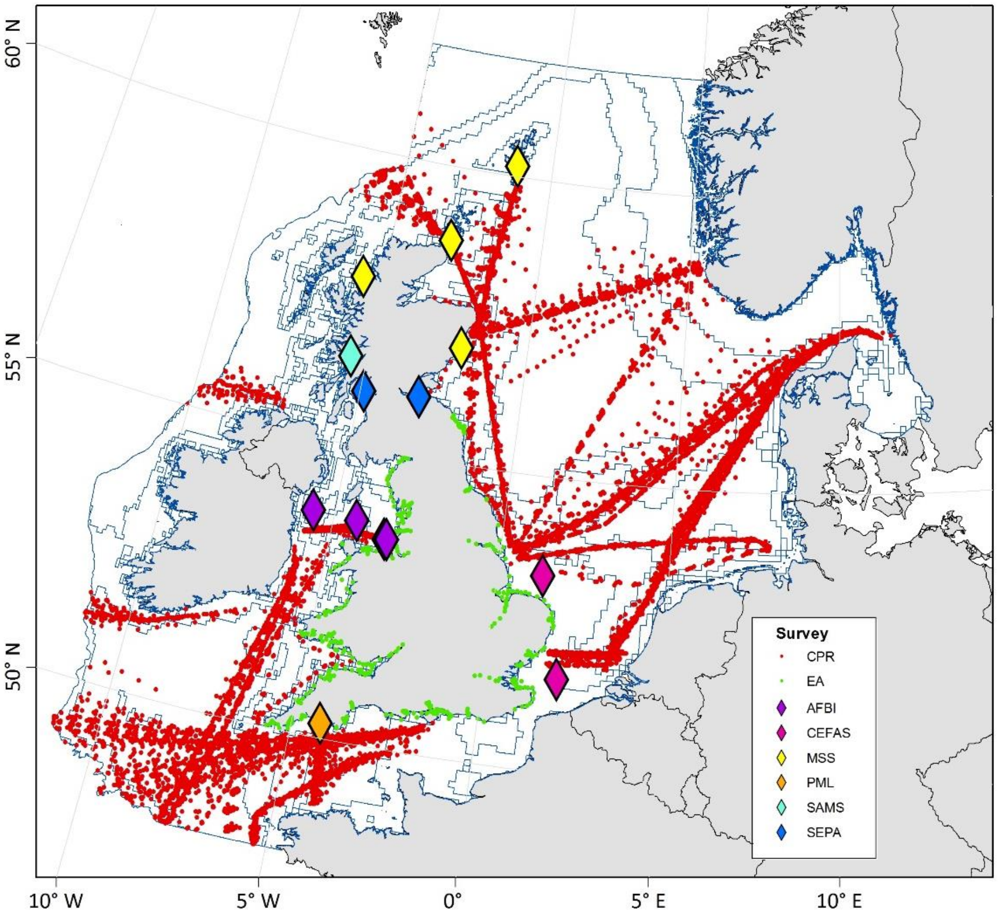


Figure 2: The UK plankton monitoring programme consists of disparate but complementary surveys. Samples from the Continuous Plankton Recorder (CPR) are displayed as red dots along routes; samples represent 10 nautical miles of water. The other surveys operate fixed-point sampling schemes. Abbreviations: AFBI – Agri-Food and Biosciences Institute; EA – Environment Agency; PML – Plymouth Marine Laboratory; MSS – Marine Scotland Science; SAMS – Scottish Association for Marine Science; Cefas - Centre for Environment, Fisheries and Aquaculture Science; and SEPA – Scottish Environmental Protection Agency.

To address this and provide a holistic view of the UK plankton, an indicator based on plankton lifeforms was developed which allows the use of all plankton datasets, regardless of differences in sampling or analysis techniques. To construct the plankton lifeform indicator, plankton taxa were grouped into lifeforms based on traits such as size, trophy, motility, and other key biological features (Table 2, 3; Litchman et al., 2012; Litchman and Klausmeier, 2008). Taxa can be assigned multiple traits, and can be included in multiple lifeforms. In instances where the trait of a taxon was unknown, the taxon was omitted from lifeforms constructed with that particular trait. Because plankton lifeforms are constructed based on traits (Table 4) rather than on species-level information, grouping plankton taxa into lifeforms allows the use of plankton data identified at different taxonomic resolutions, which suits the UK's integrated but diverse plankton monitoring programme. Additionally, plankton lifeforms are aggregations of taxa and so are less likely to experience the extreme seasonal fluctuations of single species indicators. Finally, because lifeforms consist of multiple taxa with a similar functional role, spatial intercomparability is increased, as even though the particular taxa fulfilling a functional role may vary, the corresponding lifeform is often regionally ubiquitous. When examined in ecologically-relevant plankton lifeform pairs, plankton lifeforms can provide an indication of changes in different aspects of plankton community functioning such as energy flows, benthic-pelagic coupling, and food web structure (Table 4). The eight lifeform pairs were selected according to confidence in the traits corresponding to each lifeform and to reflect multiple features of the pelagic habitat. As the knowledge base increases or policy needs change, new plankton lifeform pairs can be developed, allowing us to address additional and emerging scientific and policy questions about biodiversity, food webs, eutrophication, and responses to climate change. Given the emerging importance of community functioning as a key characteristic of biodiversity, all of the lifeform pairs in Table 4 contribute to the biodiversity and food web descriptors.

Table 2: Plankton taxa were assigned traits based on our simple definition based on key biological features.

Trait type	Trait categories
Plankton type	Phytoplankton: protista taxa that contribute to primary production Zooplankton: metazoan taxa of the kingdom Animalia
Zooplankton type	Fish/eggs: taxa of the subphylum Vertebrata Copepod: taxa of the subclass Copepoda Gelatinous: taxa of the phylum Cnidaria and Ctenophora Crustacean: taxa of the Subphylum Crustacea
Phytoplankton type	Diatom: taxa of the class Bacillariophyceae Dinoflagellate: taxa of the phylum Dinoflagellata
Zooplankton trophic mode	Carnivore: taxa which prey on zooplankton Herbivore: predominately suspension or filter feeders Omnivore: includes both carnivorous and herbivorous feeding Ambiguous: diet uncertain
Habitat	Holoplankton: taxa which spend their entire lifecycle in the plankton Meroplankton: taxa which spend part of their lifecycle in the plankton Tychopelagic: benthic diatoms which can become mixed into the water column
Size	Large: phytoplankton (≥ 20 µm diameter); zooplankton(≥ 2 mm adult body length) Small: phytoplankton (< 19 µm diameter); zooplankton (< 1.9 mm adult body length)

Table 3: Plankton lifeforms are comprised of taxa sharing the same traits.

Lifeform	Traits
Diatoms	Plankton type = 'Diatom'
Dinoflagellates	Plankton type = 'Dinoflagellate'
Gelatinous zooplankton	Plankton type = ‘Gelatinous’
Fish larvae/eggs	Zooplankton type = 'Fish' AND ‘Eggs’
Non-carnivorous zooplankton	Plankton type = 'Zooplankton' AND Trophic mode = either 'Herbivore', 'Omnivore', OR 'Ambiguous'
Crustaceans	Zooplankton type = 'Crustacean'
Large phytoplankton	Plankton type = 'Phytoplankton' AND Size = 'Large'
Small phytoplankton	Plankton type = 'Phytoplankton' AND Size = 'Small'
Pelagic diatoms	Phytoplankton type = 'Diatom' AND Habitat = 'Holoplankton'
Tychopelagic diatoms	Phytoplankton type = 'Diatom' AND Habitat = 'Tychopelagic'
Holoplankton	Plankton type = ‘Zooplankton’ and Habitat = 'Holoplankton'
Meroplankton	Plankton type = ‘Zooplankton’ and Habitat = 'Meroplankton'
Large copepods	Zooplankton type = 'Copepod' AND Size = 'Large'

Lifeform	Traits
Small copepods	Zooplankton type = 'Copepod' AND Size = 'Small'
Phytoplankton	Plankton type = ‘Phytoplankton’

Table 4: Plankton lifeform pairs consist of two contrasting and ecologically-relevant plankton lifeforms. The rationale behind their selection is also described.

Lifeform pairs	Ecological rationale
Diatoms and dinoflagellates	Systems receiving high nutrient input are often dominated by dinoflagellates at the expense of diatoms (McQuatters-Gollop et al., 2009). In the North Atlantic, stratification plays a key role in structuring phytoplankton communities with dinoflagellate abundances connected to increased stratification while diatoms are better suited to mixed waters (Barton et al., 2015). Change in the relative abundance of the two plankton lifeforms can therefore indicate changes in nutrient and stratification regimes.
Pelagic diatoms and tychopelagic diatoms	Benthic disturbance, such as from development or storms, can resuspend tychopelagic (benthic) diatoms in the water column (Ubertini et al., 2012). A shift in the proportion of tychopelagic and pelagic diatoms can therefore indicate changes in the magnitude and frequency of benthic disturbance and resuspension events.
Large microphytoplankton (≥ 20 µm diameter) and small microphytoplankton (< 19 µm diameter)	Organism size is a key factor in energy transfer efficiency in pelagic habitats and may determine the system’s potential to support higher trophic levels (Fox and Pitois, 2006; Thiebaux and Dickie, 1993). Changes in the relative abundance of large microphytoplankton (≥ 20 µm diameter) and small microphytoplankton (< 19 µm diameter) can therefore indicate alterations in energy flow to higher trophic levels.
Microphytoplankton and non-carnivorous zooplankton	Non-carnivorous zooplankton graze on microphytoplankton, thereby transferring energy from single-celled algae to metazoan animals. Changes in the relative abundance of the two plankton lifeforms can therefore indicate changes in energy flow through the pelagic food web.
Small copepods (< 1.9 mm) and large copepods (≥ 2 mm) adult body length	Copepods are a key food resource for higher trophic levels, including commercially important fish such as larval cod, whose survival is linked to the mean size of their prey (Beaugrand et al., 2003). A change in the proportion of large (≥2 mm in length) and small (<1.9 mm in length) adult copepods can therefore indicate changes in food web structure (Capuzzo et al., 2018; Fox and Pitois, 2006).
Holoplankton and meroplankton	Meroplankton only spend a part of their lifecycle within the pelagic realm, and for their most part, are the larvae of benthic organisms. A change in the proportion of meroplankton and holoplankton (plankton spending their whole lifecycle within the pelagic realm) can indicate a change in the strength of benthic and/or pelagic production with consequences for pelagic-benthic coupling (Kirby et al., 2008; Lindley et al., 1995).
Crustaceans and gelatinous zooplankton	Gelatinous organisms within the plankton can have an important predatory effect on other crustacean plankton and fish larvae when abundant, thereby acting as a pressure on fish populations. A change in the relative abundance of crustaceans and gelatinous zooplankton can thus indicate a change from an ecosystem with numerous fish of commercial interest to an ecosystem dominated by gelatinous organisms of low commercial interest (Kirby et al., 2009; Purcell and Arai, 2001; Richardson et al., 2009).

Gelatinous zooplankton and fish larvae/ eggs	Gelatinous organisms within the plankton can have an important predatory effect on other crustacean plankton and fish larvae when abundant, thereby acting as a pressure on fish populations. A change in the relative abundance of fish larvae/eggs and gelatinous zooplankton can thus indicate a change from an ecosystem with numerous fish of commercial interest to an ecosystem dominated by gelatinous organisms of low commercial interest (Kirby et al., 2009; Purcell and Arai, 2001; Richardson et al., 2009).

2.1.3 Identifying change in plankton lifeforms

A ‘Plankton Index’ (PI) has been used to identify temporal change within plankton lifeform pairs. This approach (Gowen et al., 2011; Scherer et al., 2014; Tett et al., 2008) identifies change plankton lifeform pairs from a starting period, usually at the beginning of a time-series, although the PI has been used to hindcast (Gowen et al., 2015) and compare changes in plankton in response to human pressure in different regions of the same ecohydrodynamic regime (Scherer, 2012) . Based on general systems theory (von Bertalanffy, 1972), a sample’s position at any point in time is defined in “state space” by orthogonal axes of (log-transformed) lifeform abundance. For convenience and ease of visualisation, the axes are plotted two at a time, so that, for example, a sample’s horizontal co-ordinate is diatom abundance and its vertical co-ordinate is dinoflagellate abundance (Figure 3).

To define the reference boundary, an envelope is drawn around several years of points representing monthly samples (Figure 3); here we used a 5-year period. Monthly averaged data from subsequent periods are then plotted in the same state space, and a Plankton Index (PI), and associated probability value, calculated as the proportion of new points falling within the reference boundaries. A PI value approaching 1 indicates no difference in plankton communities while a PI value approaching 0 indicates a complete change in plankton communities between the two time periods. Low PI values across spatially disparate datasets mean that wide scale changes in the plankton community (e.g. from climate change) can be identified. The PI approach is flexible in nature, allowing both abundance and biomass data to be used, and furthermore it is relatively robust to periods without data collection, making it ideal for identifying change in plankton communities when assessing environmental state by using multiple disparate datasets. Although originally developed to track change in phytoplankton communities (Tett et al., 2008), the PI has been adapted to also incorporate changes in zooplankton, making this a method to assess change in the plankton community more holistically.

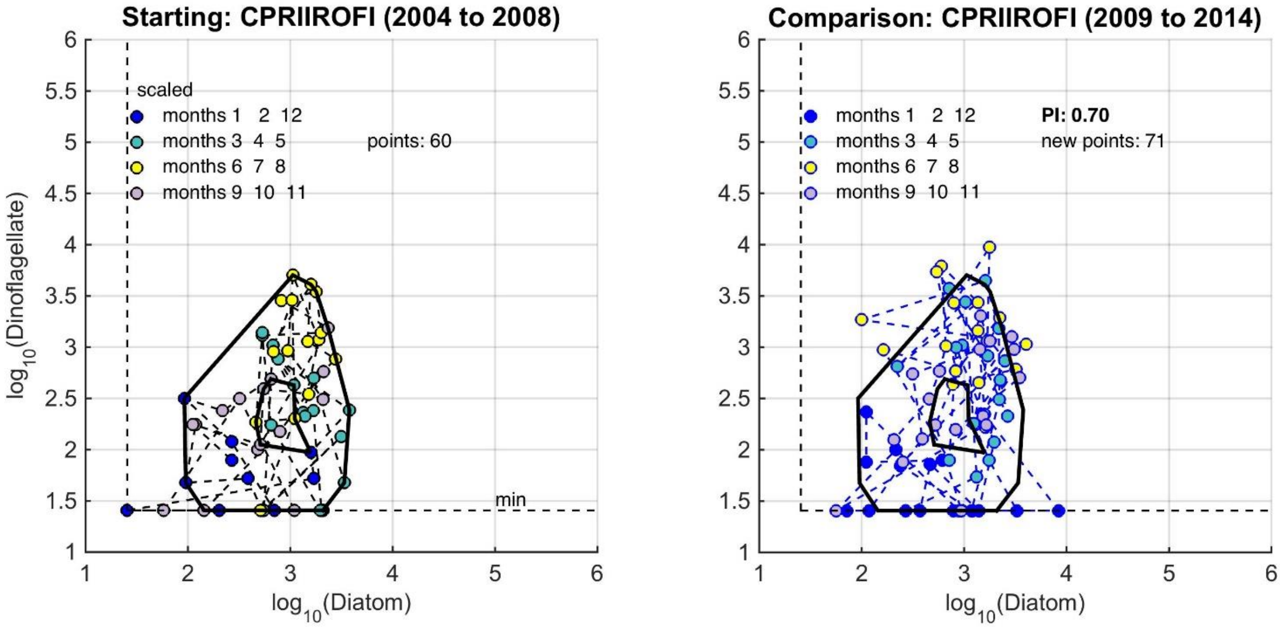


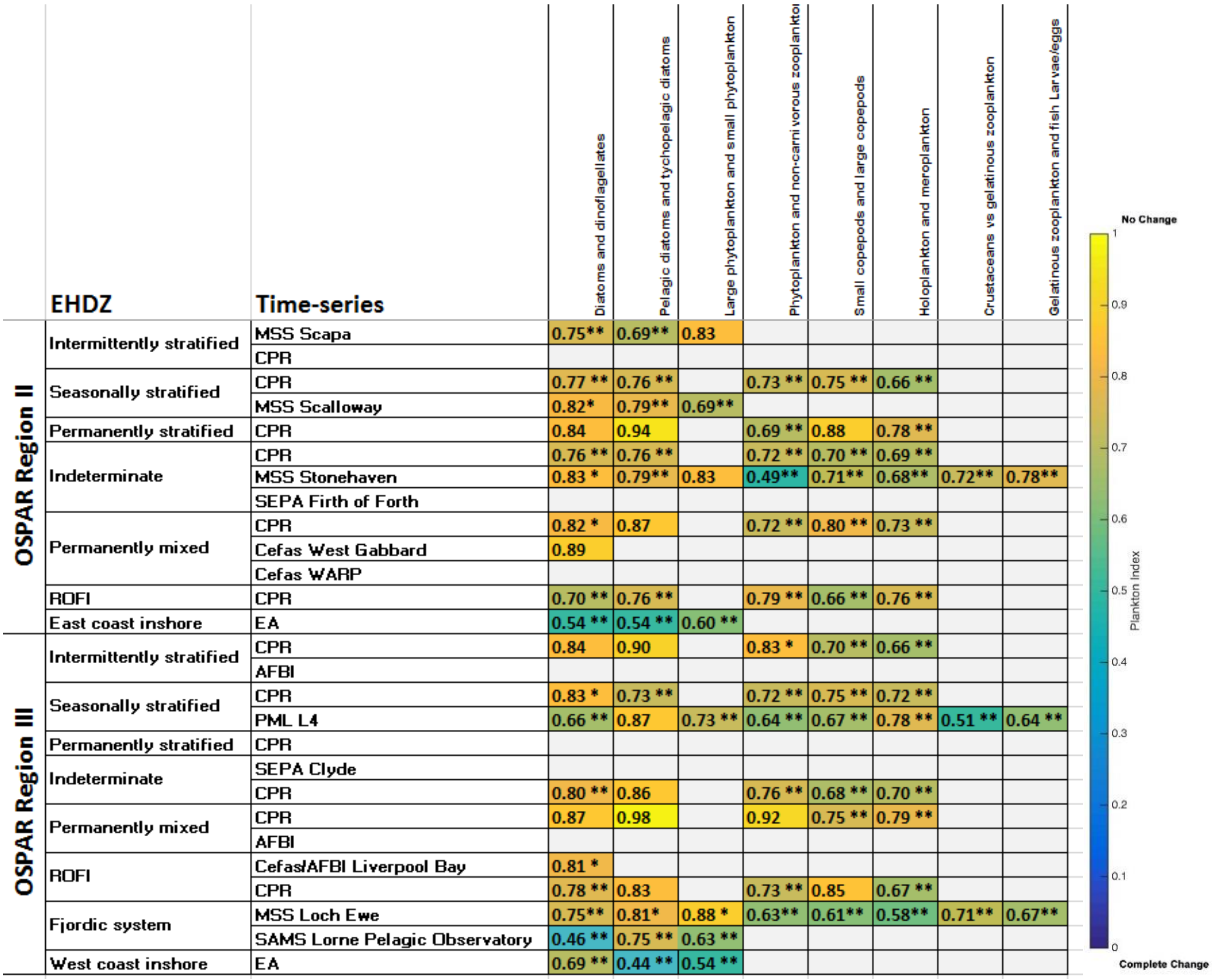
Figure 3: An example diatoms v dinoflagellate comparison between starting and contemporary conditions for Regions of Freshwater Influence (ROFIs) in the North Sea (OSPAR Region II). Left: The starting conditions envelope, outlined in black, was created using sampling points from 2004-2008. Right: points from the 2009-2014 UK 2020 MSFD Assessment period (n=71) are overlain on the starting conditions envelope. The PI value of 0.70 suggests a statistically significant difference between the two time periods (binomial p < 0.01), caused by 21 of the 71 assessment period points falling outside the bounds of the starting conditions envelope. The distribution of the points in the assessment period suggests an increase in dinoflagellates in summer months.

The PI value was calculated for all lifeform pairs for each fixed-point sampling station (with sufficient data) and for CPR data aggregated across each EHD zone. For the UK 2020 MSFD Assessment, the period 2004 to 2008 was selected to represent starting conditions to align with the starting condition period used in the OSPAR Intermediate Assessment 2017. This starting period selection was therefore driven by a policy rather than scientific requirement, a point we discuss later. The starting condition envelope was compared with data from the subsequent six-year MSFD Assessment period (2009 to 2014), also chosen for its alignment with the MSFD assessment and reporting cycle. From a policy perspective, this strategy facilitated comparability between the UK-level and OSPAR-level analyses and allowed the examination of change in UK plankton with respect to regional scale plankton change, as identified through the 2017 OSPAR Intermediate Assessment. Most importantly, alignment of the starting condition periods allowed the examination of plankton change on the MSFD policy timescale, a key goal of the UK 2020 MSFD Assessment to which this work will contribute. Here we have expanded the number of UK datasets beyond those used in the UK 2020 MSFD Assessment to include all UK plankton time-series with data spanning the same 2004-2014 time period. The datasets from Scottish Environmental Protection Agency (SEPA) and the Agri-Food and Biosciences Institute, Northern Ireland (AFBI), however, did not cover the full duration of the starting conditions period and were therefore excluded from this analysis.

3.1 Results

3.1.1 A first assessment of changes in UK plankton

Differences in the Plankton Index between starting conditions (2004-2008) and current conditions (2009-2014) were calculated for all lifeform pairs where monthly data were available during the entire time period (Figure 4). This first analysis showed similarities and differences in PI values from different EHD zones and between lifeform pairs. Of the 91 differences identified, 78 were statistically significant (Figure 4), suggesting alterations to the UK plankton community between the starting and MSFD assessment periods. Further interpretation of these results (including timing and dominance of plankton lifeforms and an investigation to the significant contributing species) were not included in the MSFD assessment and are therefore beyond the scope of this current paper.



OSPAR region	EHDZ	Time-series	Diatoms and dinoflagellates	Pelagic diatoms and tychopelagic diatoms	Large phytoplankton and small phytoplankton	Phytoplankton and non-carnivorous zooplankto	Small copepods and large copepods	Holoplankton and meroplankton	Crustaceans vs gelatinous zooplankton	Gelatinous zooplankton and fish Larvae/eggs
OSPAR Region II	Intermittently stratified	MSS Scapa	0.75**	0.69**	0.83					
		CPR								
	Seasonally stratified	CPR	0.77 **	0.76 **		0.73 **	0.75 **	0.66 **		
		MSS Scalloway	0.82*	0.79**	0.69**					
	Permanently stratified	CPR	0.84	0.94		0.69 **	0.88	0.78 **		
	Indeterminate	CPR	0.76 **	0.76 **		0.72 **	0.70 **	0.69 **		
		MSS Stonehaven	0.83 *	0.79**	0.83	0.49**	0.71**	0.68**	0.72**	0.78**
		SEPA Firth of Forth								
	Permanently mixed	CPR	0.82 *	0.87		0.72 **	0.80 **	0.73 **		
		Cefas West Gabbard	0.89							
		Cefas WARP								
	ROFI	CPR	0.70 **	0.76 **		0.79 **	0.66 **	0.76 **		
	East coast inshore	EA	0.54 **	0.54 **	0.60 **					
OSPAR Region III	Intermittently stratified	CPR	0.84	0.90		0.83 *	0.70 **	0.66 **		
		AFBI								
	Seasonally stratified	CPR	0.83 *	0.73 **		0.72 **	0.75 **	0.72 **		
		PML L4	0.66 **	0.87	0.73 **	0.64 **	0.67 **	0.78 **	0.51 **	0.64 **
	Permanently stratified	CPR								
	Indeterminate	SEPA Clyde								
		CPR	0.80 **	0.86		0.76 **	0.68 **	0.70 **		
	Permanently mixed	CPR	0.87	0.98		0.92	0.75 **	0.79 **		
		AFBI								
	ROFI	Cefas/AFBI Liverpool Bay	0.81 *							
		CPR	0.78 **	0.83		0.73 **	0.85	0.67 **		
	Fjordic system	MSS Loch Ewe	0.75**	0.81*	0.88 *	0.63**	0.61**	0.58**	0.71**	0.67**
		SAMS Lorne Pelagic Observatory	0.46 **	0.75 **	0.63 **					
	West coast inshore	EA	0.69 **	0.44 **	0.54 **					

Figure 4: Plankton Indices, by OSPAR region and EHD zone, for the period 2009 - 2014 from starting conditions (2004 – 2008). Starred cells indicate theoretical significant change (*p<0.05; **p<0.01) from starting conditions. A Plankton Index approaching '1' (bright yellow cells) denotes no change from starting conditions while an Index approaching '0' (dark blue cells) represents complete change. White shading represents where data were insufficient to determine a Plankton Index. UK datasets with incomplete data during the starting conditions period were not used in the analysis, but all existing sampling stations are included to demonstrate the future potential of the monitoring program.

The degree of difference in PI value was spatially variable within each lifeform pair (Figure 5) although, in some cases, remarkable similarity between surveys exists. Of the lifeform pairs sampled for most datasets (n >12 datasets) holoplankton and meroplankton (range = 0.21) as well as small and large copepods (range = 0.27) had the smallest ranges in PI, indicating the highest levels of spatial harmony (Figure 4, Figure 5). The lifeform pair with the greatest variability was pelagic diatoms and tychopelagic diatoms (range = 0.54), with the greatest difference between the starting and assessment period found in the west coast inshore EHD zone (PI = 0.44, p<0.01). Other than the highly dynamic west and east coast inshore zones, the most extreme differences from starting conditions of any lifeform pairs were observed in Scotland and the Western Channel, with phytoplankton and non-carnivorous zooplankton at Stonehaven (PI = 0.49, p < 0.01), and diatoms and dinoflagellates at Lorne (PI = 0.46, p < 0.01).

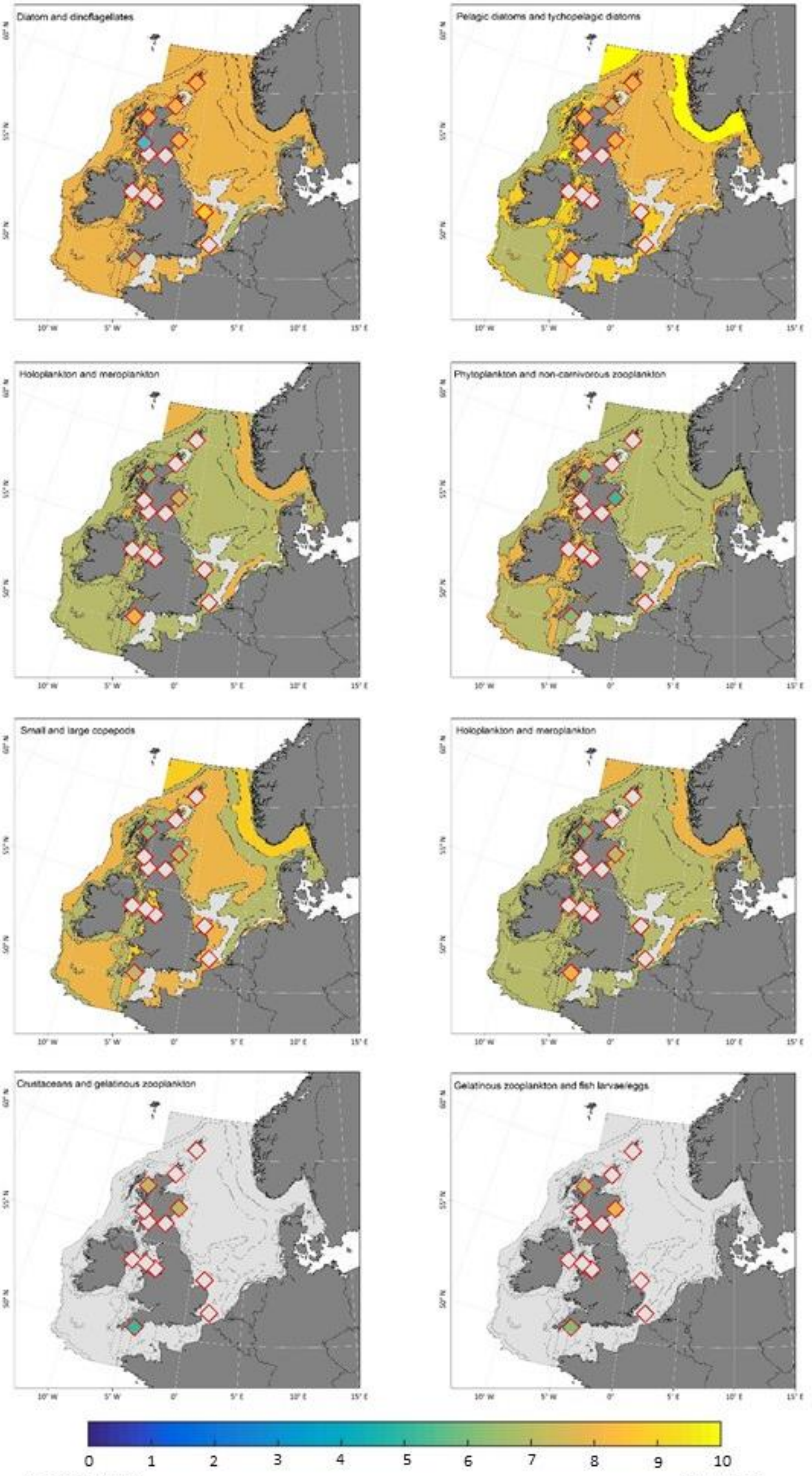

Diatom and dinoflagellates
Pelagic diatoms and tychopelagic diatoms
Holoplankton and meroplankton
Phytoplankton and non-carnivorous zooplankton
Small and large copepods
Holoplankton and meroplankton
Crustaceans and gelatinous zooplankton
Gelatinous zooplankton and fish larvae/eggs
60° N
55° N
50° N
10° W
5° W
0°
5° E
10° E
15° E
0
1
2
3
4
5
6
7
8
9
10
Complete change
No change

Figure 5: Plankton Index for each lifeform pairs in UK waters. Changes within EHDs are based on CPR data, with fixed-point stations overlain (red borders). Points or EHD zones in grey lack complete data during starting conditions and/or assessment period for particular lifeform pairs. Results for non-UK EHDs are also displayed as they enable regional interpretation of UK plankton dynamics.

Results between the near-shore fixed-point stations and CPR data in the same EHD zone were broadly consistent (Figure 4, Figure 5), suggesting spatial congruence between the two survey types. For example, the results of PML L4, located in the seasonally stratified Celtic Sea OSPAR Region III, were consistent with results from the CPR in the same EHD zone, particularly for the pairs with zooplankton lifeforms. Similarly, the results from Stonehaven, located in the indeterminate North Sea zone, matched well with CPR results from the same EHD.

4.1 Discussion

4.1.1 Change in plankton lifeform indicator

It has previously been established that the UK plankton community has undergone significant changes during the past six decades (Beaugrand, 2004). Changes include phenological alterations (Atkinson et al., 2015; Edwards and Richardson, 2004; Whyte et al., 2017), shifts in the balance of organisms (Beaugrand et al., 2002; Gregory et al., 2009; Whyte et al., 2017), and spatially variable changes in phytoplankton biomass and chlorophyll (McQuatters-Gollop et al., 2011; Whyte et al., 2017). Assessments of estuarine and coastal phytoplankton metrics have also been carried out under the requirements of the WFD, but focussed on changes in the total taxa counts and most numerous species (Devlin et al., 2009; Devlin et al., 2007). An integrated, region-wide view of plankton change assessed using a common indicator and all available UK datasets, however, has been lacking. The case study presented here illustrates the value of the plankton lifeform approach in connecting disparate geographic areas with diverse methods of plankton sampling and analysis, using a common and comparable indicator. This is the first application of this indicator across multiple plankton datasets throughout UK marine waters, illustrating change between two periods examined for the UK MSFD 2020 Assessment.

Harmony in results between fixed-point datasets and the CPR survey highlights the complementarity of the datasets comprising the UK's plankton monitoring programme (Figure 4, Figure 5). For example, results from PML L4 and the CPR survey are particularly well-matched for pairs with zooplankton lifeforms and are also in line with previous work showing that zooplankton seasonal cycles captured by the two time-series were similar, even though absolute abundances differed (John et al., 2001; Ostle et al., 2017).The similarity in PI values between CPR and fixed-point time-series suggests both are representative of EHD zones, but further validation between CPR and fixed-point data from the same EHD zones are needed.. Better spatial representivity exists for EHD zones which are monitored by CPR routes compared to locations with only a fixed-point station, though some inshore fixed-point stations (PML, MSS Stonehaven, MSS Loch Ewe) are monitored weekly and so better reflect temporal variability. Some of the EHD zones are spatially large and thus averaging over such a large spatial scale may dampen or mask variability. EHD zones with both CPR data and fixed-point stations have the most comprehensive and robust information. The stations closest to shore, the east and west inshore EHDs and SAMS Lorne Pelagic Observatory, displayed some of the most extreme differences in PI values, suggesting that coastal waters are more temporally variable than waters further offshore. In the case of the east and west inshore EHDs, however, some of this variability may be caused by changes to the sampling programme as mentioned above. These preliminary results show that UK plankton lifeforms displayed spatially-variable changes during the past decade with greater depth of knowledge obtained by the merging of many UK plankton datasets.

This study constitutes a first step in evaluating GES for UK waters by documenting widespread change. There is work to be done in establishing the causes of change, which might include (i) the intrinsic inter-annual and decadal scale cyclical variability common to many Earth systems; (ii) the longer-term effects of global change, especially that associated with climate; or (iii) the superimposed effects of manageable anthropogenic pressures such as nutrient enrichment, fisheries disturbance, pollution or seabed disturbance on food webs. The UK definition of GES for the pelagic habitat is essentially practical: if change in lifeform absolute and relative abundances (which can be signalled by the PI) is attributed to increases in manageable pressures, then the habitat is not in GES and measures need to be taken to ameliorate the pressures. Thus we have referred to the 2004-2008 period as 'starting' rather than 'reference' conditions as these years were chosen to fit with the MSFD policy assessment cycle rather than any judgement of whether the condition of the pelagic habitat was in GES or not. Ideally, the envelope used to calculate a value of the PI would be drawn around a set of points from a marine ecosystem known to be in GES. Scherer et al. (2016) have proposed a method for determining pelagic GES independent of the PI tool, but in default of application of this method to all EHD types in UK waters, the PI only provides an indication of change. However, such change in PI can be used as a 'flag' to trigger further investigation into the pressures that may be causing this change in ecosystem state.

4.1.2 Further development of the lifeform indicator and Plankton Index approach for assessing Good Environmental Status

As an indicator of plankton functioning and structure, the lifeform approach enables the use of multiple datasets with disparate methods of sample collection and taxonomic analysis. Our results demonstrate that data collected from disparate monitoring programmes established for a variety of policy drivers (e.g., Water Framework Directive, investigative monitoring and research, Urban Waste Water Treatment Directive) can also be used for the construction of plankton lifeforms for use as a MSFD indicator. Because plankton lifeform datasets can be populated with plankton data not collected specifically for informing the MSFD indicator, the use of this single regional indicator promotes synergies between disparate UK plankton monitoring surveys. This approach, whilst innovative, does require several more steps to increase its robustness, enable the best use of all available plankton data, and to support future use of the indicator in other geographic areas. Each of these steps is a precursor to determining GES for UK pelagic habitats.

EHD zones provide a way to define pelagic habitats and plankton communities, but the model used to construct the EHD zones was developed for use in, and validated with data from, offshore pelagic environments and as a result may not accurately simulate conditions in near-shore areas (van Leeuwen et al., 2015; van Leeuwen et al., 2016). Observationally-informed designations of the seasonal stratification from fixed point stations in some regions such as the Western English Channel do not always agree perfectly with the EHDs defined in Figure 1. In some cases, such as the Irish Sea, it is likely that numerous EHD zones occur in a relatively small region of complex hydrography (Gowen et al., 1995; Scherer et al., 2016) and so may need revisiting. In addition, some EHDs (e.g. North Sea seasonally stratified) are large and span a latitudinal gradient of ~ 5 degrees, and thus phytoplankton may experience differing light regimes between the northern and southern regions of this EHD. Nevertheless, we have used the Figure 1 map as a single and traceable regional classification for all our analysis. Further refinement of modelling in hydrodynamically complex areas and improvements in coupled catchment and marine models would improve the delineation of EHD zones.

A consequence of the different methods used in the UK plankton monitoring programme is that there is some inconsistency in the elements of the plankton community sampled. As a result, the full set of lifeform pairs (Table 4) could not be derived from some data sets. Although all UK stations monitor phytoplankton, only the CPR and three fixed-point stations have historically collected and analysed zooplankton samples. Additionally, not all surveys sample all taxa equally well. The CPR, for example, inadequately captures small phytoplankton or gelatinous taxa (Richardson et al., 2006) and so did not contribute to pairs containing these plankton lifeforms. Only three 'sentinel' stations, MSS Stonehaven, MSS Loch Ewe, and PML L4, can address all lifeform pairs. Adding zooplankton sampling to the remaining fixed-point stations would increase the robustness and form a 'sentinel network' providing detailed insight into coastal plankton dynamics which is complementary to the CPR's large-scale, regional sampling. It should also be noted that the smaller size portion of the pelagic assemblage, i.e. small nanoplankton, picoplankton, marine bacteria, and viruses, are poorly monitored (McQuatters-Gollop et al., 2017). Additional consideration needs to be given to taxa which are difficult to monitor or enumerate routinely, such as coccolithophores and mucilage-forming *Phaeocystis*. In general, there is a need for some further development of the trait-based theory (Litchman et al., 2012; Litchman and Klausmeier, 2008) used to define plankton lifeforms for the present work.

Not all UK plankton monitoring programmes collected data during the 2004 to 2008 starting conditions period for PI calculation, resulting in the exclusion of some important time-series from the UK 2020 MSFD Assessment and this analysis. While the Environment Agency (EA) dataset spanned the entire time period, the sampling and analysis methodology and frequency changed in 2008, as a result of implementation of the WFD. Special care must therefore be taken when interpreting change from this time-series. Additionally, some plankton surveys, such as the CPR, Marine Scotland Science, the SAMS Lorne Pelagic Observatory, and PML's L4, have multi-decadal databases; when data from only 2004 onward are included the historical data are not used to their full potential. It is therefore clear that further work into maximising the use of UK datasets is urgently required. Such investigations might test: using the entire time-series as the starting condition period for calculating the PI value; varying the starting condition period depending on the length of the dataset; using a more recent period for the starting conditions to include newer time-series; or shortening the starting conditions period to encompass only three years of data and therefore include more UK datasets. Each of these possibilities may have trade-offs. As suggested by Scherer et al. (Scherer et al., 2014), for example, starting condition envelopes which encompass > 5 years will incorporate a greater amount of natural variability and be less sensitive. Conversely, restricting the starting period to a single year (or two) would increase sensitivity but risk detecting inter-annual variability rather than longer-term change. Similarly, using different years for the starting conditions for different datasets will reduce comparability between surveys. Finally, if starting conditions are set too far in the past they will not reflect prevailing conditions. Exploration of these challenges will maximise the use of the UK's plankton datasets, increasing the robustness of future assessments through the inclusion of all UK data.

The present analysis illustrates how the PI was used to identify differences in plankton lifeforms over an 11 year (2004 - 2014) time span and applies this method to formal biodiversity assessment under the MSFD. This initial assessment used a time frame to harmonise with the OSPAR MSFD intermediate assessment. When considering the inter-annual variability that exists in the plankton community, the time period examined here is relatively short and will require the inclusion of additional years before it can confidently be established if the changes observed in Figs. 4 and 5 are part of a long-term trend (Henson et al., 2009). As mentioned above, for many UK datasets this could be a matter of adjusting the starting conditions period to be further back in time, thereby making better use of multi-decadal datasets. It is therefore imperative to maintain all UK plankton time-series in their current format, as the scientific and policy value of time-series increases with dataset length (Giron-Nava, 2017).

Notwithstanding the shortness of the assessment period, the PI value acts successfully as a flag to trigger further investigation the changes that have taken place and the pressures causing change. For example, there have been suggestions that increases in gelatinous zooplankton signify degraded ecosystem states due to stressors including overfishing, pollution, eutrophication and anoxia (Richardson et al., 2009; Tett and Mills, 1991). The lifeform pairs involving gelatinous zooplankton are instructive in this regard with a low PI value (crustaceans and gelatinous zooplankton: PI = 0.51, $p<0.01$) at PML's L4 station reflecting the substantial increase in gelatinous zooplankton that has recently been reported here (McConville, 2018). Several publications point to multidecadal cycles of jellyfish populations and even in heavily fished systems, climate change appears to be implicated in the fluctuations in gelatinous taxa that have been observed (Lynam et al., 2011). This is one example of the PI 'flagging' important trends that merit further analysis on causality. Particular care with interpretation, however, must be taken at the boundary of significance, where PI = 0.8, as time-series length and starting condition envelope size may influence statistical significance.

Another key strength of our multiple time series approach is that it allows an assessment of large-scale spatial change: are the changes observed localised or widespread? As an example, long-term declines in total copepod abundance have been reported in European shelf waters (Edwards, 2013). The fact that these trends are widespread, and observed both in oceanic and shelf waters and in geographically separate seas (e.g. Celtic and North Seas), could be argued to point more towards widespread, climate-related pressures rather than to trophic cascades induced by overfishing. Impacts from the other major anthropogenic pressure, nutrient enrichment, are more likely to be observed in coastal areas in the first instance. Comparison of PI values between coastal and offshore EHDs will flag which plankton lifeform pairs lack coherence across these broader spatial scales and require further investigation.

The work described here demonstrates a method to identify changes in UK plankton communities in support of the 2020 UK MSFD Assessment using a diverse range of datasets. To assess GES in fulfilment of the MSFD in line with the Commission Decision on GES (2017/848/EU) (European Commission, 2017), and to use the lifeform approach to inform policy decisions about management measures, two additional, critical steps are needed. Firstly, though the present study identified change in plankton lifeforms between two time periods, identification of a trend in PI away from starting conditions can identify the trajectory of change in lifeform pairs (e.g. Gowen et al., 2015). For assessment purposes, this must be accomplished for each EHD zone and fixed-point time-series, though if time-series are short (i.e. not multi-decadal) the statistical significance of trends and relationships may be difficult to identify.

Secondly, change in plankton lifeforms must be interpreted with respect to environmental variation and anthropogenic pressures, to identify factors responsible for plankton community change. This information is required to support government policy decisions about enacting management measures, ensuring effort is applied to appropriate human drivers and pressures. Causal identification is critical when assessing indicator change against the agreed UK target of ‘Plankton are not significantly influenced by direct anthropogenic pressure’. This target is process-based, rather than linked to a threshold, which means that as long as change in the plankton is not driven by direct anthropogenic pressures, such as fishing or nutrient loading, the pelagic habitat is deemed to be in GES. This process-based target allows the plankton community to shift and change due to environmental and/or climate change, known as ‘prevailing conditions’ under the Directive. The management of prevailing conditions is outside the scope of the MSFD, but failing the target will trigger management action if a directly manageable anthropogenic pressure causes change in the plankton community. Pressure identification will therefore help to recognise changes caused by prevailing environmental conditions, a state which may be different from starting conditions but which still represents GES. The pressure-state relationship in pelagic systems, however, is often unclear or non-linear and discriminating between the different pressures is challenging, requiring further research (Dickey-Collas et al., 2017). Despite challenges in understanding the pressure-state relationship for plankton communities, the use of plankton lifeforms in a surveillance role, for example in interpreting change in other ecosystem components, also requires further consideration (e.g. Bedford et al., 2018; Shephard et al., 2015).

The lifeform indicator is an OSPAR common indicator (PH1/FW5: Changes in Phytoplankton and Zooplankton Communities) and was used for the regional OSPAR 2017 Intermediate Assessment (OSPAR, 2017); that assessment, however, only considered data from PML, the CPR and one Swedish sampling station. There are a number of multi-decadal plankton time-series across the OSPAR area (O'Brien et al., 2017), and as these become available to support policy the lifeform indicator is flexible enough to incorporate them. This will provide an improved holistic understanding of change in plankton communities, increasing the robustness of future MSFD assessments which is also in line with the Commission Decision on GES (European Commission, 2017) which recognises the importance of practical criteria (technical feasibility, monitoring costs, adequate time-series of data). The flexibility of the lifeform approach means that the indicator can be used with data from other regional seas as long as appropriate lifeform pairs are selected (Brito et al., 2015; Gowen et al., 2015; Siddons et al., 2018), and in the future could be applied at a pan-European scale. Using the same indicator throughout Europe’s seas would allow clear, easily comparable assessments of plankton community change, enabling a consistent and coherent view of pelagic habitat status across Europe.

Acknowledgements

A.M-G would like to thank the UK National Environmental Research Council for support through the NERC Knowledge Exchange fellowship scheme. CO and DJ were supported by the EU DG ENV/MSFD/Action Plan project *Applying an ecosystem approach to (sub) regional habitat assessments* (EcApRHA). A. Atkinson was funded by the NERC and Department for Environment, Food and Rural Affairs Marine Ecosystems Research Program (Grant no. NE/L003279/1). A. Aubert received funding from the French Ministry of Environment, Energy, and the Sea (MEEM), the French National Centre for Scientific Research (CNRS-INEE, CNRS-INSU), the French National Museum of Natural History (MNHN) and the EU DG ENV/MSFD/Action Plan Project (11.0661/2015/712630/SUB/ENVC.2 OSPAR) *Applying an ecosystem approach to (sub) regional habitat assessments* (EcApRHA). E.B., M.M., and K.C. were supported by the Scottish Government service level agreement 20452/ST02H. P.T. was partly supported by the EU H2020 projects AquaSpace (633476) and BlueGrowthFarm (774426), and P.T. and C.S. were earlier supported by UK NERC NE/M007855/1 for work on the Lorne Pelagic Observatory. All authors would like to thank Defra for funding the Plankton Lifeforms Project, which instigated this piece of work (Contract ME5312) and also the OSPAR pelagic habitats expert group members Felipe Artigas, Isabelle Rombouts, Marie Johansen and Alexandre Budria for helping the indicator lifeform development.

References

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Blazewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandao, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.Y., Cheng, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J., Dawson, M.N., De Clerck, O., Decock, W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erseus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gomez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stohr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M.A., Turon, X., Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G.C., Wilson, S.P., Costello, M.J., 2012. The magnitude of global marine species diversity. Current biology : CB 22, 2189-2202.

Atkinson, A., Harmer, R.A., Widdicombe, C.E., McEvoy, A.J., Smyth, T.J., Cummings, D.G., Somerfield, P.J., Maud, J.L., McConville, K., 2015. Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. Progress in Oceanography 137, 498-512.

Barton, A.D., Lozier, M.S., Williams, R.G., 2015. Physical controls of variability in North Atlantic phytoplankton communities. Limnology and Oceanography 60, 181-197.

Bean, T.P., Greenwood, N., Beckett, R., Biermann, L., Bignell, J.P., Brant, J.L., Copp, G.H., Devlin, M.J., Dye, S., Feist, S.W., Fernand, L., Foden, D., Hyder, K., Jenkins, C.M., van der Kooij, J., Kröger, S., Kupschus, S., Leech, C., Leonard, K.S., Lynam, C.P., Lyons, B.P., Maes, T., Nicolaus, E.E.M., Malcolm, S.J., McIlwaine, P., Merchant, N.D., Paltriguera, L., Pearce, D.J., Pitois, S.G., Stebbing, P.D., Townhill, B., Ware, S., Williams, O., Righton, D., 2017. A Review of the Tools Used for Marine Monitoring in the UK: Combining Historic and Contemporary Methods with Modeling and Socioeconomics to Fulfill Legislative Needs and Scientific Ambitions. Frontiers in Marine Science 4.

Beaugrand, G., 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progress in Oceanography 60, 245-262.

Beaugrand, G., 2005. Monitoring pelagic ecosystems using plankton indicators. ICES J. Mar. Sci. 62, 333-338.

Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426, 661.

Beaugrand, G., Kirby, R.R., 2018. How Do Marine Pelagic Species Respond to Climate Change? Theories and Observations. Annual Review of Marine Science 10, 169-197.

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296, 1692-1694.

Bedford, J., Johns, D., Greenstreet, S., McQuatters-Gollop, A., 2018. Plankton as prevailing conditions: a surveillance role for plankton indicators within the Marine Strategy Framework Directive. Marine Policy 89, 109-115.

Bremner, J., Frid, C.L.J., Rogers, S.I., 2004. Biological traits of the North Sea benthos – Does fishing affect benthic ecosystem function? , in: Barnes, P., Thomas, J. (Ed.), Benthic habitats and the effects of fishing. American Fisheries Society, Bethesda, MD, pp. 477-489.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Marine Ecology Progress Series 254, 11-25.

Bresnan, E., Cook, K., Hindson, J., Hughes, S., Lacaze, J.-P., Walsham, P., Webster, L., Turrell, W.R., 2016. The Scottish Coastal Observatory 1997-2013. Parts 1-3. Scottish Marine and Freshwater Science 7 No 26.

Brito, A.C., Moita, T., Gameiro, C., Silva, T., Anselmo, T., Brotas, V., 2015. Changes in the Phytoplankton Composition in a Temperate Estuarine System (1960 to 2010). Estuaries and Coasts 38, 1678-1691.

Capuzzo, E., Lynam, C.P., Barry, J., Stephens, D., Forster, R.M., Greenwood, N., McQuatters-Gollop, A., Silva, T., Sonja M. van Leeuwen, Engelhard, G.H., 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. Global Change Biology 24, e352-e364.

Claussen, U., Connor, D., De Vrees, L., Leppänen, J., Percelay, J., Kapari, M., Mihail, O., 2011. Common Understanding of (Initial) Assessment, Determination of Good Environmental Status (GES) and Establishment of Environmental Targets (Art. 8, 9 & 10 MSFD). Working Group on GES, p. 71.

de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J.-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., Flegontova, O., Guidi, L., Horák, A., Jaillon, O., Lima-Mendez, G., Lukeš, J., Malviya, S., Morard, R., Mulot, M., Scalco, E., Siano, R., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Acinas, S.G., Bork, P., Bowler, C., Gorsky, G., Grimsley, N., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Raes, J., Sieracki, M.E., Speich, S., Stemmann, L., Sunagawa, S., Weissenbach, J., Wincker, P., Karsenti, E., Boss, E., Follows, M., Karp-Boss, L., Krzic, U., Reynaud, E.G., Sardet, C., Sullivan, M.B., Velayoudon, D., 2015. Eukaryotic plankton diversity in the sunlit ocean. Science 348.

Devlin, M., Barry, J., Painting, S., Best, M., 2009. Extending the phytoplankton tool kit for the UK Water Framework Directive: indicators of phytoplankton community structure. Hydrobiologia 633, 151-168.

Devlin, M., Best, M., Coates, D., Bresnan, E., O'Boyle, S., Park, R., Silke, J., Cusack, C., Skeats, J., 2007. Establishing boundary classes for the classification of UK marine waters using phytoplankton communities. Marine Pollution Bulletin 55, 91-103.

Dickey-Collas, M., McQuatters-Gollop, A., Bresnan, E., Kraberg, A.C., Manderson, J.P., Nash, R.D.M., Otto, S.A., Sell, A.F., Tweddle, J.F., Trenkel, V.M., 2017. Pelagic habitat: exploring the concept of good environmental status. ICES J. Mar. Sci. 74, 2333-2341.

Edwards, M., Bresnan, E., Cook, K., Heath, M., Helaouet, P., Lynam, C., Raine, R. and Widdicombe, C., 2013. Impacts of climate change on plankton, MCCIP Science Review, pp. 98-112.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430, 881-884.

Eloire, D., Somerfield, P.J., Conway, D.V.P., Halsband-Lenk, C., Harris, R., Bonnet, D., 2010. Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. Journal of Plankton Research 32, 657-679.

Estrada, M., Henriksen, P., Gasol, J.M., Casamayor, E.O., Pedrós-Alió, C., 2004. Diversity of Planktonic Photoautotrophic Microorganisms Along a Salinity Gradient as Depicted by Microscopy, Flow Cytometry, Pigment Analysis and DNA-based Methods. FEMS Microbiology Ecology 49, 281-293.

European Commission, 2010. Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters 2010/477/EU.

European Commission, 2017. Commission Decision (EU) 2017/848 of 17 May 2017, laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/447/EU. Official Journal of the European Union L 125(18.5.2017), 43-74.

Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. Science 305, 354– 360.

Fox, C.J., Pitois, S.G., 2006. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. ICES J. Mar. Sci. 63, 785-798.

Gallego, I., Davidson, T.A., Jeppesen, E., Perez-Martinez, C., Sanchez-Castillo, P., Juan, M., Fuentes-Rodriguez, F., Leon, D., Penalver, P., Toja, J., Casas, J.J., 2012. Taxonomic or ecological approaches? Searching for phytoplankton surrogates in the determination of richness and assemblage composition in ponds. Ecological Indicators 18, 575-585.

Garmendia, M., Borja, Á., Franco, J., Revilla, M., 2012. Phytoplankton composition indicators for the assessment of eutrophication in marine waters: Present state and challenges within the European directives. Marine Pollution Bulletin 66, 7-16.

Giron-Nava, A., James, C.C., Johnson, A.F., Dannecker, D., Johns, D.G., Kolody, B., Lee, A., Nagarkar, M., Pao, G.M., Ye, H. and Sugihara, G., 2017. A quantitative argument for long-term ecological monitoring. Marine Ecology Progress Series 572, 269-274.

Gowen, R.J., Collos, Y., Tett, P., Scherer, C., Bec, B., Abadie, E., Allen, M., O'Brien, T., 2015. Response of diatom and dinoflagellate lifeforms to reduced phosphorus loading: A case study in the Thau lagoon, France. Estuarine, Coastal and Shelf Science 162, 45-52.

Gowen, R.J., McQuatters-Gollop, A., Tett, P., Best, M., Bresnan, E., Castellani, C., Cook, K., Forster, R., Scherer, C., Mckinney, A., 2011. The Development of UK Pelagic (Plankton) Indicators and Targets for the MSFD. Advice to Defra, Belfast, UK, p. 41 pp.

Gowen, R.J., Raine, R., Dickey-Collas, M., White, M., 1998. Plankton distributions in relation to physical oceanographic features on the southern Malin Shelf, August 1996. ICES J. Mar. Sci. 55, 1095-1111.

Gowen, R.J., Stewart, B.M., 2005. The Irish Sea: Nutrient status and phytoplankton. Journal of Sea Research 54, 36-50.

Gowen, R.J., Stewart, B.M., Mills, D.K., Elliott, P., 1995. Regional differences in stratification and its effect on phytoplankton production and biomass in the northwestern Irish Sea. Journal of Plankton Research 17, 753-769.

Gowen, R.J., Tett, P., Kennington, K., Mills, D.K., Shammon, T.M., Stewart, B.M., Greenwood, N., Flanagan, C., Devlin, M., Wither, A., 2008. The Irish Sea: Is it eutrophic? Estuarine, Coastal and Shelf Science 76, 239-254.

Gregory, B., Christophe, L., Martin, E., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. Global Change Biology 15, 1790-1803.

Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends in Ecology & Evolution 20, 337-344.

Henson, S.A., Raitsos, D., Dunne, J.P., McQuatters-Gollop, A., 2009. Decadal variability in biogeochemical models: Comparison with a 50-year ocean colour dataset. Geophysical Research Letters 36, L21601.

ICES, 2015. Book 1, ICES special request advice, published 20 March 2015. EU request on revisions to Marine Strategy Framework Directive manuals for Descriptors 3, 4, and 6, Technical report. ICES, Copenhagen.

Inall, M.E., Gillibrand, P.A., 2010. The physics of mid-latitude fjords: a review. Geological Society, London, Special Publications 344, 17-33.

John, E.H., Batten, S.D., Harris, R.P., Hays, G.C., 2001. Comparison between zooplankton data collected by the Continuous Plankton Recorder survey in the English Channel and by WP-2 nets at station L4, Plymouth (UK). Journal of Sea Research 46, 223-232.

Jones, K.J., Gowen, R.J., Tett, P., 1984. Water-column structure and summer phytoplankton distribution in the Sound of Jura. Journal of Experimental Marine Biology and Ecology 78, 269-289.

Katsanevakis, S., Stelzenmüller, V., South, A., Sørensen, T.K., Jones, P.J.S., Kerr, S., Badalamenti, F., Anagnostou, C., Breen, P., Chust, G., D'Anna, G., Duijn, M., Filatova, T., Fiorentino, F., Hulsman, H., Johnson, K., Karageorgis, A.P., Kröncke, I., Mirto, S., Pipitone, C., Portelli, S., Qiu, W., Reiss, H., Sakellariou, D., Salomidi, M., van Hoof, L., Vassilopoulou, V., Vega Fernández, T., Vöge, S., Weber, A., Zenetos, A., Hofstede, R.t., 2011. Ecosystem-based marine spatial management: Review of concepts, policies, tools, and critical issues. Ocean & Coastal Management 54, 807-820.

Kirby, R.R., Beaugrand, G., Lindley, J.A., 2008. Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. Limnology and Oceanography 53, 1805-1815.

Kirby, R.R., Beaugrand, G., Lindley, J.A., 2009. Synergistic Effects of Climate and Fishing in a Marine Ecosystem. Ecosystems 12, 548-561.

Lindeque, P.K., Parry, H.E., Harmer, R.A., Somerfield, P.J., Atkinson, A., 2013. Next Generation Sequencing Reveals the Hidden Diversity of Zooplankton Assemblages. PLOS ONE 8, e81327.

Lindley, J.A., Gamble, J.C., Hunt, H.G., 1995. A change in the zooplankton of the central North Sea (55 to 58 N): a possible consequence of changes in the benthos. Marine Ecology Progress Series 119, 299-303.

Litchman, E., Edwards, K.F., Klausmeier, C.A., Thomas, M.K., 2012. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Marine Ecology Progress Series 470, 235-248.

Litchman, E., Klausmeier, C.A., 2008. Trait-Based Community Ecology of Phytoplankton. Annual Review of Ecology, Evolution, and Systematics 39, 615-639.

Litchman, E., Klausmeier, C.A., Schofield, O.M., Falkowski, P.G., 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecology Letters 10, 1170-1181.

Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E., Hays, G.C., 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? Global Change Biology 17, 767-782.

Margalef, R., 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1, 493-509.

McConville, K.M., 2018. Trophic and ecological implications for the gelatinous body form in zooplankton. PhD Thesis, University of Plymouth, p. 223 pp.

McQuatters-Gollop, A., Edwards, M., Helaouët, P., Johns, D.G., Owens, N.J.P., Raitsos, D.E., Schroeder, D., Skinner, J., Stern, R.F., 2015. The Continuous Plankton Recorder survey: how can long-term phytoplankton datasets deliver Good Environmental Status? . Estuarine, Coastal and Shelf Science 162, 88-97.

McQuatters-Gollop, A., Gilbert, A.J., Mee, L.D., Vermaat, J.E., Artioli, Y., Humborg, C., Wulff, F., 2009. How well do ecosystem indicators communicate the effects of anthropogenic eutrophication? Estuarine, Coastal and Shelf Science 82, 583–596.

McQuatters-Gollop, A., Johns, D.G., Bresnan, E., Skinner, J., Rombouts, I., Stern, R.F., Aubert, A., Johansen, M., Knights, A., 2017. From microscope to management: the critical value of plankton taxonomy to marine policy and biodiversity conservation. Marine Policy 83, 1-10.

McQuatters-Gollop, A., Reid, P.C., Edwards, M., Burkill, P., Castellani, C., Batten, S., Gieskes, W., Beare, D., Bidigare, R., Head, E., Johnson, R., Kahru, M., Koslow, J., Pena, M., 2011. Is there a decline in marine phytoplankton? Nature 472, E6-E7.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28, 167-177.

Mouillot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., Chi, T.D., 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conservation-Marine and Freshwater Ecosystems 16, 469-482.

O'Brien, T.D., Lorenzoni, L., Isensee, K., Valdes, L., 2017. What are Marine Ecological Time Series telling us about the ocean? A status report, IOC Technical Series. IOC-UNESCO, p. 297.

OSPAR, 2017. PH1/FW5: Changes in phytoplankton and zooplankton communities., in: OSPAR (Ed.), OSPAR Intermediate Assessment 2017. OSPAR, London, UK, p. 2.

Ostle, C., Artigas, F., Atkinson, A., Aubert, A., Budria, A., Graham, G., Helaouët, P., Johns, D., Padegimas, B., Rombouts, I., Widdicombe, C., McQuatters-Gollop, A., 2017. Spatial Representivity of Plankton Indicators EcApRHA Deliverable WP1.3. OSPAR, London, UK, p. 28.

Pingree, R.D., Holligan, P.M., Mardell, G.T., 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. Deep Sea Research 25, 1011-1028.

Purcell, J.E., Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451, 27-44.

Richardson, A.J., 2008. In hot water: zooplankton and climate change. ICES J. Mar. Sci. 65, 279-295.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology & Evolution 24, 312-322.

Richardson, A.J., Walne, A.W., John, A.W.G., Jonas, T.D., Lindley, J.A., Sims, D.W., Stevens, D., Witt, M., 2006. Using Continuous Plankton Recorder data. Progress in Oceanography 68, 27-74.

Scherer, C., 2012. Developing and testing an index of change in microplankton community structure in temperate shelf seas. A thesis in partial fulfilment of the requirements of Edinburgh Napier University, for the award of Doctor of Philosophy. Napier University, p. 325.

Scherer, C., Gowen, R.J., Tett, P., 2016. Assessing the State of the Pelagic Habitat: A Case Study of Plankton and Its Environment in the Western Irish Sea. Frontiers in Marine Science 3.

Scherer, C., Gowen, R.J., Tett, P., McQuatters-Gollop, A., Forster, R., Bresnan, E., Cook, K., Atkinson, A., Best, M., Baptie, M., Keeble, S., McCullough, G., McKinney, A., 2014. Development of a UK Integrated Plankton Monitoring Programme A final report of the Lifeform and State Space project, prepared for Defra. Agri-food and Biosciences Institute, Belfast, p. 450.

Secretariat of the Convention on Biological Diversity, 2004. The Ecosystem Approach (CBD Guidelines). Secretariat of the Convention on Biological Diversity, Montreal, p. 50 p.

Shephard, S., Greenstreet, S.P.R., Piet, G.J., Rindorf, A., Dickey-Collas, M., 2015. Surveillance indicators and their use in implementation of the Marine Strategy Framework Directive. ICES J. Mar. Sci.

Siddons, B., Glegg, G., McQuatters-Gollop, A., 2018. Inter-regional coherence: can Northeast Atlantic pelagic indicators be applied to the Arctic? Marine Policy 96, 53-64.

Stoetaert, K., Heip, C., 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Marine Ecology Progress Series 59, 305-307.

Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501, 539.

Tett, P., 1973. The use of log-normal statistics to describe phytoplankton populations from the Firth of Lorne area. Journal of experimental marine Biology and Ecology 11, 121-136.

Tett, P., Carreira, C., Mills, D.K., van Leeuwen, S., Foden, J., Bresnan, E., Gowen, R.J., 2008. Use of a phytoplankton community index to assess the health of coastal waters. ICES J. Mar. Sci. 65, 1475-1482.

Tett, P., Gowen, R., Painting, S., Elliott, M., Foster, R., Mills, D., Bresnan, E., Capuzzo, E., Fernandes, T., Foden, J., Geider, R., Gilpin, L., Huxham, M., McQuatters-Gollop, A., Malcolm, S., Saux-Picart, S., Platt, T., Racault, M.-F., Sathyendranath, S., Molen, J.v.d., Wilkinson, M., 2013. A framework for understanding marine ecosystem health. Marine Ecology Progress Series 494, 1-27.

Tett, P., Mills, D., 1991. The plankton of the North Sea - pelagic ecosystems under stress ? Ocean and Shoreline Management 16, 233-257.

Tett, P., Wallis, A., 1978. The general annual cycle of chlorophyll standing crop in Loch Creran. Journal of Ecology 66, 227-239.

Thiebaux, M.L., Dickie, L.M., 1993. Structure of the Body-Size Spectrum of the Biomass in Aquatic Ecosystems: A Consequence of Allometry in Predator–Prey Interactions. Canadian Journal of Fisheries and Aquatic Sciences 50, 1308-1317.

Ubertini, M., Lefebvre, S., Gangnery, A., Grangeré, K., Le Gendre, R., Orvain, F., 2012. Spatial variability of benthic-pelagic coupling in an estuary ecosystem: consequences for microphytobenthos resuspension phenomenon. PloS one 7, e44155-e44155.

UKTAG, 2014. UKTAG Coastal Water Assessment Method, Phytoplankton, Coastal Water Phytoplankton Tool. Water Framework Directive - UK Advisory Group (WFD-UKTAG), Stirling, Scotland, p. 26.

van Leeuwen, S., Tett, P., Mills, D., Molen, J.v.d., 2015. Stratified and nonstratified areas in the North Sea: Long-term variability and biological and policy implications. Journal of Geophysical Research Oceans 120, 4670-4686.

van Leeuwen, S.M., Le Quesne, W.F., Parker, E.R., 2016. Potential future fisheries yields in shelf waters: a model study of the effects of climate change and ocean acidification. Biogeosciences 13, 441-454.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290-2301.

von Bertalanffy, L., 1972. The history and status of General Systems Theory. The Academy of Management Journal 15, 407-426.

Weston, K., Greenwood, N., Fernand, L., Pearce, D.J., Sivyer, D.B., 2008. Environmental controls on phytoplankton community composition in the Thames plume, U.K. Journal of Sea Research 60, 246-254.

Whyte, C., Davidson, K., Gilpin, L., Mitchell, E., Moschonas, G., McNeill, S., Tett, P., 2017. Tracking changes to a microplankton community in a North Atlantic sea loch using the microplankton index PI(mp). ICES J. Mar. Sci. 74, 311-325.

Widdicombe, C.E., Eloire, D., Harbour, D., Harris, R.P., Somerfield, P.J., 2010. Long-term phytoplankton community dynamics in the Western English Channel. Journal of Plankton Research 32, 643-655.

Williams, R., Conway, D.V.P., Hunt, H.G., 1994. The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. Hydrobiologia 292, 521-530.

Wood, B.J.B., Tett, P.B., Edwards, A., 1973. An Introduction to the Phytoplankton, Primary Production and Relevant Hydrography of Loch Etive. Journal of Ecology 61, 569-585.