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Applying long temporal scale plankton data to marine strategy development under climate change

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**UNIVERSITY OF
PLYMOUTH**

**APPLYING LONG TEMPORAL SCALE PLANKTON DATA TO
MARINE STRATEGY DEVELOPMENT UNDER CLIMATE CHANGE**

by

JACOB BEDFORD

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

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Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

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For all papers, I was the lead author, generating the ideas and aims, carrying out all analyses and interpretation and completing all of the writing. The other authors gave overall guidance and insight to the development of the papers. David Johns provided raw data from the Continuous Plankton Recorder upon data requests.

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Abstract

Assessing changes in the state of marine biodiversity is critical for underpinning sustainable marine management. As the cumulative effects of multiple anthropogenic pressures on marine ecosystems are increasingly understood, and the importance of marine ecosystems in providing goods and services to society is increasingly recognised, marine management frameworks are transitioning towards an ecosystem-based approach, explicitly addressing biodiversity change. Under the European Marine Strategy Framework Directive (MSFD), biodiversity indicators are used to assess the state of marine ecosystems against defined targets. Plankton communities are a key component of these biodiversity assessments and indicators for both phytoplankton and zooplankton are used to assess for change in the state of 'pelagic habitats'. Key challenges exist however, in the attribution of change in plankton indicators to the underlying drivers. The effects of climate change must be understood and accounted for when interpreting indicator changes against targets.

Long-temporal scale information is needed to understand the effects of climate on plankton communities. So far, when assessing pelagic habitats under the MSFD in the North East Atlantic, the full temporal extent of plankton data available hasn't been used. Specifically, the role of long temporal scale data in the setting of reference conditions from which pelagic habitats are assessed for change is unclear. The dynamics of the plankton indicators used in MSFD pelagic habitat assessment have also not been fully explored over long temporal scales. In this thesis, long-temporal scale data is used to identify 'shifting baselines' in plankton communities within the North Sea, and resolve the use of historical data in setting reference conditions.

Furthermore, long temporal scale data is applied to further develop the indicators used in pelagic habitat assessments in the North East Atlantic, including indicators based on functional lifeform groups, by understanding their response to changing climatic and oceanographic conditions. Zooplankton communities show clear directional change in response to climate over multidecadal time scales, with phytoplankton communities being highly stochastic in time. This directional zooplankton community change was driven by select taxa. To this extent, the dynamics of policy indicators, including functional 'lifeform' groups are driven by the dynamics of select individual taxa, highlighting that fine taxonomic resolution data is needed to interpret changes in indicators during policy assessments.

Recommendations for policy are then outlined as to how this information from long-temporal scale plankton data can be formally incorporated into the ecosystem assessment process. Notably, a surveillance role for long temporal scale plankton data in the formal assessment of biodiversity under the MSFD is developed. Under the MSFD, climate variation and anthropogenic climate change is an ecosystem driver outside the scope of management, and instead referred to as 'prevailing conditions'. It is important to track changes in prevailing conditions however, in order to interpret the outcomes of biodiversity assessments and design appropriate and adaptive targets and management measures. As illustrated by analyses in this thesis, changes in plankton can track and inform on changing prevailing conditions, and so when applied as surveillance indicators, can provide useful supplementary and contextual information. Therefore, although the full temporal extent of plankton information has been so far underused in ecosystem assessments under the Marine Strategy Framework Directive, it can have multiple roles in the sustainable management of the marine environment under climate change.

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Chapter 1

Introduction- Assessing pelagic habitats within the development of marine strategies: nested challenges at the science-policy interface

Chapter 1 Introduction- Assessing pelagic habitats within the development of marine strategies: layered challenges at the science policy interface

European marine ecosystems are changing, and marine biodiversity, from the plankton communities at the bottom of the food web through to the charismatic megafauna at higher trophic levels, is being adversely affected by human activities (Cloern et al., 2016; Sala and Knowlton, 2006; Selig et al., 2014). As well as direct anthropogenic pressures, ecosystems are being altered as a result of large-scale climate change (Henson et al., 2017; Hoegh-Guldberg and Bruno, 2010; Poloczanska et al., 2016). Changes in marine ecosystems therefore need to be well understood, and levels of human activities carefully managed, in order to balance societal needs with the conservation of biodiversity and achieve the 'blue growth' political agenda (Klinger et al., 2018). In Europe historically, different aspects of the marine system were managed separately, as were the human pressures affecting them. For example, the Water Framework Directive manages water quality in coastal and transitional waters (Directive 2000/60/EC; Hering et al., 2010), the Habitats Directive protects key species and habitats (Council Directive 92/43/EEC; Qiu and Jones, 2013) whilst the EU Common Fisheries Policy manages commercial fish stocks (Council Regulation (EC) No 2287/2003; Prellezo and Curtin, 2015). The lack of integration, or overall integrated ecosystem assessment process, meant cumulative pressures and interacting processes were insufficiently assessed and managed, requiring a new way of thinking about the management of European seas (Boyes and Elliott, 2014; Curtin and Prellezo, 2010; Salomon, 2009).

In response, the management of marine biodiversity is transitioning towards a more holistic approach through the development of ecosystem-based 'marine strategies'. The development of marine strategies generically involves the regular assessment of marine ecosystem status as a whole, the continued monitoring of changes in this status towards defined targets and the design of an integrated programme of management measures to address the main pressures causing these changes (Patrício et al., 2016; Scharin et al., 2016).

Adopted in 2008, the European Union's (EU) Marine Strategy Framework Directive (MSFD) (Directive 2008/56/EC) mandates the development of marine strategies by EU member states. Whilst previous environmental directives (e.g. the Water Framework Directive) are still in place, the MSFD aims to bring different aspects of marine management together, to assess and manage the marine environment holistically (Borja et al., 2010; van Leeuwen et al., 2014). Often described as the 'environmental pillar' of EU maritime policy, the underlying principle of the Marine Strategy Framework Directive is sustainability; where the multiple human uses of the marine environment are conducted at a sustainable level so that the overall target of 'Good Environmental Status' (GES) is achieved by 2020- where seas are clean, healthy and productive (Berg et al., 2015; Juda, 2010). The MSFD consists of 11 qualitative descriptors, three of which, Biodiversity, Food webs and Seafloor integrity, relate to ecosystem state, whereas the remaining descriptors relate to pressures (Figure 1.1). These descriptors must be managed using both existing and, where necessary, new management measures (Boyes et al., 2016).



Figure 1.1. The 11 descriptors making up the Marine Strategy Framework Directive. Descriptors 1, 4, and 6 are known collectively as the 'Biodiversity descriptors'. Image adapted from <https://oap.ospar.org/en/>.

A fully developed marine strategy, under MSFD regulations, consists of an assessment of ecosystem state through the development of indicators and targets, a coherent monitoring programme to track progress towards Good Environmental Status (GES), and programme of measures based on the outcome of assessments (Juda, 2010). The original timeframe set out by the MSFD is given in Figure 1.2. Over this timeframe, an extensive programme to define targets and indicators for use in the MSFD assessments has been undertaken by the member states. For example, in the UK, the Healthy and Biodiverse Seas Evidence Group (HBDSEG) selected indicators for use in UK assessments (Moffat et al., 2011). The scientific principles underlying indicator development are discussed later in this chapter. Implementation of the MSFD occurs on a 6-yearly cycle, so that an assessment occurs every 6 years incorporating most

recent monitoring data, and an associated evaluation and adjustment of the programme of measures (Nygård et al., 2016).

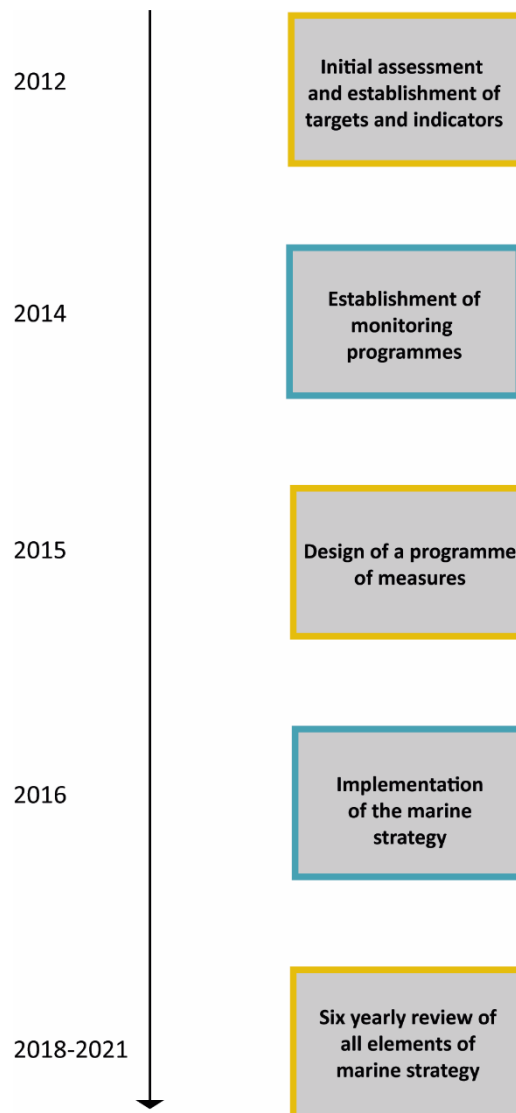


Figure 1.2. The original timeline set out for MSFD implementation. MSFD works on a 6 yearly implementation cycle.

The European Commission provides formal guidance of criteria and methodological standards through Commission decisions in order to aid member states in implementing the high level directive, and to divide the concept of GES into defined criteria. These details were first outlined in the Commission decision of 2010 but

further refined in 2017 (European Commission, 2010, 2017). The biodiversity descriptor is divided into different ecosystem components (marine birds, mammals, reptiles, fish and cephalopods, benthic habitats and pelagic habitats) and broken down into different criteria, helping make the high level descriptors more concrete and quantifiable. As an example, the focus of this thesis is on pelagic habitats, which are assessed under both the biodiversity and food web descriptors. The relevant criteria for pelagic habitats listed in the 2017 commission decision are given in Table 1.1. The biotic component of pelagic habitats comprises plankton communities (McQuatters-Gollop et al., 2017). Phytoplankton are primary producers, and provide over 90% of marine primary production (Boyce and Worm, 2015). Zooplankton are the primary consumers in pelagic food webs, and channel this primary production up to fish and marine top predators (Richardson, 2008). In direct response to the commission decision therefore, plankton indicators that describe the structure and functioning of 'pelagic habitats' have been selected to track changes in European pelagic habitats and detect any impacts of anthropogenic pressures (McQuatters-Gollop et al., 2017).

Table 1.1. The descriptors and criteria relating to the pelagic habitat, quoted from European Commission (2017). Descriptor images from <https://oap.ospar.org/en/>.



'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.'

Relevant criteria for pelagic habitats



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'.



'All elements of 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'.

Relevant criteria for pelagic habitats



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.



D4C3 The size distribution of individuals across the trophic guild is not adversely affected due to anthropogenic pressures.

The Marine Strategy Framework Directive requires that member states use existing regional cooperation structures to coordinate their development of marine strategies.

This is key because ecosystems do not adhere to political boundaries, and cooperation between member states is needed to achieve Good Environmental Status at the regional scale. The regional seas conventions, such as the Oslo Paris Convention for the protection of the environment of the North East Atlantic (OSPAR), already in place in Europe can support individual member state's marine strategy development, and by being signatories to regional seas conventions, individual member states can fulfil the requirements of regional cooperation under the MSFD. OSPAR for example, develops its own regional scale marine strategy termed the North East Atlantic Environment Strategy (OSPAR, 2010), whose implementation contributes to achieving GES in the North East Atlantic. Similarly, a set of common biodiversity indicators developed by OSPAR help coordinate biodiversity monitoring at the regional scale. In summary, OSPAR facilitates the coordinated implementation of the MSFD in the North East Atlantic (van Tatenhove et al., 2014).

Conceptually, the development of marine strategies can be viewed as a layered process, including the assessment of Good Environmental Status and the design and implementation of management measures (Link and Browman, 2014). For example, plankton indicators describe the structure and functioning of 'pelagic habitats' and have been developed by both individual member states and regional seas conventions to track changes in European pelagic habitats (McQuatters-Gollop et al., 2017). In turn, pelagic habitats are one of multiple ecosystem components that are assessed under the biodiversity descriptors, forming part of a biodiversity monitoring programme at both the member states and regional seas convention level.

In this introductory review, the 'pelagic habitat' assessment process is placed within the development of marine strategies, such as that driven by the Marine Strategy

Framework Directive. Whilst previous reviews have mapped the process of scaling up from single commercial fish stock assessments up to wider ecosystem based fisheries management strategies e.g. (Möllmann et al., 2013), fewer reviews have focused on this layered process for biodiversity status assessments. In this chapter, using pelagic habitats as an example, I identify the main scientific concepts underpinning the different levels of biodiversity management under an ecosystem based approach and highlight relevant scientific priorities and knowledge gaps. This synthesis is structured around three conceptual 'layers': first at the broadest level the scientific principles underpinning the overall development of marine strategies, secondly the assessment and monitoring of biodiversity which feeds evidence to marine strategy development, and lastly at the most fine scale level, the assessment of pelagic habitats which feeds into wider biodiversity assessments. Cross-scale issues faced at each of these conceptual layers are then identified. Following this review, the aims and rationale of the thesis are presented, to address these identified scientific challenges facing pelagic habitat assessments within marine strategy development, before the methodological approaches taken are discussed and the structure of the thesis outlined.

1.1 Ecosystem-based marine strategies

The overall process of developing marine strategies for achieving Good Environmental Status follows the main tenets of ecosystem-based management (EBM), and the MSFD promotes the ecosystem approach (Rouillard et al., 2018). EBM aims to manage marine ecosystems holistically, recognising that different components of the

ecosystem are interlinked, and need to be considered together. Specifically, different pressures from the same human activity can act cumulatively on marine ecosystems, as well as in combination with pressures from different activities (Crain et al., 2008; Smith et al., 2016). Furthermore, impacts on one component of the ecosystem can have consequences on other components, if they spatially co-occur (Stelzenmüller et al., 2010) or have trophic links (Torres et al., 2017). Examples of taking an ecosystem-based approach to management are the management of forage fisheries considering the biomass needed to sustain higher trophic levels (Dickey-Collas et al., 2013) and the spatial management of benthic trawling activities, where a focus is on understanding the trade-offs between fisheries landings and seabed impacts (Jennings et al., 2012). These examples follow a key tenet of the ecosystem approach which is to understand the consequences of anthropogenic pressures on the flow of ecosystem services to humans, and the necessary management measures required to sustain them (Atkins et al., 2011). Ecosystem services are defined as “the direct and indirect benefits people obtain from ecosystems” and by incorporating socio-economic elements of marine ecosystems, explicitly considering humans as part of the ecosystem, ecosystem services frameworks facilitate the evaluation of biodiversity impacts and management measures in a societally-relevant way (Bouwma et al., 2017; Broszeit et al., 2017; O'Higgins and Gilbert, 2014).

A second key tenet of ecosystem-based management is adaptive management (Curtin and Prellezo, 2010). Adaptive management of marine ecosystems adjusts to changing circumstances, both the accumulation of new scientific understanding, as well as the adjustment of management to account for non-linear ecosystem dynamics. Under the MSFD, adaptive management means that the process of designing marine strategies,

including the assessment process and the programme of measures to achieve GES, can change over time and, importantly, decisions can still be made even with evidence gaps and uncertainty (Garmendia et al., 2017). Adaptive management is especially important because direct anthropogenic pressures are not the only influences on the state of ecosystems and associated flow of ecosystem services. Large-scale environmental variability, such as caused by the North Atlantic Oscillation (Hurrell et al., 2003), causes structural changes to marine ecosystems. The drivers of these structural changes, including changes in thermal, salinity and emergence regimes, as well as changes in water flow and pH, however, are unmanageable at immediate political time-scales, (Smith et al., 2016).

Superimposed on this variability is a signal of directional change in environmental variables caused through anthropogenic climate change (Hoegh-Guldberg and Bruno, 2010). Climate change has been shown to affect both the state of biodiversity, as well as act synergistically with direct anthropogenic pressures. For example, warming temperatures have been shown to increase eutrophication symptoms in marine ecosystems (Winder and Sommer, 2012), and climate change and fishing pressure have been shown to act together and synergistically on fish stocks and fish communities (Engelhard et al., 2014; Kirby et al., 2009; Perry et al., 2010). As the drivers of these changes are outside of the scope of regional-scale control, the MSFD labels these drivers as 'prevailing conditions', and GES is achieved when *"the quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions"* (Directive 2008/56/EC). Ultimately, adapting management to incorporate climate change impacts is a key challenge for developing ecosystem-based marine strategies (Elliott, 2011).

1.1.1 Evidence needs and role of Integrated Ecosystem Assessments

Clearly, in order to understand the cumulative effects of human pressures on marine ecosystems, evaluate how these can be managed to sustain the flow of ecosystem services, and successfully implement adaptive management to climate change, scientific input is needed to provide information on these elements which can support the development of marine strategies under the MSFD. The main route by which scientific information is synthesized to influence marine strategies is through Integrated Ecosystem Assessments (IEAs) (Walther and Möllmann, 2013). IEAs aim to summarize the state of the marine environment, drawing on both natural and socioeconomic factors, and importantly evaluate progress towards a specified ecosystem objective. In the case of the Marine Strategy Framework Directive, this ecosystem objective is the overall vision of Good Environmental Status. Levin et al. (2009) outline the core framework of an IEA as involving initial scoping, the development of indicators, risk analysis, assessing ecosystem status and finally evaluating current management strategies.

A key role for scientific assessments is the prioritisation of the predominant activities and pressures for management to address. Resources for marine management are limited, and there is political impetus to ensure resource allocation is strategic to maximise benefits (Breen et al., 2012). Furthermore, as activities and pressures can vary between areas, there is a need to ensure this prioritisation process is spatially explicit. Breen et al. (2012) use a risk-based framework to prioritise management areas at the regional scale. Here, they evaluated the risk of not achieving GES for different

descriptors within the MSFD, based on criteria including the extent and frequency of the pressure occurring in each region, and the level of impact. They found that some descriptors were high risk in all regions, including food web structure, and marine litter. In contrast, some descriptors varied in their risk; for example, eutrophication was high risk in the Baltic Sea, but only moderate risk in all other regions. Piet et al. (2015) then also apply this risk-based framework to the evaluation of management measures, in order to aid in prioritising management measures for both present and future adverse pressures on the ecosystem.

Integrated Ecosystem Assessments under the MSFD should aim to efficiently inform both regional prioritisations of activities to manage and then inform effective management measures, through the assessment of Good Environmental Status. Importantly, they should not aim to understand every ecosystem interaction, but maximise the use of available information to give a broad overview of ecosystem functioning, with the aim of enabling communication of trade-offs between human exploitation of the ecosystem, and ecosystem state to a range of stakeholders (Dickey-Collas, 2014; Yvonne et al., 2010).

1.2 Biodiversity assessment and monitoring

Integrating the state of biodiversity into the development of marine strategies is a data- and science-intensive process (Edgar et al., 2016). Under the MSFD, coordinated biodiversity monitoring and assessment programmes are undertaken at both the member state and regional seas level (e.g. through the OSPAR convention) (Patrício et al., 2016). The biodiversity components are made up of two 'habitats' (pelagic and

benthic), and then constituents of those habitats (birds, non-commercial fish, mammals). Hayes et al. (2015) summarise that in order to achieve ecosystem-level management of biodiversity, we need to “understand what is changing, where change is occurring and why it is occurring”.

Marine ecosystems however, are complex and difficult to quantify, and therefore monitoring anthropogenic drivers on the state of ecosystems is difficult. Measuring key variables, or ‘indicators’, that reduce these ecosystem complexities down to key ecosystem factors allows information on the state of the ecosystem to be conveyed in a simplified form to a range of stakeholders (Rombouts et al., 2013). After identifying ambiguity in the scientific definitions of an indicator, Heink and Kowarik (2010) suggest a broad definition of an indicator as “a component or a measure of environmentally relevant phenomena used to depict or evaluate environmental conditions or changes or to set environmental goals”. In this thesis therefore, ‘indicator’ is used in both the sense of the “components” or variables that reflect wider conditions (e.g. ‘community diversity’), as well as the “measures” or metrics used to quantify that component or variable (e.g. ‘diversity index’).

Biodiversity indicators under the MSFD are used to assess the state of biodiversity components and descriptors, and to track progress towards defined targets. When an indicator is included in an assessment it is considered ‘operational’. To distinguish these operational indicators from the extensive potential metrics for assessing biodiversity, in this thesis these operational indicators are referred to as ‘policy indicators’, and described as undergoing ‘formal assessments’ i.e. have been approved by policy makers and are included in MSFD assessments by either member states or a

regional seas convention. This thesis specifically focuses on biodiversity indicators used in the North East Atlantic by the OSPAR commission.

1.2.1 Characteristics of an effective state indicator

A large volume of literature has been built up addressing indicator evaluation, i.e. defining the properties and characteristics of an indicator that are ideal for operational assessment. For example, Rice and Rochet (2005) outline the availability of historical data, the strength of the conceptual basis and cost-effectiveness of monitoring as important features of an indicator. Another important feature they outline is the responsiveness to underlying pressure. Conceptually, this relates to how well a biodiversity state indicator can follow a ‘Driver-Pressure-State-Impact-Response’ (DPSIR) framework that is core to monitoring strategies for the UK (Rogers and Greenaway, 2005). ‘Drivers’, are the forces that exert pressure onto an ecosystem, ‘State’ refers to the changes in ecosystem properties and processes resulting from the drivers. Ultimately, ‘Impacts’ refer to the changes in ecosystem services provided to humans as a result of state changes, whilst ‘Response’ refers to the management measures society implements to tackle the drivers (Berg et al., 2015). Furthermore, tracking indicators that have defined ecological significance, as well as sensitivity to defined anthropogenic stressors, allows the monitoring of each stage of the DPSIR management framework.

For the MSFD however, this scientific consensus of what makes an effective indicator is being expanded, as the role of biodiversity indicators in integrated ecosystem assessments is explored. For example, Tam et al. (2017) suggest including full coverage

of functional groups as well as structural, resilience and energy flow aspects of food webs into indicator suite selection for the assessment of food webs under the MSFD.

Similarly, Shephard et al. (2015) define a new type of indicator called 'surveillance indicators', which are indicators where the pressure-state relationship is unclear and therefore setting quantitative targets is difficult. Due to their lack of clear pressure-state relationships, surveillance indicators cannot follow directly a DPSIR framework. Shephard et al. argue however, that although these indicators can't have a direct role in the assessment of Good Environmental Status, they can provide contextual information on wider ecosystem impact of pressures, as well as underlying environmental change. Accordingly, Shepherd et al. modified the traditional DPSIR framework to include surveillance indicators (Figure 1.3). A key feature of their surveillance indicator framework is that there are no GES targets for surveillance indicators. Instead, when a surveillance indicator moves outside of a defined bound, new research is triggered as the potential implication of this indicator change may not be clear. This research focuses on addressing whether the change in surveillance indicators means that the targets and management measures for associated assessed indicators need to be re-evaluated. Precautionary management may be implemented as a result of surveillance indicator change, in respect to the management responses to changes in associated formally assessed indicators. Further exploration of the role and implementation of surveillance indicators in the assessment of Good Environmental Status and the design of management measures is warranted.

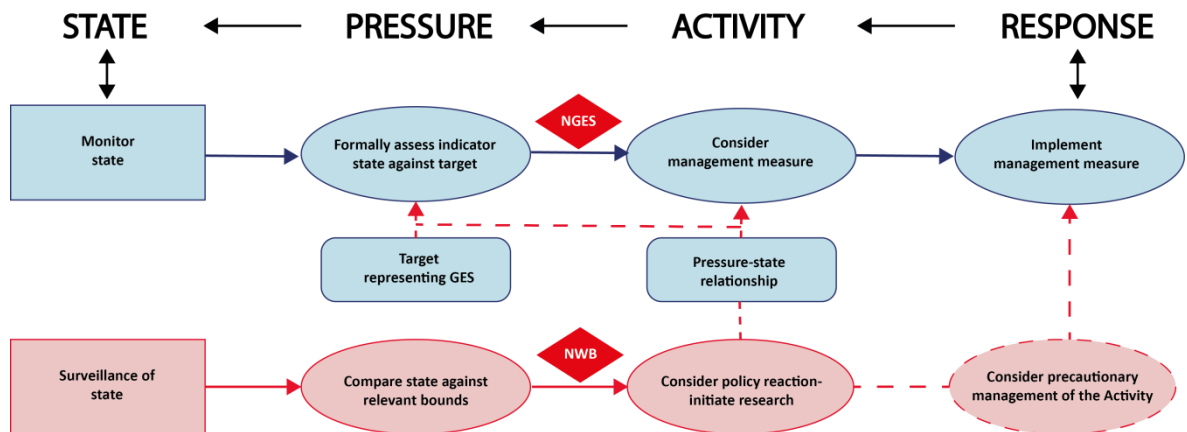


Figure 1.3 The 'surveillance indicator' framework adapted from Shephard et al. (2015). Assessed indicator (blue) change is detected. If indicator moves to being not in GES (NGES), a management measure is considered, based on the pressure-state relationship of the assessed indicator with a direct pressure. Surveillance indicators (red, bottom) are monitored simultaneously to the assessed indicator, and surveillance indicator change is detected when the surveillance indicator moves out of predefined bounds (not within bounds: NWB). This surveillance indicator change triggers research targeted at the pressure-state relationships and GES targets of associated assessed indicators (blue, top).

1.2.2 Integration of indicators to overall biodiversity assessment

Individual indicator assessments can be scaled up to an overall assessment of GES both within ecosystem components, and then throughout the overall biodiversity descriptors, a process known as 'integration'. As highlighted by Link and Browman (2014) there is linguistic uncertainty on the use of 'integration', and different interpretations of the process of integrating individual biodiversity indicators into an overall biodiversity assessment can be made. Firstly, the integration of biodiversity indicators can refer to the process of aggregating the results of individual indicator assessments into an overall assessment of Good Environmental Status both within ecosystem components, and within the biodiversity descriptors (Figure 1.4). Multiple

methods exist for aggregating indicators to overall GES assessments. Borja et al. (2014) outline some of the potential methods including ‘One out all out’, which is used in the WFD, where if one indicator does not meet a target the whole descriptor falls out of GES. It is acknowledged that this method is over-sensitive, and potentially makes GES unrealistic to achieve. Instead, options involving averaging, scoring or weighted averages may be more viable options for integrating biodiversity indicators.

Furthermore, Probst and Lynam (2016) highlight that a challenge in many integration methods is that the probability of achieving GES is dependent on the number of elements included in the descriptor or component, so components with a larger indicator suite are more likely to be assessed as out of GES. This issue is exemplified with the One out all out approach to aggregation. They suggest a ‘Principle of Equal Probability’ as a way of ensuring that the chances of GES being achieved are equal between different descriptors, and not influenced by the integration process.

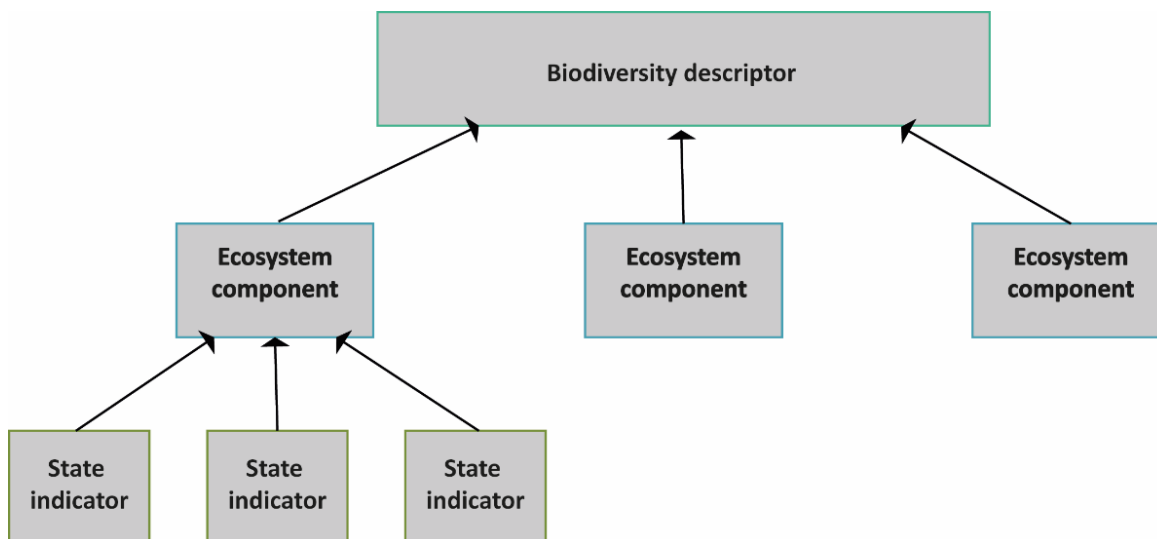


Figure 1.4 'Integration' of assessment outcomes of individual indicators up to ecosystem components, and ecosystem components up to overall biodiversity.

'Integration' between indicators can also refer to understanding cumulative pressures on different biodiversity components. Particularly, one activity or pressure is likely to affect multiple biodiversity components at once, and by integrating biodiversity state indicators linked to pressure pathways, the main pressures facing biodiversity and ecosystem functioning as a whole can be summarised. For example, eutrophication resulting from anthropogenic nutrient pollution affects both pelagic and benthic systems (Ferreira et al., 2011). Here, conceptual frameworks such as 'bow-tie' approaches, can be useful tools for summarising these pathways between pressures and biodiversity state changes (Smith et al., 2016). Lastly, integration can refer to the interactions between different biodiversity components affecting each other, for example, through trophic feedback mechanisms (Casini et al., 2008). Understanding these interactions is particularly key to the food webs descriptor of the MSFD. Here, biodiversity indicators are required to assess the structural integrity of food webs, in relation to pressures exerted on food web functioning through human activities (Rombouts et al., 2013). Key challenges therefore to overall biodiversity monitoring and assessment programmes come in relating biodiversity indicator change to wider food web functioning and drivers of change.

1.3 Pelagic habitat assessments

1.3.1 The suite of plankton indicators selected for formal assessment

Pelagic habitat assessment forms part of the overall assessment and monitoring programme for marine biodiversity under the MSFD. Plankton make useful ecosystem indicators because of their sensitivity to environmental change and their key position

at the base of the marine food web (Racault et al., 2014). As a result plankton communities are assessed under both the biodiversity and food-web descriptors of the MSFD (European Commission, 2017). Plankton communities are highly species rich, meaning plankton community data is highly multivariate in nature, as well as spatially patchy and temporally variable, providing challenges to assessing when a change in pelagic habitat state has occurred. Furthermore, these changes in state can manifest themselves in many ways, including changes in total plankton abundance as well as changes in the composition and dominance structure of communities (McQuatters-Gollop et al., 2017).

In response to this, at the OSPAR level of MSFD implementation, three plankton indicators have been selected for assessing the state of pelagic habitats under the MSFD, by the OSPAR working group ICG-COBAM (coordinated biodiversity assessment and monitoring), and the indicator approaches they represent are outlined below. One of these consists of 'bulk' variables describing change in productivity, and two of which focus on community change using taxonomically resolved data (Figure 1.5). Plankton indicator selection and development represents a balance between fulfilling scientific consensus on what makes an effective state indicator, and informing on functional changes in pelagic habitats, whilst also being practical for regional scale monitoring and assessment. For example, indicators may need to be assessed across disparate survey programmes (Zingone et al., 2015). These indicators were selected by the ICG-COBAM and accepted as OSPAR indicators for pelagic habitat assessments ('PH1/FW5', 'PH2' and 'PH3') before my thesis research began, and underwent an initial assessment during the OSPAR Intermediate Assessment 2017, which forms a starting point for much of the further indicator development work undertaken in this thesis.

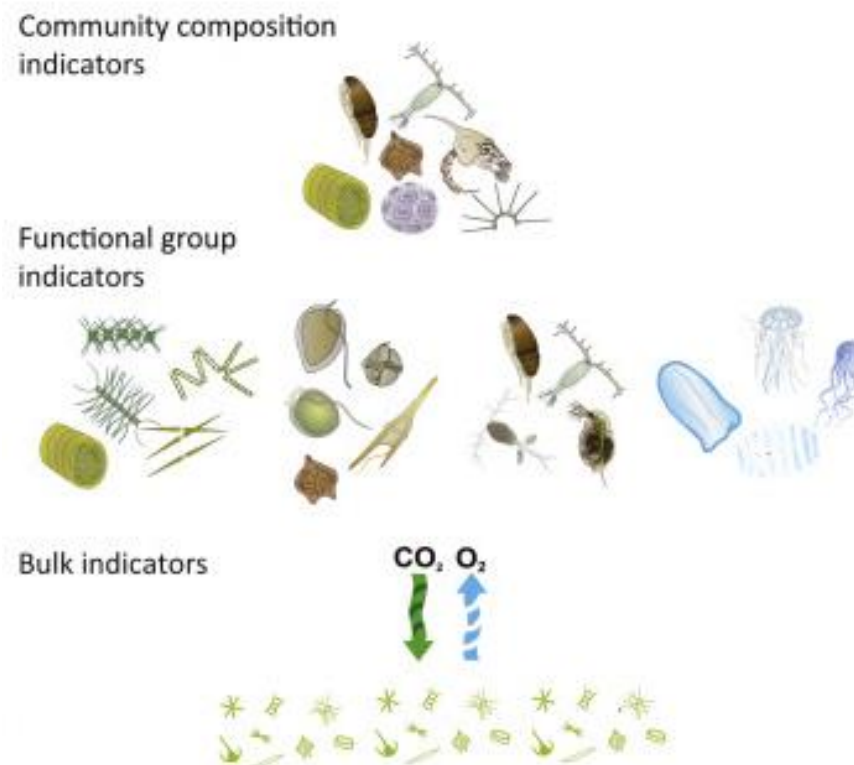


Figure 1.5. Classifications of plankton indicators by taxonomic resolutions, from lowest (bulk indicators) to highest (community composition indicators). Diagram from McQuatters-Gollop et al. (2017).

1.3.1.1 PH1/FW5- Changes in Phytoplankton and Zooplankton Communities (functional group approach)

A useful approach to understanding change in plankton communities is the use of functional trait concepts. A functional trait is a characteristic that mediates growth, reproduction and survival, and many roles within food webs are trait-mediated (Barton et al., 2013). Furthermore, trait distributions can reflect on the dominant factors structuring plankton ecosystems, when responses to environment can be predicted from traits (Edwards et al., 2013a) and therefore taking a functional trait approach has particular value of the development of ecosystem indicators (Beauchard et al., 2017).

A method based on functional traits has been selected for assessing for functional changes in plankton community structure under the MSFD. The method is based on grouping species into their respective 'lifeforms' based on shared functional traits. Lifeforms are groups of species that play the same functional role within an ecosystem (Tett et al., 2013) and are analogous to broad-scale functional groups. As ecosystems experience change and are subjected to pressures, the relative proportions and ratios of different life forms can change. Monitoring key lifeform ratios can therefore help assess change in ecosystem state.

For example, diatoms are a key spring-blooming phytoplankton functional group and form the base of the copepod-fish food web, have fast sedimentation rates and are known to be important for fixing atmospheric carbon to the sea floor (McQuatters-Gollop et al., 2007a; Spilling et al., 2018; Wasmund, 2017). In contrast, summer-blooming dinoflagellates are seen to be less palatable than diatoms to higher trophic levels and have slower sedimentation rates than diatoms, meaning less energy is transferred to the benthos. A switch in dominance from diatoms to dinoflagellates therefore can result in changes in trophic pathways, changes to carbon fixation and changes to benthic-pelagic coupling. Furthermore, many dinoflagellate taxa are associated with Harmful Algal Blooms (HABs) (Garmendia et al., 2013), so change in the relative proportion of diatoms and dinoflagellates may result in changes to toxin production within the pelagic habitat (Edwards et al., 2006; Hallegraeff, 2010; Heisler et al., 2008). The two lifeforms contrast in their nutrient requirements, with dinoflagellates able to capitalise on inputs of nitrogen and phosphorous better than diatoms which have a unique requirement for silicate to build their cell wall. Change in the ratio of diatoms to dinoflagellates therefore can indicate changing eutrophic conditions (McQuatters-Gollop et al., 2007a).

The method currently employed by OSPAR ICG-COBAM to quantify changes in the lifeform indicator is based around a 'state-space' approach. This approach involves selecting key lifeform pairs, based on their link to ecosystem structure and functioning, then plotting the abundance of the first lifeform for each month in a time series on the X axis, and the second lifeform on the Y axis (Tett et al., 2013). For example in figure 1.6 the abundance of diatoms is plotted on the x axis and the abundance of dinoflagellates on the y axis, so that monthly plankton communities are plotted in 'state-space'. As ratios of lifeforms vary naturally, e.g. seasonal variation, plotting multiple coordinates from months taken throughout a defined time period can produce a 'domain' within the plot of ecosystem state. Further time periods can be compared to this reference domain by overlaying the months for the new time period in question. In figure 1.6, the new time period B represents a changed ecosystem state from the reference domain A, revealing community change within the pelagic habitat (Tett et al., 2013).

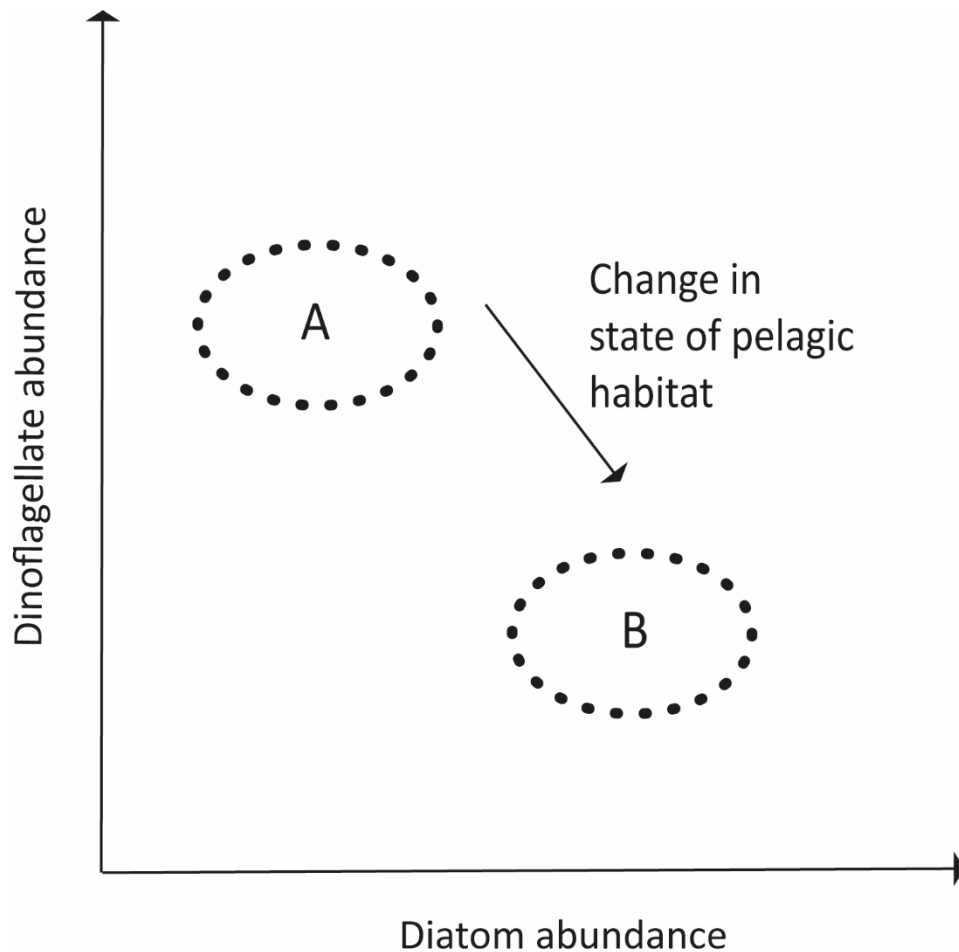


Figure 1.6. The 'State-Space' approach for pelagic monitoring within the MSFD. Diagram modified from Tett et al. (2013). Here changes in the relative abundance of Diatoms to Dinoflagellates in the system represent a difference in the state of pelagic habitats.

1.3.1.2 PH2- Plankton biomass and/or abundance (bulk properties approach)

Bulk properties of plankton communities focus on total abundance and biomass of phytoplankton and zooplankton as a whole, i.e. the data are not taxonomically resolved (McQuatters-Gollop et al., 2017). Chlorophyll a concentration is often used as a proxy for phytoplankton biomass (Henson et al., 2010), with change indicating

changes in primary productivity, while alterations in zooplankton biomass indicates changes in secondary productivity (Gorokhova et al., 2016). Changes in these bulk indicators can reveal structural changes to the food web, and are therefore particularly useful for assessing the food-web descriptor under the MSFD. For example, Capuzzo et al. (2018) found a decline in primary productivity in the North Sea over the last 25 years, associated with a decline in small copepods and a decline in fish recruitment. Bulk variables are also sensitive to anthropogenic pressure. Phytoplankton biomass for example, is used as an indicator for eutrophication, due to nutrient inputs stimulating increased growth (McQuatters-Gollop et al., 2009). The focus of this thesis is on community change, and does not cover bulk properties; although key variables for understanding ecosystem dynamics, it is established that bulk variables are most usefully interpreting alongside more taxonomically-resolved data informing on community composition (McQuatters-Gollop et al., 2017).

1.3.1.3 PH3- Changes in biodiversity indices (diversity approach)

At the OSPAR level, species diversity metrics are used as a formally assessed state indicator for pelagic habitats, and in contrast to PH1 and PH2 have an implicit requirement for species-resolved taxonomic data to assess for changes in species composition. Broadly, species diversity metrics are metrics of taxonomic composition that focus on the number of species and the evenness of species abundances. Species richness is a simple metric of the number of species in a community, and can be calculated from presence-absence resolution data. In contrast, species evenness

metrics require abundance data, and indicate changes in dominance structure of communities (Hillebrand et al., 2008).

In this thesis, one diversity metric used in a pilot assessment of PH3 during the OSPAR IA2017 is examined; The Local Contribution to Beta Diversity (LCBD) (OSPAR, 2017f). This metric identifies atypical or unique plankton community composition in a time-series, compared to the other time-points (Legendre and Gauthier, 2014). As a metric, it is effective in flagging changes in diversity because it accounts for not only changes in the identity of taxa, but also changes in the number of taxa in a community and importantly the dominance structure of communities that may be a result of anthropogenic perturbation or environmental variation (Legendre and Cáceres, 2013; Magurran and Henderson, 2010). Within IA2017, LCBD was tested only on three coastal stations, and only for phytoplankton, so requires extensive further development as an indicator.

The concept of diversity is often the basis of assessments of benthic communities (Muxika et al., 2007) and has been used in understanding long-term change in benthic communities (Capasso et al., 2009). In the context of benthic systems, changes in diversity indicators are often directly related to the level of human disturbance (van denderen et al., 2014). In contrast, within plankton communities, the response of diversity metrics to perturbation is more unclear. Theoretically, perturbation to pelagic habitats, as well as large-scale environmental change, should favour some species over others, causing changes in dominance patterns and evenness based metrics (Flöder et al., 2010). For example plankton diversity indicators have been linked to nutrient inputs (Jiang et al., 2014) and Beaugrand et al. (2010) found that increasing zooplankton diversity was a result of increases in sea surface temperature, indicating a

link between diversity and climate change. The consequences of changing diversity of plankton communities on the wider food web are also unclear. Although there is evidence for a link between species diversity and ecosystem functioning, Strong et al. (2015) conclude that the information required for operationalizing this relationship into the monitoring of ecosystem functioning is lacking. Beaugrand et al. (2010) found that the increasing plankton diversity shown in their study was coupled with a decrease in the mean size of copepods, which could have negative consequences for wider ecosystem stability and resilience, as well as trophic implications. Increased phytoplankton diversity has also been linked to increased resource use efficiency, due to niche complementarity (Olli et al., 2014). However, the consequences of this increased resource use efficiency for secondary productivity and trophic energy transfer are not well understood. Key challenges remain on progressing understanding of what 'diversity' in the classical concept of the term, means for pelagic habitats, and the applications of using diversity indices, including the Local Contribution to Beta Diversity, as formally assessed indicators.

1.3.2 Key scientific challenges to assessing pelagic habitat status

1.3.2.1 *Establishing reference conditions for plankton indicators*

Reference or comparison conditions for plankton indicators are challenging to set.

Firstly, these reference conditions must represent GES, and a vision for GES is difficult to define for pelagic habitats, not least because it requires a degree of societal choice in environmental ambition (Gilbert et al., 2015). An attempt to articulate a vision of GES has been made by Dickey-Collas et al. (2017). They argue that for pelagic habitats to be in GES, three conditions should be met: species must be able to close their

lifecycles within their pelagic habitat, biogeochemical processes are maintained and movement of biota and water masses are not obstructed. Similarly, Scherer et al. (2016) formally evaluated the Western Irish Sea pelagic habitat for GES, using concepts of expected levels of vigor and organization, and concluded that the area was representative of GES. Once these GES criteria are consolidated, temporal and spatial reference conditions for indicator assessments can be evaluated.

Another challenge to setting a temporal reference period is to account for shifting baselines syndrome in ecosystem state that has been identified within other areas of marine conservation (McClenachan et al., 2015; Pauly, 1995; Thurstan et al., 2015) . This is the phenomenon where neglecting past changes obscures the magnitude of change or variability in ecosystem components. For example, Zu Ermgassen et al. (2012) compared the extent of wild oyster bed habitat in the US for 24 estuaries, between the periods of 1878-1935 and 1968-2010. They found a 64% decline in oyster bed extent between the two periods. Similarly, Ferretti et al. (2013) compared the elasmobranch community in the Adriatic Sea from 1948 to 2005, and found a decline of 94.5%, with 11 species ceasing to be detected. In these examples, using contemporary data to provide a baseline for management purposes would mask significant declines. This may lead to conservation intervention not being triggered, or targets for restoration lower than could/should be achieved (Mihoub et al., 2017; Plumeridge and Roberts, 2017). Historical plankton data from either the beginning of long-term time-series, or other 'rescued' historical sources therefore provide a possibility for setting reference conditions for pelagic habitat assessments. For example, Wasmund (2017) used historical plankton data to define a threshold value for the ratio for the diatom/dinoflagellate index, an indicator of plankton community structure used in assessments of the Baltic Sea, arguing that using pre-eutrophication

period from the first half of the 20th century in the Baltic Sea provides a relatively pristine reference period.

The reference condition for pelagic habitat assessments under the MSFD, however, is used as a threshold to understand whether a change has occurred and in contrast to the Water Framework Directive, it is not meant to reflect pristine conditions as the MSFD specifically allows for human use of the system. Furthermore, Duarte et al. (2009) show that a reduction in nutrient inputs within four eutrophic coastal ecosystems did not lead to the return to a pristine reference status. This lack of a consistent recovery trajectory can be as a result of many factors. Firstly, the biodiversity of a given ecological community can be seen as having a temporal component, and turnover in a community occurs regardless of human pressures (Magurran et al., 2010). Secondly, 'legacy' effects, where the state of an ecosystem at a given point in time (such as an MSFD assessment period) are representative of previous accumulated human pressures, as well as the pressures for that period (O'Higgins et al., 2014). Lastly, climate change can cause changes to an ecosystem baseline beyond the scope of direct conservation intervention (McQuatters-Gollop, 2012). The specific role of historical data in setting reference conditions for pelagic habitats warrants further investigation; fluctuations and trajectories in ecosystem baselines must be taken into account for management of pelagic habitats to be adaptive, and to set realistic and meaningful reference conditions (Gatti et al., 2015; Kraberg et al., 2011).

1.3.2.2 Attributing drivers of change in plankton indicators

The overall biodiversity assessment challenge of disentangling signals of direct anthropogenic pressures from prevailing climatic and oceanographic influences is exemplified with plankton indicators. Changes in plankton community structure can result from direct anthropogenic pressures, manageable at the regional seas scale. Plankton communities however, are highly dynamic in the face of climatic variability and directional anthropogenic climate change (Barton et al., 2016; Hays et al., 2005). There is a clear need within the implementation of the Marine Strategy Framework Directive to understand how large scale climatic and oceanographic influences ('prevailing conditions') influence pelagic habitats in order to effectively attribute drivers of change to plankton indicators during formal assessments (McQuatters-Gollop et al., 2015). Much of our understanding of large-scale environmental change on plankton communities is gained through long-time series datasets. For example, the Continuous Plankton Recorder Survey (described in detail later in this chapter) provides geographically extensive, taxonomically resolved plankton data, available from 1958 onwards which has helped increase our understanding of multi-decadal plankton dynamics (Edwards et al., 2010; Giron-Nava et al., 2017). 'Rescued and reused' historical datasets can also further increase temporal scale of understanding the drivers of change (Tingley and Beissinger, 2009; Ward et al., 2008).

Temperature is considered the most important physical variable driving large-scale change in plankton communities; individual plankton taxa have different thermal niches, and plankton assemblages have different temperature preferences (Dell et al., 2011; Gvoždík, 2018). With warming temperatures, locations that were historically too cold for survival will become habitable, thus facilitating range shifts (Bates et al., 2014;

Beaugrand and Kirby, 2018; Richardson, 2008). Multiple changes in plankton communities have been documented as a result of climate variability and climate change, which can cause changes in plankton state indicators. For example, The North Atlantic Oscillation (NAO), is shown to influence phytoplankton community structure on a decadal scale (Henson et al., 2012; Zhai et al., 2013). Similarly, The Atlantic Multidecadal Oscillation (AMO) causes alternating temperature regimes (Ting et al., 2009) at an even broader temporal scale than the NAO and has a strong signal in North Atlantic plankton records (Edwards et al., 2013b; Harris et al., 2014; Nye et al., 2014) . In the 1980s, a global regime shift occurred, triggered by both natural and anthropogenic climatic change, as well as changes in regional hydrography (Beaugrand, 2004; Reid et al., 2015; Weijerman et al., 2005). In the North Sea, for example, extensive changes in the plankton community were documented; phytoplankton biomass increased, with a 13% higher chlorophyll concentration in the open North Sea after the regime shift (McQuatters-Gollop et al., 2007b), and there was an increase in the abundance of warmer water copepod species (Edwards et al., 2013c; Helaouët and Beaugrand, 2007).

Therefore, prevailing conditions are likely to have a large influence on plankton state indicators, obscuring the clear detection of relative influence of direct anthropogenic pressures on pelagic habitats. For example, further work is needed to understand the responses of plankton lifeform groups to changes in prevailing conditions, to provide context to assessment of direct anthropogenic pressures.

1.4 Cross-scale challenges

The Ecosystem Approach to marine management can be adopted in practice at different levels (Link and Browman, 2014) from developing individual biodiversity indicators, to developing overall marine strategies. Scientific challenges and knowledge gaps are faced at each 'layer' of the MSFD implementation process; especially as integrating biodiversity state assessments into holistic marine policy in this way is relatively new. Each level of MSFD implementation comes with associated scientific challenges (Figure 1.7). For example at the individual plankton indicator level, deciding on appropriate temporal scales for setting reference conditions, as well as using disparate data sources are key technical challenges facing indicator development and assessment. These challenges are likely to be common to other individual indicators across different biodiversity components. There are however, key challenges that are common across different levels of MSFD implementation.

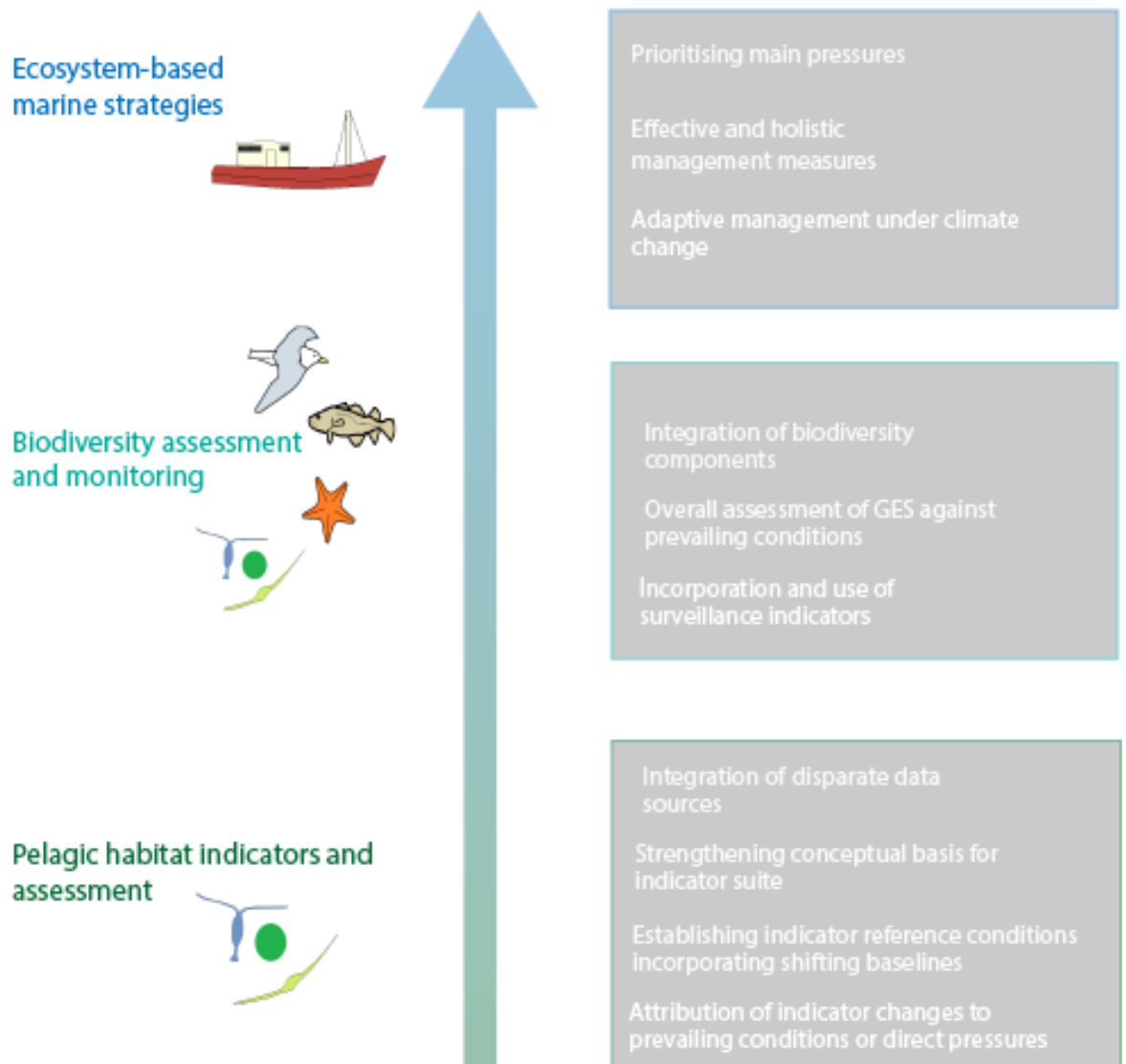


Figure 1.7. Challenges associated with pelagic habitat assessments are 'layered' within wider ecosystem based management.

1.4.1 Integration

'Integration' is inherently a key scientific challenge as management of marine ecosystems progresses towards cross-sectoral ecosystem-based approaches. Holistic management involves integrating different biodiversity indicators during biodiversity

state assessment, through to integrating the regulation of multiple human activities at the regional seas scale (Elliott, 2011). Further work is required however, to consolidate the concepts of integrated management, in order to make it operational. At the biodiversity assessment level for example, further work is needed to distinguish the aggregation of indicators into an overall assessment of GES from the understanding of the interactions between different ecosystem components, as well as the integration of information from surveillance indicators into the assessment process. Similarly, at the broader level of developing marine strategies, further work is needed to identify management mechanisms that can effectively manage multiple pressures at once. Marine Spatial Planning for example, is identified as a key management mechanism that if properly implemented, can support integrated ecosystem based management (Douve, 2008; Jones et al., 2016).

Using the example of pelagic habitat assessments to illustrate the challenge of integration, further work is required to aggregate indicator assessment results into an overall assessment of GES, as well as understand how changes in plankton indicators reflect changes in other ecosystem components, which will particularly aid in assessing the food web descriptor of the MSFD. If a detrimental influence of a direct human pressure on the ecosystem, such as eutrophication, is identified as a result of formally assessing pelagic habitat status, integrating management of eutrophication into the wider marine strategy is required to achieve overall Good Environmental Status.

1.4.2 Prevailing conditions

Another key cross-scale challenge is in understanding and adapting to changes in prevailing conditions caused by both natural variability and the signal of anthropogenic

climate change. At the biodiversity assessment level, this involves understanding the sensitivity of MSFD biodiversity indicators to climate change, as identified as a key scientific priority by Frost et al. (2016). This remains a scientific priority for pelagic habitat assessments, because plankton indicators are particularly sensitive to changes in prevailing conditions (McQuatters-Gollop, 2012). At the wider level of developing marine strategies, a key challenge comes in adapting management of human activities in response to changing prevailing conditions. Ultimately, sustained monitoring and detection of underlying environmental change is required for effective ecosystem based management (Mieszkowska et al., 2014).

1.5 Conclusions and aims of project

'Mapping' individual biodiversity indicator development into the wider ecosystem-approach context as done in this review in a useful way of summarizing the knowledge gap areas to progress indicator development, biodiversity monitoring and ultimately overall ecosystem-based management strategies. As many of the challenges facing the assessment of pelagic habitats are cross-scale challenges, namely assessing indicators against the backdrop of changing prevailing conditions, addressing them will increase the robustness of pelagic habitat assessments, as evidence bases for the wider development of ecosystem-based marine strategies.

Continued exploration of the influence of temporal scale on the perception of change in pelagic habitats is needed to progress their formal assessment under the MSFD. Specifically, continued research into how changes in prevailing conditions over these

large temporal scales alter plankton community composition is needed to understand the drivers of change in plankton communities, to understand reference levels of variability, and to set appropriate reference conditions (McQuatters-Gollop et al., 2015). Furthermore, exploration of how to maximise the applications of this long-temporal scale data, given the identified potential for surveillance indicators within the MSFD, warrants further exploration.

A wealth of long-temporal scale data is available for plankton communities within the North Sea, and can aid in addressing these 'layered' challenges, progressing the robust assessment of pelagic habitats under the MSFD. This includes consistent time-series running up to the present day, such as the Continuous Plankton Recorder dataset (described below), as well as 'rescued' historical datasets spanning fixed periods of time. Specifically, it is established, that long temporal scale data is essential for understanding the influence of climate variability on plankton communities, and identifying signals of long-term climate change (Giron-Nava et al., 2017). The full temporal scale of plankton data available, however, has yet to be fully utilised under the MSFD. The OSPAR Intermediate Assessment 2017, for example, used CPR data from 2004 onwards for its assessment of PH1 (OSPAR, 2017a), with the role of additional historical plankton data unclear. The overall aim of this thesis is therefore to:

Apply long temporal scale plankton data to the challenges facing the formal assessment of pelagic habitats under changing prevailing conditions.

Specifically, this main overall aim will be explored centring on the following three aims:

- 1. The selection of appropriate reference periods in the context of changing prevailing conditions**
- 2. The responses of policy indicators to changing prevailing conditions**
- 3. Using plankton as surveillance indicators to monitor and inform on changing prevailing conditions**

1.5.1 The Continuous Plankton Recorder Survey

The Continuous Plankton Recorder (CPR) survey is the longest running, and most geographically extensive, marine ecological survey in the North-East Atlantic (Giron-Nava et al., 2017). The CPR survey provides regional scale data to the UK and OSPAR assessment of pelagic habitats under the MSFD, and is the core dataset employed in this thesis. Continuous Plankton Recorders (CPRs) consist of a filtering mechanism housed in an external body that is towed behind ships of opportunity at a depth of approximately 6-7m (Figure 1.8). The speed at which the silk is drawn from a storage spool is controlled by a propeller, so that when the filtering silk is later cut into individual samples, ~10cm of silk corresponds to ~18.5 km of tow through the sea (Batten et al., 2003).

These samples are then analysed for both phytoplankton and zooplankton taxa, using consistent four-stage methodology: 1) overall phytoplankton biomass (quantified by the 'greenness' of the silk), 2) large phytoplankton (> 20 µm) cells, where a semi-quantitative abundance value is calculated 3) smaller zooplankton (< 2.0mm) count

based on a traverse of the silk, and 4) large zooplankton (>2.0mm) count based on the total count on the whole sample (Richardson et al., 2006).

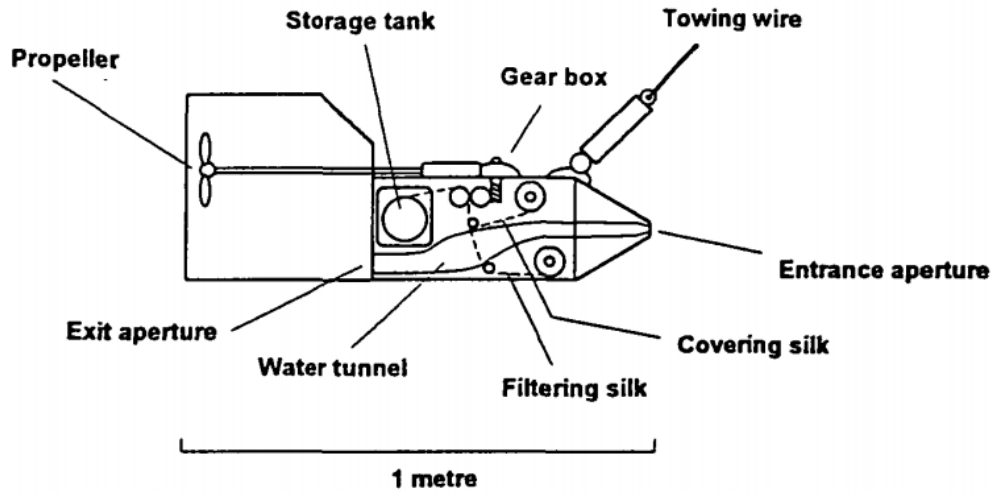


Figure 1.8 The internal mechanism of a Continuous Plankton Recorder (Hays, 1994). Water enters the entrance aperture, is filtered through the filtering silk and covered by the covering silk. Water then exits the exit aperture. The speed at which the silk is drawn is controlled by the propeller.

1.5.2 Study area

This thesis focuses on the Greater North Sea (GNS) OSPAR region (Figure 1), which includes the North Sea, English Channel and Skagerrak and Kattegat, with a permanently mixed water column in the south and east and seasonal stratification regimes in the North (ICES, 2017). The GNS region has a rich history of ecosystem and biodiversity monitoring, and is therefore a useful focal site for exploring the application of long temporal scale plankton data for the development of marine strategies. Furthermore, the GNS is a key region for developing an ecosystem approach

to management, due to it being a multi-sector, multi-use platform providing ecosystem services to bordering countries (Emeis et al., 2015). Diverse human activities including fishing and offshore oil and gas developments in turn place diverse pressures on the ecosystem, including the selective extraction of species and substrate loss (ICES, 2017). Land-based activities including agriculture and coastal development can also influence GNS nutrient regimes via pollution across the land-sea interface (de Jong, 2016). Superimposed on these direct human activities, the GNS is also a known hotspot of climate change. The Northern North Sea transitioned from a cold-temperature boreal regime to a warm-temperature regime following the 1980s regime shift (Beaugrand, 2004). This climate warming has occurred more rapidly in the Southern North Sea due to it being shallower (ICES, 2017). Sea Surface Temperatures in the region are influenced by North Atlantic thermal regimes such as the Atlantic Multidecadal Oscillation, interacting with the influence of anthropogenic global carbon emissions (Nye et al., 2014). For each subsequent chapter, the region is further split into different sub-areas depending on the specific analysis, which are described in detail within each respective chapter.

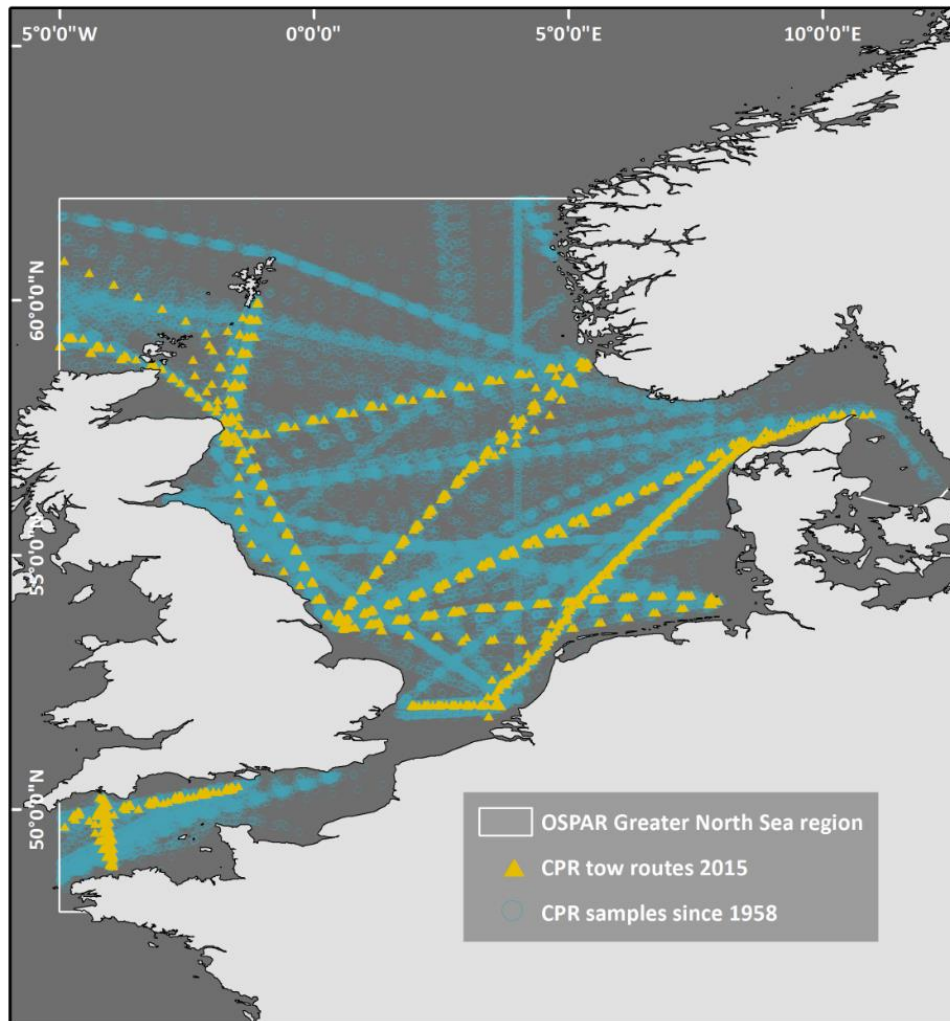


Figure 1.9. CPR samples within the OSPAR Greater North Sea region. Sampling is based on tows from ships of opportunity, so are clustered along linear transects. Sampling routes have varied through time, and routes from 2015, the latest year of data included in the thesis, are coloured yellow for context.

1.5.3 General analysis approaches

Plankton communities are highly species rich and therefore the data are highly multivariate in nature (i.e. there are many dependent variables (different taxa) to analyse at once). In order to identify how the plankton community responds holistically to environmental variation, and thus address questions about reference conditions (Aim 1), and the interpretation and use of policy indicators (Aims 2 and 3)

multivariate analyses were employed. A plethora of statistical analyses are available for multivariate plankton community data (Mackas et al., 2012). Traditionally, multivariate analyses focus on reducing the number of variables down to a more 'manageable' number of variables through, for example, the analysis of principle components (Harris et al., 2014), or the calculation of a matrix of pairwise distances between samples and using PERMANOVA (Van Ginderdeuren et al., 2014). Warton et al. (2015) however, highlight the merits of specifying a statistical model for the raw community data (i.e. not attempting to reduce the number of variables prior to analysis). By specifying a model and testing how well that model explains variation in the data, it allows for the testing of defined questions and theories to a greater extent than distance-based analyses. This approach is termed 'multivariate abundance modelling' and is used in this thesis. For example, in Chapter 3, multivariate generalised linear models are used to test for the influence of time period and SST on community composition (Hui et al., 2015).

Another merit of multivariate abundance modelling over other available approaches is the ability to explicitly account for the structure of the data. For example, count data often has a mean-variance relationship (variation in abundance of taxa is larger when their mean abundance is larger). Warton et al. (2012) show that not accounting for these relationships through using classical distance-based multivariate analyses (i.e. those based on a matrix of pairwise distances) can lead to the failure to detect multivariate effects when taxa don't express high variance, and the failure to identify taxa in which an effect is expressed. Instead, by directly specifying a statistical model for the observed multivariate data, these mean-variance structures in the data can be accounted for (Warton et al., 2015).

Similarly, another approach to understanding plankton community responses to environmental drivers is to identify species assemblages where individuals respond similarly to environmental forcing, for example, through distance based cluster analyses (Beaugrand, 2005). Whereas many cluster analysis approaches are based on the abundance of species in different conditions, fewer allow clustering based specifically on the response to changing environmental conditions, which uniquely requires the specification of a statistical model (Dunstan et al., 2011; Warton et al., 2015). Model -based clustering approaches, based on finite mixtures of generalised linear models allow the specification of a statistical model to classify organisms (Foster et al., 2015). As I was interested specifically in this ‘response’ of plankton taxa and indicators to changing prevailing conditions, in chapter 6 a model-based clustering approach termed ‘Species Archetype Modelling’ (SAMs) is used to cluster taxa based on their response to Sea Surface Temperature (Dunstan et al., 2011).

1.5.3.1 Applied indicator approach

In order to specifically address Aim 2 of the thesis, an indicator approach was taken within chapters 3 and 4. By looking at the dynamics of OSPAR indicators that have been approved by policy-makers for the assessment of pelagic habitats under the MSFD, the analyses can be tightly aligned with the policy process. Although these metrics have undergone extensive screening through the policy process, I independently assessed the indicator metrics included in this thesis to be ecologically valid and effective for understanding the influence of prevailing conditions on plankton communities. Firstly, I assessed that the included indicator approaches had specific

merits over other available methods. For example, in chapter 3, the metric 'Local Contribution to Beta Diversity' for each year in the time-series was calculated, which identifies unique or atypical plankton community compositions compared to the wider time-series (outlined in the above literature review and in detail in chapter 3). Compared with other metrics of temporal beta diversity (Anderson et al., 2011), and indeed other methods of quantifying variability in plankton composition such as time-series decomposition (Broekhuizen and McKenzie, 1995), the LCBD metric facilitated the partitioning of total variability into the contribution each individual time-point makes. This is particularly useful for the aim 1 of the thesis because it can identify periods of time that are representative, or not representative, of typical community structure and therefore may be suitable, or not suitable, for use as reference conditions. Furthermore, a pilot assessment of LCBD indices for phytoplankton communities was included in the OSPAR intermediate assessment 2017, but was not assessed for CPR data in the North Sea, not assessed for zooplankton communities, nor were any links to drivers looked for, including large scale changing prevailing conditions. Therefore using this metric progressed understanding of the influence of prevailing conditions on plankton communities and also contributed to the development of a policy indicator.

Secondly, I assessed that the indicators included in the thesis provided full coverage of plankton community structure. For example, although there are many different functional groups that can be used to describe the structure and dynamics of plankton communities, in chapter 6, lifeform groups used in the OSPAR IA2017 assessment of pelagic habitats were used in order to explore the response of these indicators to prevailing conditions. I assessed that the lifeform groups included by OSPAR cover the majority of the main broad functional groups of plankton and so provide good

coverage of plankton community structure. I therefore assessed that using these pre-selected groups both appropriately answered the ecological aims of the chapter, as well as contributed to policy indicator development, addressing aim 2 of the thesis. The potential for selecting and developing further plankton lifeforms is discussed in chapter 4 and chapter 6.

1.6 Thesis outline

Broadly, the thesis first contributes to understanding of the influence of large scale climate variability and climate change on plankton communities, to understand shifting baselines, to explore temporal options for setting reference conditions, and to provide historical context to pelagic habitat assessments. It then takes an applied indicator approach to explore the responses of OSPAR pelagic habitat indicators to changing prevailing conditions. Following this, the application of this understanding of climate-driven community change as surveillance indicators in ecosystem assessments is explored, before the aims of the thesis are evaluated in relation to the findings within.

Chapter 2 further extends understanding of the influence of prevailing conditions (focusing on SST change) on plankton communities by integrating the CPR dataset with the ICES historical plankton dataset, consisting of net samples undertaken between 1902 and 1912. The results are discussed in the context of shifting baselines and the selection of reference periods from historical plankton data.

Chapter 3 explores reference levels of variability in plankton communities through quantifying temporal Beta Diversity of the time series. This variability in community composition is quantitatively linked to data on prevailing oceanographic and climatic conditions. The application of temporal Beta Diversity as an ecosystem indicator and as a tool to evaluate suitable reference periods are also presented.

Chapter 4 scales up from describing pelagic habitats using species level data to using aggregated lifeform groups (broad-scale functional groups). Lifeform groups form the core of both UK and OSPAR pelagic habitat assessments, and this chapter looks at whether changes in lifeform abundances can indicate the influence of prevailing conditions on plankton community change, focusing on Sea Surface Temperature.

Chapter 5 analyses in detail the concept of surveillance indicators, and applies a conceptual surveillance indicator monitoring and assessment framework to plankton indicators, to illustrate the potential use of plankton indicators in informing on changing prevailing conditions for the wider marine food-web during ecosystem assessments.

Chapter 6-In this chapter, the main findings of the thesis are summarized and evaluated in relation to the core project aims. Finally, policy recommendations are made to progress pelagic habitat assessments under the MSFD.

Chapter 2

A century of change in North Sea plankton communities explored through integrating historical datasets

Aspects of this chapter have been included in the following:

Bedford, J., Johns, D., McQuatters-Gollop, A. (2018) A century of change in North Sea plankton communities explored through integrating historical datasets, ICES Journal of Marine Science, 76 (1) 104-112

For this published paper, I integrated the digitised database of raw ICES historical samples with raw CPR data provided by the CPR survey, researched and carried out all analyses and completed all of the writing. AMG and DJ provided supervision and feedback on the paper.

Chapter 2 A century of change in North Sea plankton communities explored through integrating historical datasets

2.1 Introduction

Climate change is causing widespread changes in marine ecosystems, superimposed on a background of climate variability that acts at different temporal scales (Hoegh-Guldberg and Bruno, 2010). Plankton communities are sensitive to changes in the physical marine environment, and have been shown to be responsive to interannual and multi-decadal climate variability as well as anthropogenic climate change (Hays et al., 2005). As the base of the pelagic food web, phytoplankton are primary producers (Boyce and Worm, 2015), transferring energy through zooplankton to higher trophic levels (Richardson, 2008). This sensitivity to environmental conditions and their role in the pelagic foodweb makes tracking plankton community change useful as an indicator of change in the wider ecosystem. Much of our understanding of multi-decadal change in plankton communities in the North Sea comes from the Continuous Plankton Recorder (CPR) survey (McQuatters-Gollop et al., 2015). Consistent monitoring data available from 1958 through the present has documented widespread shifts in both phytoplankton and zooplankton communities, specifically the occurrence of basin-scale regime shifts in the North Atlantic (Beaugrand et al., 2014; Reid et al., 2015).

The value of plankton time series as evidence for policy and management increases with time. Through using long temporal scale data, the influence of multi-decadal changes in environmental conditions on plankton communities can be investigated, and the most important environmental influences structuring plankton communities

on this scale can be identified (Edwards et al., 2010; Giron-Nava et al., 2017). For example, the Atlantic Multidecadal Oscillation is a term for the natural low-frequency SST variability in the North Atlantic that oscillates between warm and cool phases on a ~60yr time scale (Edwards et al., 2013b). It has been identified as the second largest macroecological signal in North Atlantic plankton communities, but requires long temporal-scale time-series in order to detect the influence of transitions between oscillatory phases on community change (Edwards et al., 2013b). Furthermore, the long temporal scale of the CPR survey can help separate these wider oceanographic and climatic influences on plankton communities, such as the key influence of SST, from direct anthropogenic pressures such as eutrophication, which is particularly useful during formal policy assessments (McQuatters-Gollop et al., 2015).

'Rescuing' historical ecological datasets, that otherwise may be lost or deemed redundant, has been identified as a useful way of increasing temporal scale in ecological studies, and can be used to address contemporary marine policy challenges, including understanding effects of long-term climate change (Hawkins et al., 2013).

Specifically, the use of rescued historical datasets in avoiding 'shifting baselines syndrome' in biodiversity state has received much attention (Pauly, 1995). This is the phenomenon where neglecting historical changes obscures the magnitude of change or variability in ecosystem components. Therefore, rescued historical plankton data can be a tool for avoiding shifting baseline syndrome in our understanding of the multi-decadal dynamics of plankton communities (Ward et al., 2008). The ICES historical plankton dataset used in this study is a dataset of plankton samples collected in the North Atlantic between 1902 and 1912, digitised from historical log books.

Hällfors et al. (2013) compared phytoplankton records from this 'rescued' ICES

historical dataset in the Baltic Sea with contemporary phytoplankton samples, and documented compositional differences between the two time periods, potentially driven by both climate change and eutrophication. By comparing the ICES historical dataset with North Sea data from the CPR survey, we can better understand changes occurring in North Sea plankton communities pre-1950s, facilitating further exploration of the effects of large scale temperature change to the Continuous Plankton Recorder temporal coverage.

Disparities in sampling and analysis methodologies between the ICES historical data and the CPR survey, however, present challenges in their direct comparison, which need to be addressed before using the datasets together. Handling disparate data-types is a key challenge facing regional scale monitoring and assessment where data from multiple different sampling programmes often needs to be incorporated (Olli et al., 2013; Zingone et al., 2015). For example, the OSPAR IA2017 regional-scale assessment of plankton communities incorporated multiple time-series from across Europe, where taxa were sampled using different methods, and analysed to differing taxonomic resolutions (OSPAR, 2017a). In this study, by integrating and combining the CPR historical time series with the rescued ICES historical dataset, I aim to provide additional contextual information to the changes in North Sea plankton communities between 1958 and 2015 detected by the CPR survey, specifically to address the following questions:

- **Is there a difference in plankton community structure (both phytoplankton and zooplankton) between the early 20th century and the beginning of the consistently-sampled CPR time period (1960s)?**

- **Which plankton communities and individual taxa are most responsive to SST when examining the two datasets combined (1902-12, 1958-2015)?**

2.2 Data and Methods

2.2.1 Data sources

2.2.1.1 *Plankton samples*

Data from the period 1902-1912 have become available through the ICES historic plankton digitisation project, which occurred prior to the current thesis study, where 13,379 plankton samples were digitised from seven historical ICES volumes (McQuatters-Gollop et al., 2011). The data are collated from different sampling programmes, across the North-East Atlantic, North Sea, Irish Sea, Baltic Sea and Arctic Sea. After digitisation, data tables from the historical volumes were quality checked. The samples are all spatially referenced and consist of records of taxa at the presence/absence level or with semi-quantitative abundance information. In this study, I used all data at the presence/absence level, as to be able to compare with the Continuous Plankton Recorder survey data. I extracted data from the months February, May, August and November, as these had the greater numbers of samples. This historical plankton dataset is now freely available via the ICES data portal (ecosystemdata.ices.dk/HistoricalPlankton/Download.aspx).

The Continuous Plankton Recorder survey has been collecting samples in the North Sea on a routine, consistent basis since 1958 (Kirby and Beaugrand, 2009). CPRs consist of

a filtering mechanism housed in an external body that is towed behind ships of opportunity at a depth of approximately 6-7m. The speed at which the silk is drawn from a storage spool is controlled by a propeller, with 10.16 cm of silk corresponding to 18.5 km of tow through the sea (Batten et al., 2003). CPR data for the months February, May, August and November were obtained for the North Sea area for phytoplankton (DOI 10.7487/2016.236.1.999) and zooplankton (DOI 10.7487/2016.236.1.998). Although abundance information is collected for each taxon identified on each sample, for this study data were converted to presence/absence to make comparable to the ICES historical database.

As well as differences in quantitative resolution between the datasets, there are major structural differences between the historical ICES surveys and the CPR survey (McQuatters-Gollop et al. 2010). Firstly, the CPR is a continuous plankton sampling method, using a 270 micron mesh size silk (Richardson et al., 2006). The ICES database, in contrast, consists of net samples collected at fixed point locations by a multitude of disparate sampling cruises by northern European nations. Therefore, whereas the analysis methodology has remained consistent throughout the CPR series, the composite nature of the ICES dataset means that the sampling and analysis methodologies are not reliably consistent throughout the database. However, both sampling methodologies incorporated sub-sampling, where only a proportion of the sample is analysed, reducing any differences as a result of volume of water filtered (e.g. Hällfors et al. 2012).

The mesh sizes of the net samples in the ICES historical database are missing from the sample metadata, and are likely to be varied. The mesh size of the Continuous Plankton Recorder, 270 microns, is larger than the majority of standard plankton nets,

which tend to range between 5µm - 80 µm for phytoplankton and 125 µm – 200 µm for zooplankton (Castellani and Edwards, 2017; John et al., 2001) . Importantly therefore, any biases in sampling as a result of mesh size differences between the ICES historical plankton dataset and the CPR data are likely to come from the side of the CPR survey, evidenced by a lower number of species recorded overall than the ICES historical dataset. For example, CPR methodology likely undersamples smaller phytoplankton taxa, although they often are retained on the silk strands of the mesh (taxa as small as 5-10 µm are regularly recorded), which constitutes 30-40% of the mesh area (Batten et al., 2003). Similarly, the CPR survey likely undersamples small zooplankton taxa. A previous study however, comparing CPR data to net samples taken at the L4 sampling station in the Western English Channel, that used a mesh size of 200 microns, concluded that although the abundance of zooplankton taxa was generally lower, all dominant zooplankton species recorded at L4 were also common to CPR data (John et al., 2001). In this study, occurrence frequencies of select plankton taxa, based on presence/absence resolution data, were compared between datasets.

Samples from both datasets located in the North Sea region were divided into a 'Northern' North Sea region and a 'Central/Southern' North Sea region based on the border between ICES regions 4b and 4c (Figure 2.1). The two spatial areas represent a balance between the need for spatial specificity in comparing plankton communities with known differences occurring across latitudes, and the retention of a reliable sample size within each area. To ensure the depth of the ICES samples were comparable to the CPR dataset all ICES historical samples collected below 15m, or vertical hauls that started below 15m were removed from the resulting sample list, along with samples for which no depth information was given. To compare plankton

communities from the same area, CPR samples within half a degree of the ICES historical sample locations were then selected.

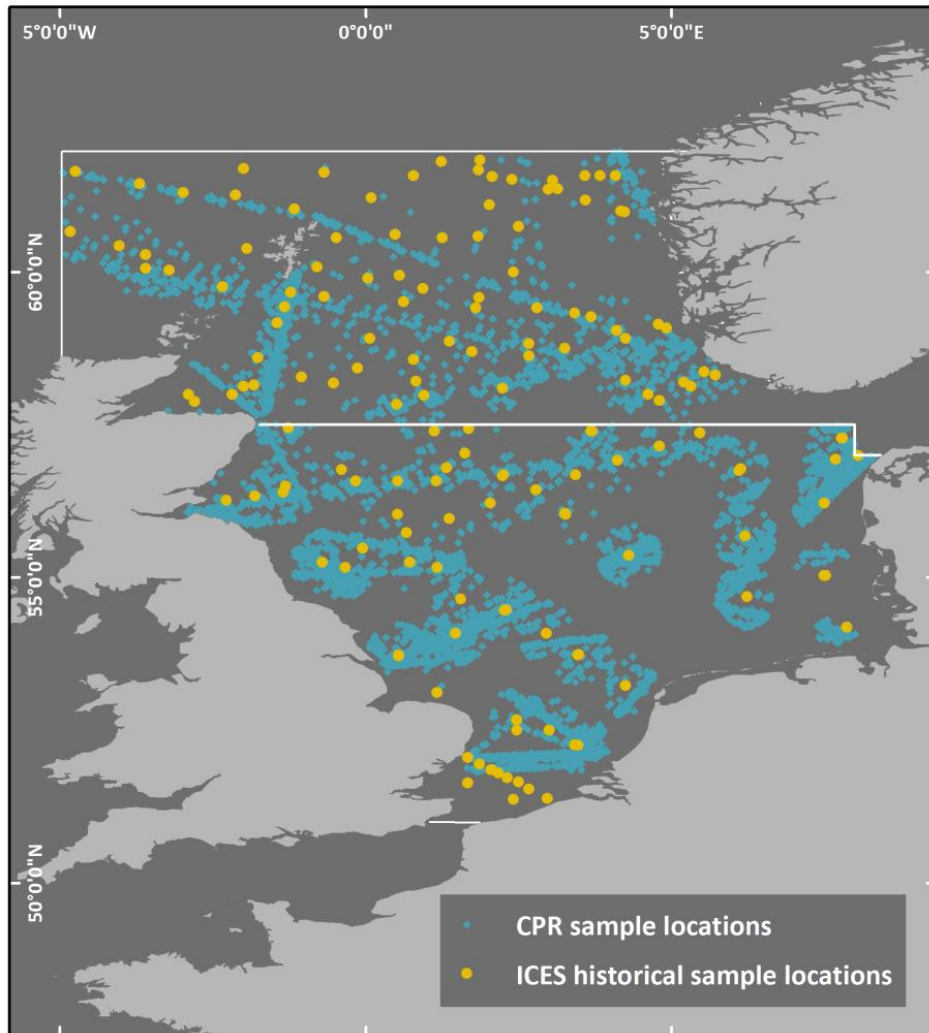


Figure 2.1. Locations of historical samples (large yellow) and centre points for CPR samples (small blue), included in this study . North Sea area (dashed white line) divided into 'Northern' and 'Central/Southern' areas based on boundary between ICES subregions 4b and 5c (solid white line).

2.2.1.2 *Sea surface temperature (SST) data*

Sea Surface Temperature was selected for this analysis due to it being a key component of the prevailing conditions affecting the North Sea, the key role of temperature in structuring plankton communities (Garzke et al., 2015; Richardson, 2008), and the relative availability of data for the historical time-period (1902-1912) compared to other variables, where data for the beginning of the 20th century is more limited; further variables on prevailing conditions including wind speed and salinity are included in analyses in chapter 3, which focuses on the CPR time-series only. Monthly SST data were downloaded for the North Sea region from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) at a 2 degree resolution. Data points were extracted from the Northern and Central/Southern North Sea area, and averaged for each year between 1902 and 2015.

2.2.2 Data preparation

Due to the disparate nature of the two datasets, data needed to undergo a cleaning and harmonization process in order to compare community composition between the two time-periods. The integration process is summarised in figure 2.2. Taxa lists of both phytoplankton and zooplankton were extracted from the historical ICES and CPR databases and both the ICES taxa lists and the CPR taxa lists were run through the Taxon Match Tool available on the WoRMS (World Register of Marine Species) website (<http://www.marinespecies.org>) to update all names to the most up-to-date accepted nomenclature. Due to the ICES database being a composite of multiple sampling

programmes, sporadically occurring taxa were removed, as these may not have been recorded or identified inconsistently between the different sampling programmes. For both datasets, a threshold of 1% frequency of occurrence was selected as a cut-off point for taxa to include in analyses of taxonomic composition. This represented a balance between the need to remove sporadic taxa, as highlighted by Hällfors et al. (2013), but still include rare species in analyses. Because of the decade time-span of the ICES historical dataset, this list for the CPR data was constructed based on a 1% occurrence frequency threshold *in any decade*, to ensure consistency.

The taxa lists differed in the taxonomic resolutions of recorded taxa. As the CPR time-period is the longer of the two, and the taxa are generally more coarsely taxonomically resolved, the taxa within the ICES list were aggregated to their equivalent resolution within the CPR taxa list. For example, the CPR taxon name 'Radiozoa' is a phylum, whereas in the ICES taxa list there were four taxon names within the phylum Radiozoa. These taxa were therefore aggregated to the coarser CPR resolution. In some cases, new groups were constructed to aggregate multiple taxa. 'Gelatinous zooplankton' was created as Cnidarians and Ctenophores were sometimes recorded as 'Coelenterata' within the ICES dataset. This nomenclature is outdated, and is not a monophyletic group, and so it would be impossible to determine whether these records related to '*Cnidaria*' taxa or '*Ctenophora*' taxa. Some taxa had resolutions too low for aggregation, for example records of '*Crustacea*' with associated life stages 'larvae' or 'nauplius'. Samples containing these records were removed before analysis, so the low taxonomic resolution did not skew results. Lastly, taxa that are not consistently recorded throughout the CPR time series, as a result of analysis changes, were removed. Similarly, any taxa within the ICES taxa list that would not be reliably

sampled by the CPR due to their small size or delicate nature were removed, thus reducing biases from differing mesh sizes.

After integrating the taxonomic nomenclature and resolution of the two taxa lists, of taxa that occurred in over 1% of samples, 39 phytoplankton taxa and 27 zooplankton taxa were unique to the ICES list, whilst 10 phytoplankton taxa and 13 zooplankton taxa were unique to the CPR list. These differences could represent large changes in occurrence frequency over the time period, but could also still be a result of sampling biases between the two datasets, for example though different mesh sizes. I therefore only used taxa that occurred in over 1% of samples in both datasets. These lists of common phytoplankton and zooplankton taxa shared between the two datasets represented taxa that were assumed to be consistently sampled by both surveys (Hällfors et al., 2013), further minimising biases from differing mesh sizes , and consisted of 44 phytoplankton taxa and 30 zooplankton taxa respectively (Table 2.1). Records of these shared common taxa were then extracted from the CPR and ICES samples, before determining the occurrence frequency of each taxon for each sampling month. Months with fewer than 5 samples were removed before analysis.

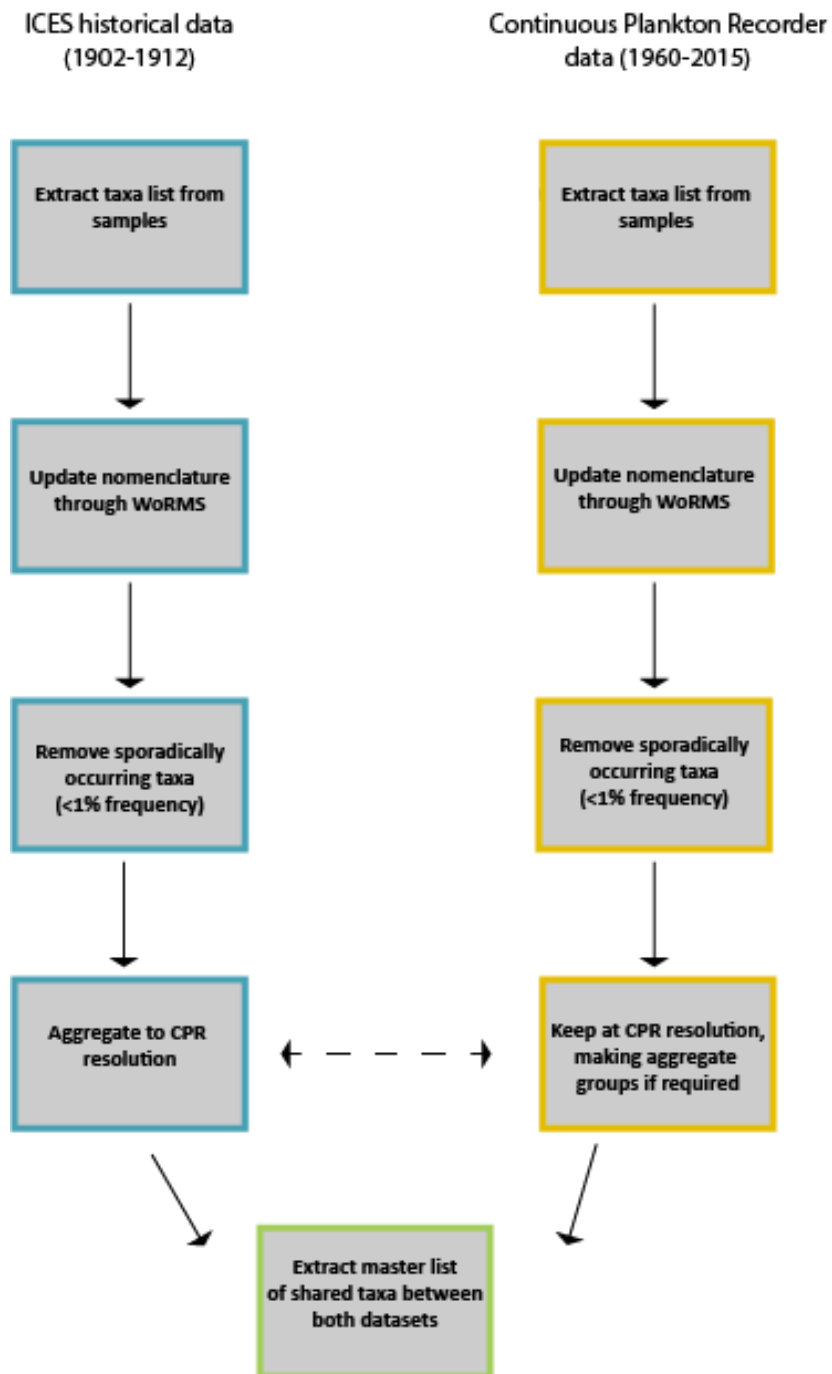


Figure 2.2 Data management workflow for integrating the CPR dataset with the ICES historical plankton dataset.

Table 2.1. 'Matching' taxa lists, at aggregated taxonomic resolution, used in analysis

Phytoplankton Matching List	Zooplankton Matching List	
Diatoms		Holoplankton
<i>Asterionellopsis glacialis</i>	<i>Navicula spp.</i>	<i>Acartia spp.</i>
<i>Bacillaria paxillifera</i>	<i>Odontella aurita</i>	<i>Anomalocera patersoni</i>
<i>Bacteriastrium spp.</i>	<i>Odontella sinensis</i>	<i>Appendicularia spp.</i>
<i>Bellerocha horoglacialis</i>	<i>Paralia sulcata</i>	<i>Calanus spp.</i>
<i>Ceratoneis closterium</i>	<i>Proboscia alata</i>	<i>Centropages spp.</i>
<i>Chaetoceros spp.</i>	<i>Pseudo-nitzschia delicatissima</i>	<i>Centropages hamatus</i>
<i>Corethron spp.</i>	<i>Pseudo-nitzschia seriata</i>	<i>Centropages typicus</i>
<i>Coscinodiscus spp.</i>	<i>Rhaphoneis amphiceros</i>	<i>Chaetognatha spp.</i>
<i>Coscinodiscus concinnus</i>	<i>Rhizosolenia hebetata f.semispina</i>	<i>Copepoda spp.</i>
<i>Ditylum brightwellii</i>	<i>Rhizosolenia setigera</i>	<i>Corycaeus spp.</i>
<i>Eucampia zodiacus</i>	<i>Rhizosolenia styliformis</i>	<i>Euphausiacea spp. and Mysida spp.</i>
<i>Fragilaria</i>	<i>Skeletonema costatum</i>	<i>Evadne spp.</i>
<i>Guinardia delicatula</i>	<i>Thalassionema spp.</i>	<i>Foraminifera spp.</i>
<i>Guinardia striata</i>	<i>Thalassiosira spp.</i>	<i>Isias clavipes</i>
<i>Halosphaera spp.</i>	<i>Thalassiothrix longissima</i>	<i>Labidocera wollastoni</i>
<i>Lauderia danicus</i>		<i>Metridia lucens lucens</i>
Dinoflagellates, silicoflagellates and haptophytes		Meroplankton
<i>Ceratium fusus</i>	<i>Tripes furca</i>	<i>Bivalvia spp.</i>
<i>Ceratium horridum</i>	<i>Tripes lineatus</i>	<i>Bryozoa spp.</i>
<i>Ceratium tripos</i>	<i>Tripes longipes</i>	<i>Cirripedia spp.</i>
<i>Dictyochophyceae</i>	<i>Tripes macroceros</i>	<i>Decapoda spp.</i>
<i>Dinophysis spp.</i>		<i>Echinodermata spp.</i>
<i>Gonyaulax</i>		<i>Pisces spp.</i>
<i>Phaeocystis</i>		<i>Polychaeta spp.</i>
<i>Prorocentrum spp.</i>		
<i>Protoperidinium spp.</i>		

2.2.3 Multivariate analysis

To investigate whether significant change occurred in the plankton community between the ICES historical time-period and the beginning of the time-period covered by the CPR survey, I tested for an effect of time period (historical dataset, 1902-1912, to the 1960s decade of the CPR time period) on plankton community composition using multivariate generalised linear models with the '*mvabund*' package in R (Wang et al., 2012). This method fits a generalised linear model to each taxon separately, and then gives a summed likelihood ratio for the given predictors for each model, which can be used as a test statistic ('Sum-of-LR') for the effect of predictors on the community as a whole. Resampling is then done at the whole-sample level (here the sampling month) to test for significance while accounting for correlations between taxa (Wang et al., 2012). The method accounts for a mean-variance relationship in the data (Warton et al., 2012). The generalised linear models were fitted for the occurrence frequency of each taxa in each sampling month, with a complementary log-log link to accommodate the proportional, binomial data (Wang et al., 2012). For each model, the log of the sampling month occurrence frequency total was used as an offset as an approximate method of analysing relative compositional change, and weights were included so that sampling months with higher sample sizes were given stronger weighting. I extracted the univariate statistics for each taxon in the model, to examine the contribution of each taxon to any overall effect.

Furthermore, I visualised change in the plankton community over the extended time period using non-metric Multidimensional Scaling (nMDS) ordination plots. Plots were constructed for each area and plankton type using the *vegan* package in R (Oksanen et

al., 2007). These were constructed based on the relative occurrence frequency of each of the matching list taxa in each sampling month.

After testing for the effect of time period on community composition, I tested whether SST difference between the two periods could explain any observed differences in community composition using multivariate generalised linear models. Here, models including SST were compared to models including SST and time-period, as a significant effect of time-period over and above SST suggests there is variation between the time-periods not explained by changes in SST alone. Lastly, I tested for any overall effect of SST on plankton community composition, over the whole extended time period, when examining the two datasets combined. Models with SST and season as predictors were compared against models with just season as a predictor to look for the influence over and above seasonality.

2.3 Results

2.3.1 Changes in plankton community composition over time

Significant differences in overall community composition were found for both phytoplankton and zooplankton in both the Northern and Central/Southern North Sea areas, suggesting a change in the North Sea plankton community between the beginning of the 20th century and the 1960s. The zooplankton communities showed a stronger overall difference, with larger overall summed likelihood ratios for an effect of time period, despite a lower number of taxa within the list of shared common taxa. In contrast, the overall effect of time period, although significant, was lower for phytoplankton communities, suggesting a smaller community change (Table 2.2)

Table 2.2 Plankton community responses to dataset (time-period). Taxa contributing >20% of overall community effect are listed (+/- = increase/decrease in occurrence frequency, *= significant p <0.05).

Plankton community	Overall community response to time-period		Taxa contributing >20% of community variation between time periods
	Sum-of-LR	p	
Northern NS phytoplankton	299.44	<0.01	<i>Protoperdinium</i> -
Central/Southern NS phytoplankton	825.65	<0.01	<i>Guinardia striata</i> -
Northern NS zooplankton	1891.3	<0.01	<i>Tintinnidae</i> * -
Central/Southern NS zooplankton	2355.5	<0.01	<i>Euphausiacea and Mysida</i> +

However, when extracting the individual contributions of each taxon to the overall community response, a low number of taxa in all communities showed significant contributions to overall community responses. Furthermore, the overall community responses were largely dominated by a low number of taxa. For example, in each community over 20% of the variation was driven by one individual taxon (Table 2.2), which showed changes in relative occurrence frequency in all months. These were *Protoperdinium* (a heterotrophic group) and *Tintinnidae* in the Northern North Sea

area for phytoplankton and zooplankton communities respectively, which showed declines. In the Central/Southern North Sea area *Guinardia striata* showed a decline, whilst 'Euphausiacea and *Mysida*' showed an increase. Out of these taxa, only the decline in *Tintinnidae* in the Northern North Sea was a statistically significant contribution to community change. Other taxa showing large contributions to overall effect were *Dinophysis* within the Northern North Sea phytoplankton community, and *Anomalocera patersoni* within the Northern North Sea zooplankton community, both of which showed a decline, although the decline in *Dinophysis* was not a statistically significant contribution to community change. Aside from these particular taxa, the overall community change between the beginning of the 20th century and the 1960s was distributed relatively evenly between the taxa, suggesting a holistic community change between the two time periods.

As sampling biases between the datasets, such as varying mesh sizes, may have influenced the taxa that had disproportionate contributions to overall community change, I removed taxa contributing over 20% of variation between time periods before visualising community composition over the extended time period using nMDS plots (Figure 2.3). This was to avoid identifying what appears to be a holistic community change but is actually dominated by these individual taxa. There was also a lack of an immediate ecological explanation as to why these taxa would show such large contributions to community change. 'May 1912' was removed due to being highly anomalous. Here, the stronger effect of time-period on zooplankton composition can be seen with a clearer distinction between the historical (1902-1912) decade and the 1960s. Furthermore, there is a clearer distinction between the 1960s and the 2000s within the zooplankton plots, especially for the Central/Southern North

Sea, suggesting phytoplankton to be more stable in terms of change in community composition over multi-decadal scales.

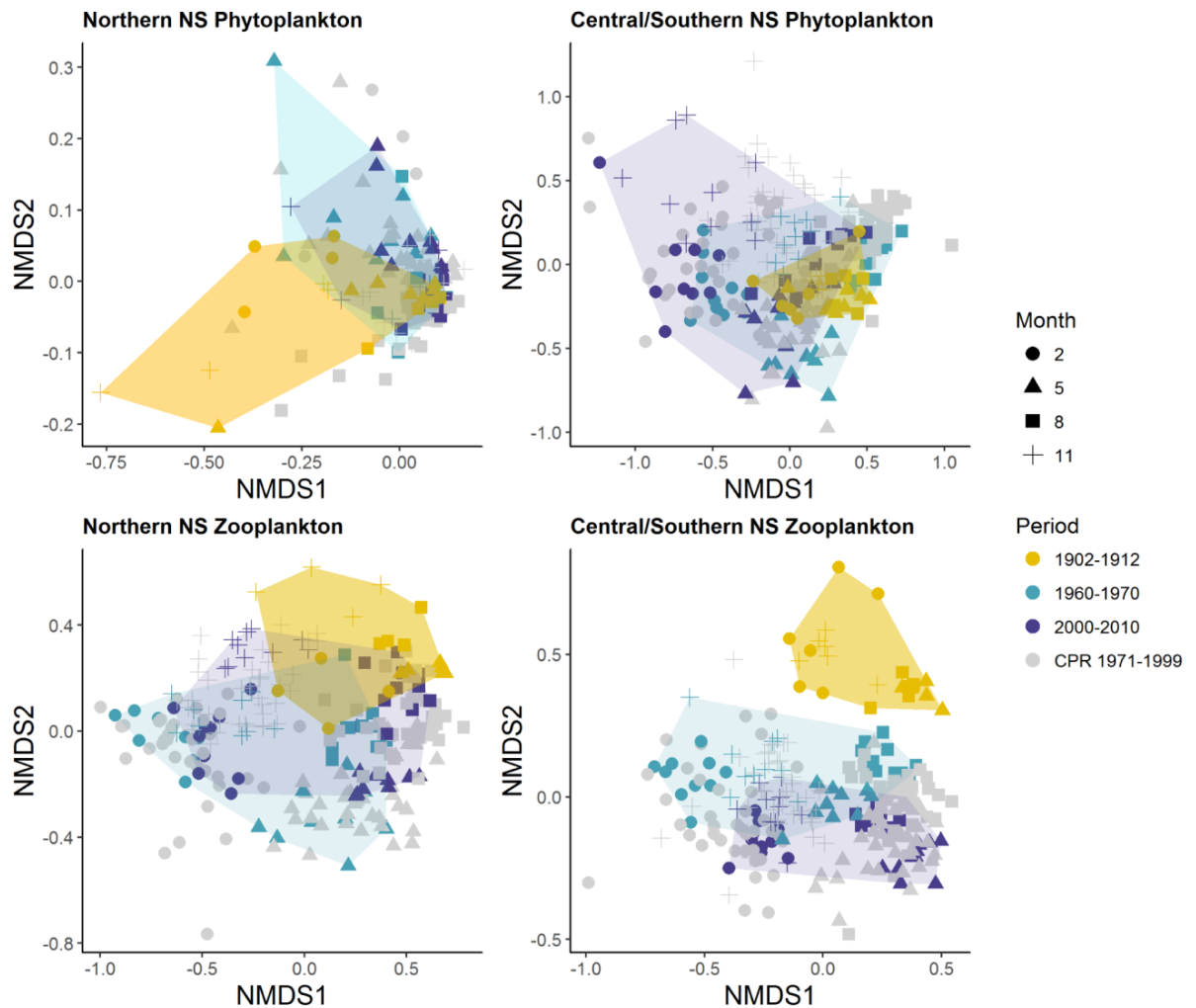


Figure 2.3. nMDS plots using Bray Curtis dissimilarity, based on monthly occurrence frequency of the matching list taxa in each North Sea region. Data points from the ICES historical dataset (1902-1912) are shown in orange and are bound by orange polygon (convex hull). $K=3$ for all except Northern NS zooplankton, where $k=4$ to lower stress. Data points from 1971-1999 from the CPR survey are shown in grey, with data from the 1960s shown in blue and bounded by blue polygon. Data from the 2000s decade are in purple and bounded by purple polygon, for additional context.

2.3.2 Influence of SST change on plankton communities

Taxa contributing over 20% of between-dataset variation were still omitted when analysing the effect of SST on plankton community composition, to ensure any effects of SST found on the overall community were not being driven solely by this small proportion of taxa. SST has increased in both the Northern and Central/Southern North Sea areas and particularly sharp increases occurred during the late 1920s and 1980s (Figure 2.4). The average annual SST for the ICES historical time period (1902-1912) was 9.00 °C for the Northern North Sea area, rising to 9.53 °C in the 1960s. In the Central/Southern North Sea area, the average SST for the ICES historical time period was 9.59 °C, rising to 9.86 °C in the 1960s.

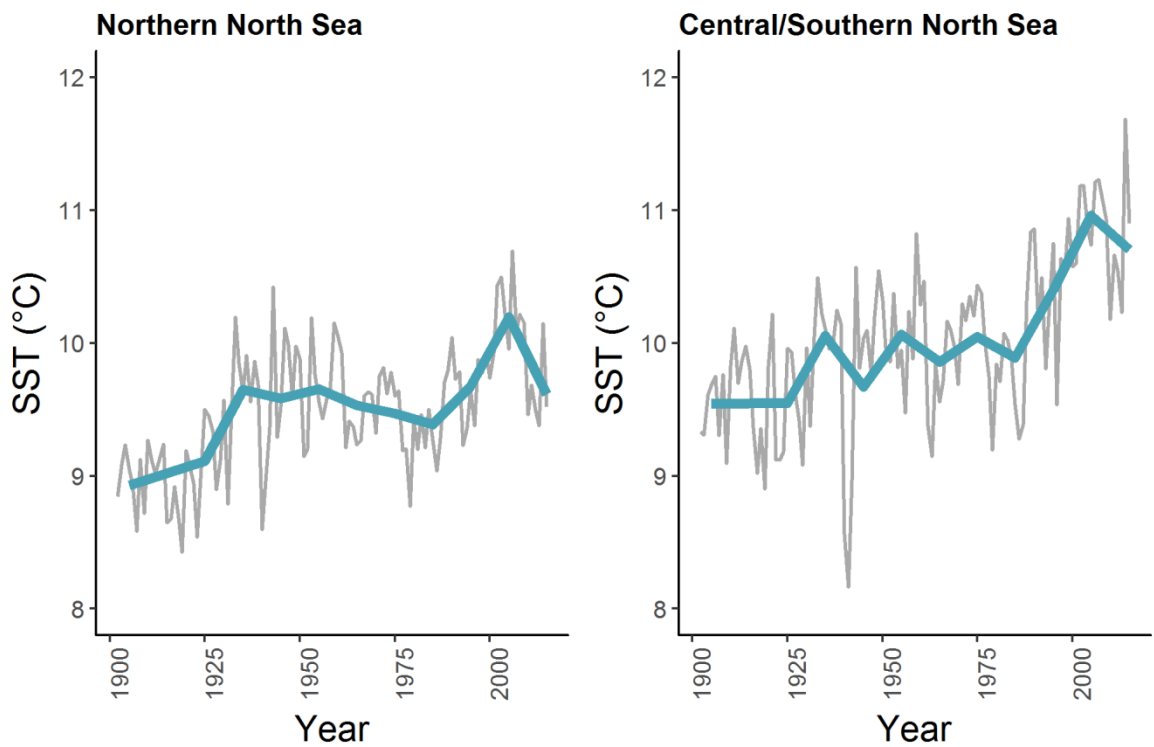


Figure 2.4. North Sea SST variation between 1902 and 2015. Annual data are in grey and the 5 year mean is in blue.

Differences in SST between the time periods suggest that changes observed in overall plankton community composition between 1902-1912 and the 1960s coincided with changes in environmental conditions within the North Sea. I tested this further using multivariate generalised linear models; a significant effect of time-period over and above SST suggests there is variation between the time-periods not explained by changes in SST alone. A significant effect of time period over and above SST was found only in the Central/Southern North Sea phytoplankton community ($p=0.023$), suggesting variation between time-periods could not be explained by SST change only in this community. In the Northern North Sea zooplankton and phytoplankton

communities, as well as the Central/Southern zooplankton community there was no significant effect, suggesting variation could be linked to large-scale SST change.

When then using both the ICES historical dataset and the full temporal extent of the CPR dataset together, giving an extended temporal coverage, I found significant effects of SST on phytoplankton and zooplankton communities in both the Northern and Central/Southern North Sea areas (Table 2.3). SST had a greater influence in the Central/Southern North Sea than the Northern North Sea area on both phytoplankton and zooplankton composition, and a larger influence on zooplankton than phytoplankton overall. No phytoplankton taxa showed individual significant contribution to overall community response. In contrast, there were multiple individual significant contributions to the overall response within zooplankton communities, with the most number of significant individual contributions shown in the Central/Southern North Sea. These included both meroplankton and holoplankton taxa, with the largest contributions to overall community response from *Centropages typicus* and the multi-species group *Bivalvia*. *Centropages typicus* showed an increase in relative occurrence frequency over time, whilst *Bivalvia* showed a decrease in relative occurrence frequency over time, coinciding with increasing annual SST (Figure 2.5).

Table 2.3. Plankton community responses to SST when examining both datasets combined (1902-1912, 1958-2015). Sum-of-LR= Summed likelihood ratio.

Plankton community	Overall community response to SST		Taxa with significant contributions to community response to SST over the extended time period
	Sum-of-LR	p	
Northern NS phytoplankton	195.7	0.044	N/A
Central/Southern NS phytoplankton	542.86	<0.001	N/A
Northern NS zooplankton	669.94	<0.001	<i>Anomalocera patersoni</i> <i>Decapoda spp.</i> <i>Echinodermata spp.</i>
Central/Southern NS zooplankton	1999.7	<0.001	<i>Bivalvia</i> <i>Calanus spp.</i> <i>Centropages typicus</i> <i>Corycaeus spp.</i> <i>Decapoda spp.</i> <i>Oithona spp.</i> <i>Para-Pseudocalanus spp.</i> <i>Polychaeta spp.</i>

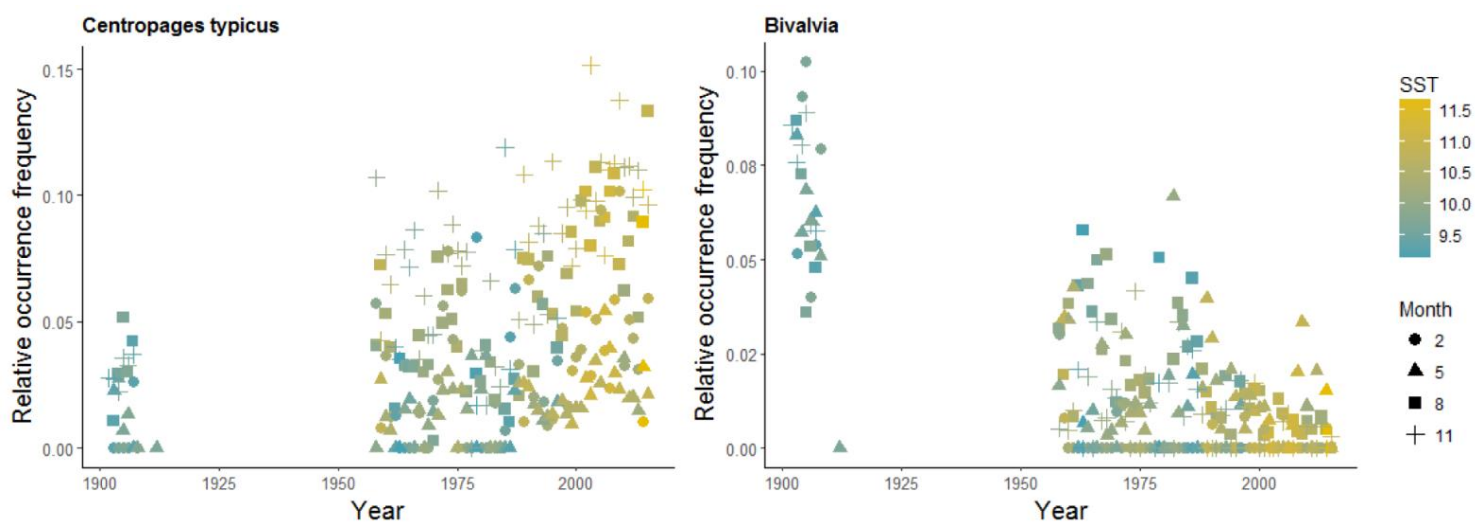


Figure 2.5. A) Occurrence frequency of *Centropages typicus* by month from wider time-period. B) Occurrence frequency of *Bivalvia* by months for wider time-period.

Although overall community composition change between 1902-1912 and the 1960s may be linked to changes in SST, taxa that had the largest univariate contributions to community change did not necessarily have large responses to SST across the wider time period (1902-1912, 1958-2015). This suggests that although a change in temperature conditions may have contributed to the overall community response, it does not necessarily explain individual taxon changes between the two time periods. Furthermore, any potential influences of specific environmental drivers on community composition differences between the two time-periods may be at least partially obscured by the differences in sampling and analysis methodologies between the two datasets used, and the low quantitative resolution available.

2.4 Discussion

Here, I have demonstrated the value of 'rescued' historical plankton data in increasing the temporal scale of understanding community change. By harmonising the taxonomic lists from the two datasets in order to ensure comparability and then further selecting a subset of shared, common taxa based on a 1% occurrence frequency threshold, and using presence/absence semi-quantitative resolution, I have reduced the influence of disparate sampling and analysis methodologies. Results suggest that the 1960s had a significantly different plankton community composition compared to the early 1900s, indicated by variation in the relative occurrence frequency of shared common taxa. Differences in community composition between time periods were largely driven by a small number of taxa. The remaining effect was shared relatively evenly between the remaining taxa, suggesting the overall significant changes in community composition are a result of subtle change across the taxa list, with individual taxa having mainly non-significant contributions to overall community response.

Zooplankton communities showed a greater difference between the ICES historical time period and the 1960s decade of the CPR time period than phytoplankton communities. The nMDS plots also revealed clearer visual distinctions between the 1960s decade and the 2000s decade within the zooplankton communities than within the phytoplankton communities. This suggests that although differences between the time periods were found within phytoplankton communities, over the whole time period the phytoplankton community showed less directional change in community composition at the multi-decadal scale than zooplankton communities. A similar result

was found during the OSPAR (Oslo-Paris Convention for the Protection of the North-East Atlantic) Intermediate Assessment 2017, where larger changes in indicators of zooplankton community structure were found compared to phytoplankton communities (OSPAR, 2017a). This assessment result could therefore be representative of multi-decadal patterns of variation occurring at the century-scale.

Furthermore, I found that the plankton community change identified between 1902 - 1912 and the 1960s could be explained through changes in SST in Central/Southern North Sea zooplankton and Northern North Sea phytoplankton and zooplankton, suggesting a correlation between community changes and increasing Sea Surface Temperature. These community changes coinciding with increasing SST may therefore be attributed to a regime shift that has been shown to have occurred in the North Atlantic during the 1920s and 1930s, which is argued to be the largest and most significant climate-induced regime shift of the 20th century (Drinkwater, 2006), and which is associated with increases in SST. Furthermore, change in the Central/Southern North Sea phytoplankton community could not be explained by SST change. It is likely, therefore, that finer scale changes, in variables other than SST, drove the change in the Central/Southern North Sea phytoplankton community. The influence of oceanographic and climatic variables other than SST on plankton community composition in the North Sea is explored in chapter 4.

Hällfors et al. (2013) similarly described an unknown 'period effect' between the ICES historical time period and contemporary phytoplankton samples in the Baltic Sea, where variation could not be explained by environmental change alone, and instead they hypothesise a potential signal of eutrophication in the change observed. In the North Sea, changes in nutrient inputs due to variation in Atlantic inflow, as well as

anthropogenic nutrient pollution also affect the overall nutrient balance, and changes in nutrient inputs over time, which have not been explicitly explored here, could also potentially contribute to the changes in plankton communities observed (Vermaat et al., 2008). The full potential impacts of coastal eutrophication from land sources have not been fully explored here as the CPR survey does not sample very inshore regions. Previous research, as well as OSPAR eutrophication assessments, have suggested that eutrophication in the North Sea is primarily restricted to coastal regions, and is not a driver of phytoplankton dynamics in the open sea (McQuatters-Gollop et al., 2009; OSPAR, 2017h). Furthermore, the potential influence of atmospheric deposition of nutrients on the community changes observed in this study has not been explored here. Atmospheric nitrogen deposition contributes up to 16% of total nitrogen in the North Sea, and has been shown to provide enough nitrogen to support enhanced coastal phytoplankton growth under certain meteorological conditions (Spokes and Jickells, 2005; Troost et al., 2013). The degree to which it causes changes in phytoplankton community composition in open sea regions, however, is a knowledge gap, but any impacts are unlikely to manifest themselves at the coarse quantitative resolution of this study. Furthermore, although I am confident that differences in taxonomic nomenclature and resolution are not driving any patterns observed, I cannot rule out an influence of the low quantitative resolution resulting from sampling and analysis biases, especially for those taxa showing disproportionate contributions (e.g. >20%) to the overall community response.

Integrating the CPR survey with the ICES historical data facilitated exploration of the influence of warming SSTs on multidecadal plankton community change at the century-scale, although focusing on occurrence frequency, rather than abundance

values. Over the extended time period (1902-1912, 1958-2015), SST had a stronger influence on zooplankton communities than phytoplankton, in both the Northern and Central/Southern North Sea areas. In particular, it is known that temperature is an important structural variable for zooplankton communities and is a key determinant of the limits to distributions (Richardson, 2008). In contrast, although SST was a significant driver of community composition in phytoplankton in both the Northern and Central/Southern North Sea, no single taxa showed significant contributions to the overall community effect. Previous studies have suggested the importance of physical variables other than SST directly influencing phytoplankton community composition including salinity and wind stress (Hinder et al., 2012).

Multiple zooplankton taxa in the Central/Southern North Sea area showed significant univariate responses to SST change, with *Centropages typicus* and the multi-species group *Bivalvia* showing the largest responses. A positive association between the abundance of *Centropages typicus* and SST has previously been identified in the North Sea (Lindley and Reid, 2002), and this pattern is also shown here when examining the CPR time-series at a presence/absence resolution. The lack of a large difference in relative occurrence frequency between the beginning of the 20th century and the 1960s found here however suggests that the response of *Centropages typicus* to SST occurred since the 1960s. In contrast, the larger difference in the occurrence frequency of *Bivalvia* found here between the beginning of the 20th century and the 1960s suggests the decline in the abundance of bivalve larvae previously identified in the North Sea (Kirby et al., 2008) occurred over a longer time scale. Kirby et al. hypothesise that the long-term decline in bivalve larvae found through the CPR survey is a result of predation from increasing abundance of decapod larvae, also observed

through the CPR survey, and the increase in decapod larvae is associated with increasing SST (Lindley et al., 2010). In this study, decapod larvae in the Central/Southern North Sea had a significant response to SST, and increased in relative occurrence between 1902-1912 and the 1960s, suggesting that trophic amplification of a climate signal could explain the decrease in bivalve larvae also at the century scale. The differences in whether the taxa with strong overall responses to SST also showed large differences in occurrence frequency between time periods suggests that the temporal scale of responses to SST change, and temporal scale of baseline shifts, is variable between individual taxa.

2.4.1 Conclusions

Through integrating and directly comparing the CPR dataset to the ICES historical database, important considerations have been identified for using disparate plankton datasets together, with applications for large scale assessment and integrated monitoring programmes, such as regional scale assessments undertaken at the OSPAR level (OSPAR 2017). Particularly, zooplankton taxa varied greatly in the taxonomic resolution in which they were recorded between surveys, and much attention needs to be drawn to this when designing integrated monitoring programmes constructed from different surveys. However, I have shown that a subset list of shared common taxa can inform on community change when combining data from disparate sources. Furthermore, occurrence frequency seems to be a relevant proxy for abundance, when abundance data is non-comparable, for example occurrence frequency resolution still revealed strong seasonality signals. As sampling and analysis biases cannot ever be fully reconciled in contemporary comparisons of rescued historical datasets, such as

varying mesh sizes, often resulting in low quantitative resolution, I suggest that 'rescued' historical datasets can be useful as an additional contextual tool for understanding climate change effects on plankton communities, but caution should be employed when using disparate historical datasets as robust evidence bases on their own.

A stable historical baseline may be hard to define in the North Sea, as the plankton communities vary on inter-annual, multi-decadal and, suggested here, century-wide scales in response to environmental change. Phytoplankton community composition may show less directional change in community composition, in terms of the relative occurrence frequency of common taxa, over multi decadal time scales than zooplankton communities. Although statistically significant changes were observed in particular individual taxa between time periods, and across the wider time-series in response to SST, this does not necessarily inform on the ecological significance of changes. When formally assessing change in North Sea plankton communities under policy drivers, it is important to consider the functional consequences of community change, as well as the century-scale shifts in community composition baselines.

Chapter 3

Understanding temporal Beta Diversity
of North Sea plankton communities for
regional assessments of pelagic habitat
status

Chapter 3 : Understanding temporal Beta Diversity of North Sea plankton communities for regional assessments of pelagic habitat status

3.1 Introduction

Monitoring of marine biodiversity underpins the achievement of healthy marine ecosystems, by ensuring that their management can be flexible, adaptive and effective (Addison et al., 2017). Across European seas, cumulative pressures from human activities, along with underlying large scale climate change, are causing changes in marine biodiversity that are being addressed through both local and regional scale management frameworks (Apitz et al., 2006; Berg et al., 2015). Focusing at a regional scale, the European Union (EU) Marine Strategy Framework Directive (MSFD) incorporates biodiversity status into ecosystem-based management strategies, where different components of the marine ecosystem are formally monitored and assessed against targets representing 'Good Environmental Status' (Zampoukas et al., 2013). As the base of the marine pelagic food web, plankton communities form one of the key components of these biodiversity assessments, and are used to assess the status of 'pelagic habitats'. Indicators of plankton community structure have been selected for formal assessment (i.e. for use in biodiversity state reporting under the MSFD), which can detect change in the structure and function of plankton communities, from a temporal reference period (McQuatters-Gollop et al., 2017). Deviations in indicator values away from these reference periods can then be detected, providing an initial flag of whether pelagic habitats may have moved away from Good Environmental Status.

Plankton communities are highly dynamic and naturally variable at seasonal, inter-annual, and multidecadal time scales, providing technical challenges to assessing pelagic habitat status under the MSFD by obscuring the detection of effects of direct anthropogenic pressures such as nutrient pollution (McQuatters-Gollop, 2012). This inherent variability in plankton community composition has been attributed to variation in environmental conditions (Hátún et al., 2009), as well as biotic interactions and 'chaos in the plankton' (Barton et al., 2015). Similarly, variability between points within a time-series can also be caused by directional turnover in community composition so that points that are further apart in time are more different to each other than points closer in time (Collins et al., 2000; Dornelas et al., 2014; Legendre and Cáceres, 2013). Magurran et al. (2010) highlight that such 'turnover' in composition is an inherent feature of biological communities; biodiversity can change through time in the absence of human pressures.

A first challenge that variability in plankton community composition provides to formal assessments of pelagic habitats is in the selection of appropriate reference conditions from which to assess indicator change. For example, reference periods can be a defined period of time within a time-series, which are used as reference conditions to show trajectories in indicator change (Scherer et al., 2016; Tett et al., 2008). A period of time which is atypical of wider community composition would arguably be inappropriate as a reference period, as it is not representative of the most common community structure within the time-series. A second challenge is that an indicator value may show a change from a reference period as a result of community variability, or underlying turnover, rather than a result of anthropogenic pressure. Furthermore, under the MSFD, changes in indicators linked to climatic and oceanographic variability, termed 'prevailing conditions' by the Directive, are considered outside of the scope of

management. Variation in plankton community composition caused by variation in these 'prevailing conditions' therefore also can cause indicator values to change, and these drivers need to be separated from any signals of direct anthropogenic pressures (McQuatters-Gollop, 2012).

The total variability in community composition over time can be measured as the Beta Diversity of points within a time-series (Legendre and Gauthier, 2014). Plankton time-series with high temporal Beta Diversity have higher levels of uniqueness between points in the time-series, whereas plankton communities with lower temporal Beta Diversity are relatively more stable. The level of uniqueness of each time point in a time-series can be measured by partitioning the total Beta Diversity into the individual 'Local Contribution to Beta Diversity (LCBD)' that each point in the time-series makes. Time points with high LCBD values are more unique in terms of community composition compared to time points with low LCBD values, which are more typical of wider community composition (Legendre and Cáceres, 2013).

As well as being useful to quantify patterns of variability in plankton communities, LCBD indices can themselves make valuable biodiversity state indicators for ecosystem assessments (Hillebrand et al., 2018). Due to the differing sensitivities of plankton taxa to anthropogenic pressures, changes in the taxonomic composition, relative abundances and dominance rankings of communities can indicate a potential anthropogenic pressure on pelagic habitats (Flöder et al., 2010; Magurran and Henderson, 2010). Therefore, a year within a time-series that has a unique plankton composition compared to the wider time-series (a high LCBD value) may represent a change in pelagic habitat status, and may be an indication of anthropogenic perturbation. As such, a pilot assessment of plankton LCBD indices was included in the

OSPAR Intermediate Assessment of North East Atlantic biodiversity indicators (OSPAR, 2017f).

Here, I first quantify temporal Beta Diversity in plankton community composition over multidecadal time scales in the North Sea, assess the degree to which Beta Diversity is caused by directional turnover in community composition, and identify the taxa that exhibit the most variability through time. By then calculating the individual Local Contributions to Beta Diversity for each year in the multi-decadal time series, atypical communities in time can be identified and related to potential environmental drivers. I aim to use an understanding of temporal Beta Diversity and time-series of LCBD indices in the North Sea to:

- 1. Evaluate different options for the setting of appropriate reference periods for indicator assessments**
- 2. Assess whether prevailing conditions can explain the presence of atypical plankton communities over multi-decadal time scales.**

3.2 Materials and Methods

3.2.1 Plankton community data

Plankton community data were obtained from the Continuous Plankton Recorder (CPR) survey. The CPR survey has been collecting samples in the North Sea on a routine, consistent basis since 1958. CPRs consist of a filtering mechanism housed in an external body that is towed behind ships of opportunity at a depth of approximately 7-

10m, with each sample representing approximately 10 nautical miles (18.5km) of tow, and approximately 3m³ of sea (Batten et al., 2003). Both phytoplankton and zooplankton data are then enumerated on a semi-quantitative scale (Richardson et al., 2006). Records of species from a species list compiled to assess the North Sea at the OSPAR level (OSPAR, 2017a) were extracted from the OSPAR Greater North Sea area (Figure 3.1).

Geographical subsets of plankton samples were compiled following methodology used in the OSPAR Intermediate Assessment (2017) for assessment of pelagic habitats in the OSPAR Greater North Sea (which includes the channel). Based on a model of stratification regimes by van Leeuwen et al. (2015), the North Sea is divided into different 'Ecohydrodynamic Zones' (EHDZs): 'permanently stratified', 'seasonally stratified', 'permanently mixed', 'intermittently stratified' or 'indeterminate'. Plankton samples were extracted from each EHDZ, but 'indeterminate' areas were not included in this analysis (Figure 3.1).

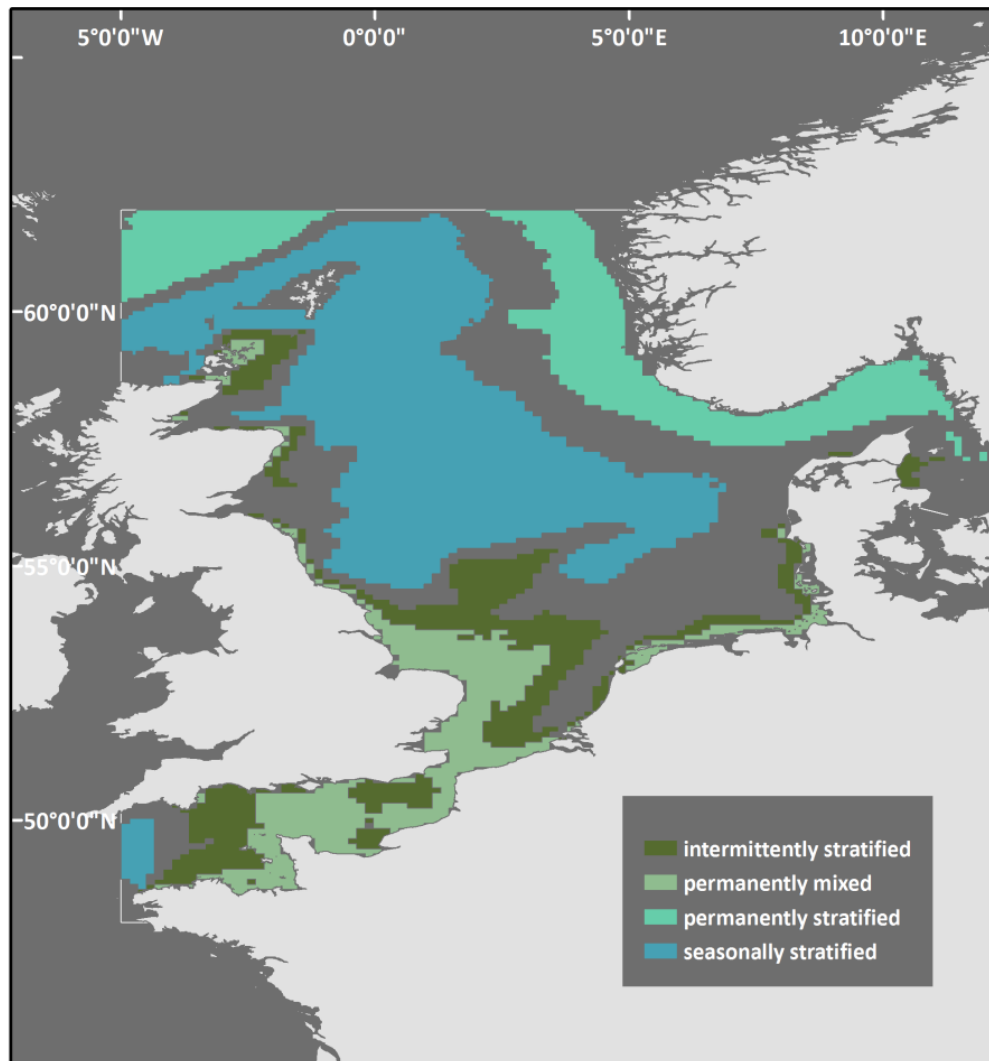


Figure 3.1. Ecohydrodynamic zones within the OSPAR Greater North Sea region, based on stratification regimes, identified by van Leeuwen et al. (2015).

3.2.2 Oceanographic variables

Monthly Sea Surface Temperature (SST) and Scalar Wind Speed (SWS) data were downloaded for the Greater North Sea area from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) at a 1 degree resolution from 1960 to 2015 (Woodruff et al., 1987). Data points were extracted from each EHDZ and the annual mean calculated for each year in the time-series. Surface salinity data were obtained from the ICES Oceanographic Data Portal (<http://www.ices.dk/marine-data/data-portals/Pages/ocean.aspx>) and monthly means were calculated before being aggregated to annual means for 1960-2015, for each EHDZ. Lastly, data on the Winter North Atlantic Oscillation (WNAO) were obtained from the Hurrell Centre (<https://climatedataguide.uca.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>), which is calculated from December-March.

3.3 Data analysis

3.3.1 Total Beta Diversity

Total Beta Diversity of both phytoplankton and zooplankton communities was calculated for each EHDZ, following Legendre and Cáceres (2013) Total Beta Diversity (BD_{Total}) under this method is calculated as the total variance of the year-by-species community data, so is calculated without reference to alpha and gamma diversity as in other metrics of Beta Diversity (Anderson et al., 2011). A matrix of squared deviations from species means is calculated for each year for each species, so that if the

abundance of a particular species is the same in all years, the values for that species are zero in each year. The total of these squared deviations are then summed across the species-by-year abundance data (SS_{Total}). BD_{Total} is then calculated as $(SS_{\text{Total}}/(n-1))$, where n refers to the number of years. The $\log_{10}(x+1)$ plankton abundance data were chord transformed prior to analysis to make the data suitable for Beta Diversity analysis and to not put a large emphasis on rare species (Legendre and Borcard, 2018; Legendre and Gallagher, 2001). Total Beta Diversity analyses were undertaken using the `beta.div` function in the R package '*adespatial*' (Dray et al., 2016). Further analyses were then focused on the areas showing the highest BD_{Total} for phytoplankton and zooplankton respectively.

I then further decomposed this total Temporal Beta Diversity by identifying the taxa that contribute the most to total community variability across the time-series. For each plankton community time-series, I identified the Species Contributions to Beta Diversity (SCBD) for each taxon, with species with high SCBD values showing the highest variation across the time-series, i.e. the highest contributions to BD_{Total} . SCBD indices for each taxa included in the community analysis were calculated using the '*adespatial*' R package.

3.3.2 Local Contributions to Beta Diversity

Total Beta Diversity was then partitioned into the contribution of each individual year to the BD_{Total} , referred to as the Local Contribution to Beta Diversity (LCBD); years with high LCBD indices were atypical compared to wider community composition. LCBD indices were tested for significance through permutation testing. The time-series was then divided into data pre-1985 and post-1990, to split the time-series into 'pre 1980s regime shift' and 'post 1980s regime shift', which was centred around 1988 (Reid et al.,

2015). This facilitated the investigation of the effect of temporal scale on which years are identified as unique or anomalous, compared to time-series data of varying length. Stepwise multiple regression was then used to determine which environmental variables could best explain variation in annual LCBD values, based on minimising the Akaike Information Criterion (AIC). To then further investigate environmental drivers of LCBD variation, I also used Granger causality tests, where lagged environmental variables are used to predict future LCBD indices, over and above lagged LCBD indices, thus adjusting for temporal autocorrelation and testing for potential lags in the effects of environmental drivers on plankton communities.

3.4 Results

3.4.1 Total Beta Diversity

The Total Beta Diversity (BD_{Total}) of plankton communities quantifies the variability in community composition. Following methodology outlined in (Legendre and Cáceres, 2013), using chord transformed data a BD_{Total} value of 1 means that each point in the time-series has a unique community composition. For phytoplankton communities, the permanently mixed EHDZ had the highest BD_{Total} value (0.32), whereas the seasonally stratified area had the lowest BD_{Total} (0.14), suggesting that areas that are permanently mixed are less stable in community composition than the other areas, and particularly less stable than areas with seasonal stratification patterns. For zooplankton communities, the permanently stratified EHDZ had the highest BD_{Total} value (0.14), whereas the intermittently stratified area had the lowest BD_{Total} value (0.06), suggesting this area to be the most stable in terms of community composition. Subsequent analyses focused on phytoplankton in permanently mixed areas, and

zooplankton in permanently stratified areas, as these areas had the highest BD_{Total} values.

The species contributing most to BD_{Total} were then calculated, giving the individual Species Contributions to Beta Diversity for each taxon, and the taxa were then ranked based on their individual SCBD values. For the phytoplankton community in permanently mixed areas, *Thalassiosira.sp* had the largest SCBD (0.106), followed by *Ceratium fusus* (0.078) and *Ceratium furca* (0.073). *Thalassiosira.sp* and *Ceratium fusus* have previously been identified as taxa that most frequently form exceptional blooms in the North Sea/ (Reid et al., 1987). For zooplankton in permanently stratified areas, *Calanus finmarchicus* had the highest SCBD value (0.132), followed by Echinoderm larvae (a multi-species group, 0.105) and *Calanus helgolandicus* (0.077).

3.4.2 Local Contributions to Beta Diversity

The BD_{Total} for each community was then partitioned into the individual contributions of each point in the time-series, or the Local Contributions to Beta Diversity. Here, I focus analysis on the Local Contributions to Beta Diversity (LCBD) for the areas that had the largest BD_{Total} values, which were the permanently mixed and permanently stratified areas for phytoplankton and zooplankton, respectively. When examining the full time-series (1960-2015) for phytoplankton in permanently mixed areas (Figure 3.2), the years 1972, 1978,1979,1980,1982 and 1990 had significant LCBD values, meaning they had relatively unique community compositions in comparison to wider temporal variability. When repeating the LCBD analysis on only years before the 1980s regime shift (<1985), the year 1972 no longer showed a significant contribution. Post-regime shift, the years

1995 and 1996 showed a significant LCBD value, which did not show a significant local contribution when comparing against the full time-series.

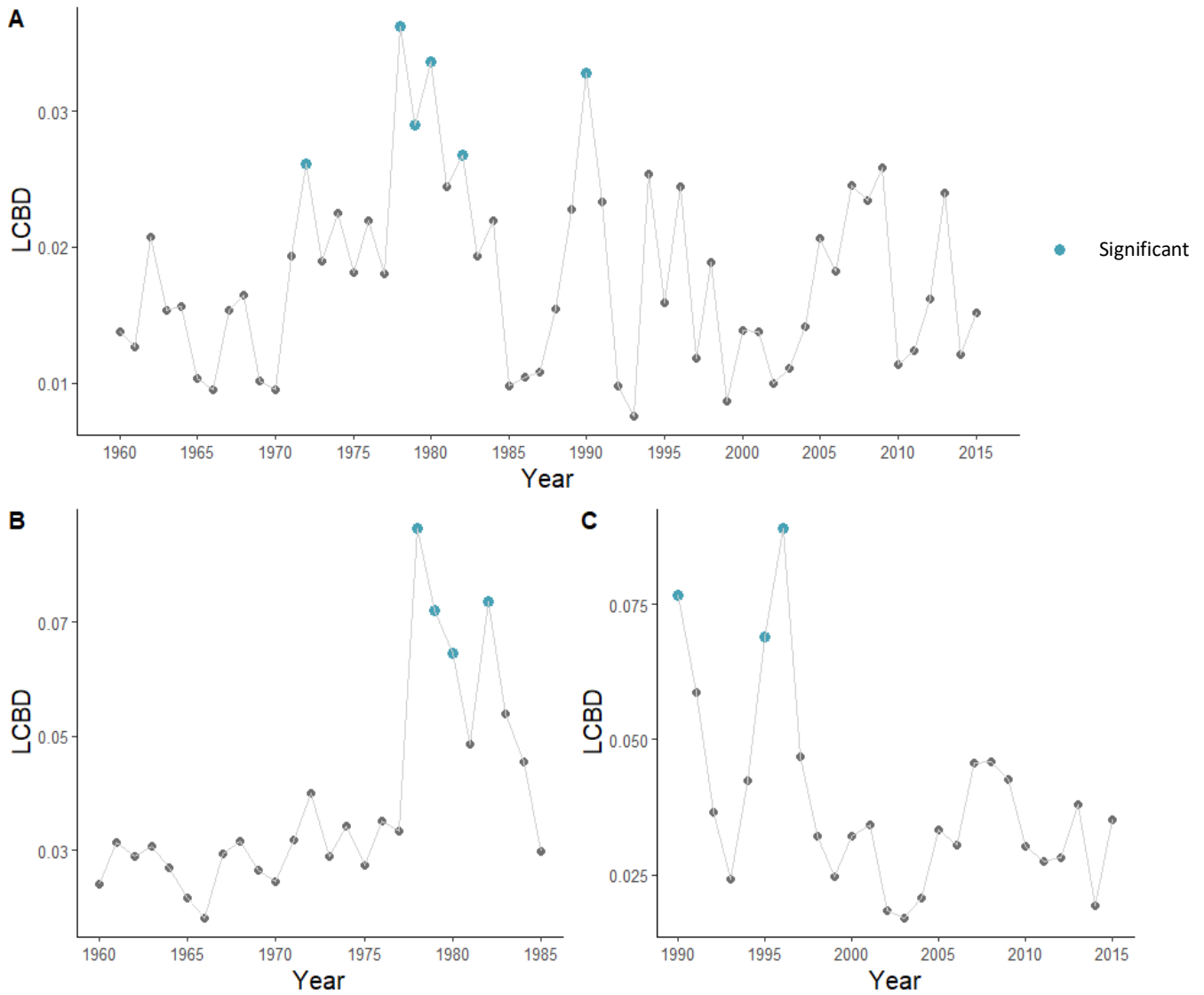


Figure 3.2 A) Local Contributions to Beta Diversity (LCBD) indices for phytoplankton communities in permanently mixed areas. B) LCBD indices when only including pre- regime shift data. C) LCBD indices when only including post regime shift data.

When examining the full time-series for zooplankton communities in permanently stratified areas, the years 1996, 1999, 2007 and 2009 had significant LCBD values (Figure 3.3). When repeating the LCBD analysis on only years pre-1985, the years 1961 and 1975 had significant LCBD values.

Post regime shift, the years 1999 and 2007, no longer showed significant LCBD values.

For zooplankton, including pre-regime shift data therefore increases the number of years post regime shift that come out as having significant Local Contributions to Beta Diversity.

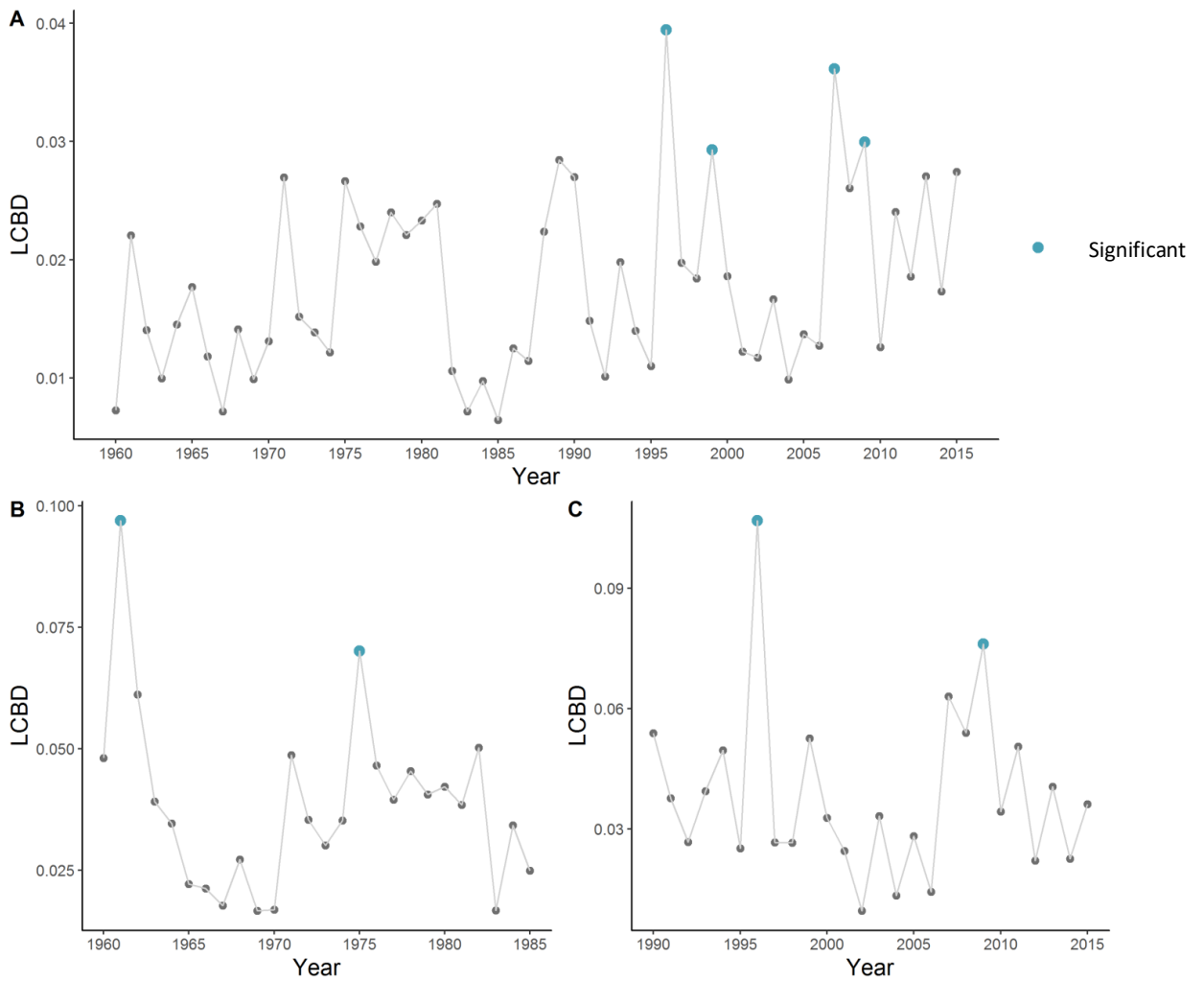


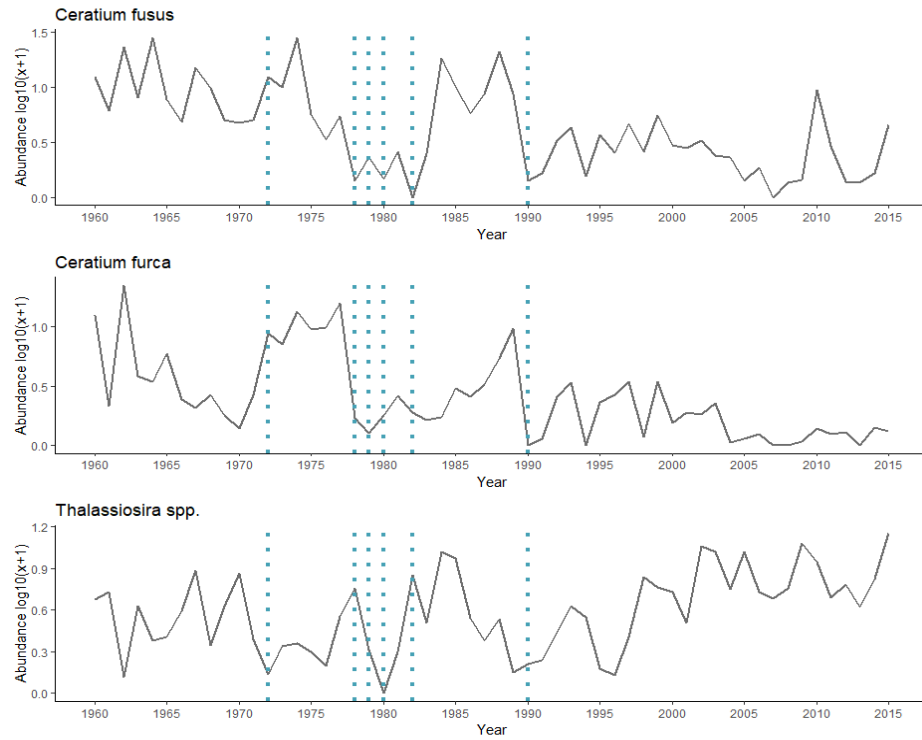
Figure 3.3 A) Local Contributions to Beta Diversity (LCBD) indices for zooplankton communities in permanently stratified areas. B) LCBD indices when only including pre- regime shift data. C) LCBD indices when only including post regime shift data.

3.4.3 Covariates with LCBD indices

3.4.3.1 Species Contribution to Beta Diversity

When plotting the annual abundances of the phytoplankton taxa that had the greatest Species Contribution to Beta Diversity (SCBD values) (Figure 3.4A), patterns emerge between variation in species' abundance and years with significant Local Contributions to Beta Diversity. The years 1978-1980 have significant LCBD values, and coincide with a period of low abundance of *Ceratium fusus*. There was also a very low abundance of *Ceratium furca* and a decline in *Thalassiosira spp.* When plotting the annual abundance of the zooplankton taxa that had the greatest Species Contribution to Beta Diversity (Figure 3.4B) changes in abundance occur after ~1988. There was a decrease in *Calanus finmarchicus* abundance to a minimum abundance in 1999 which had a significant LCBD value. There was an increase in *Echinoderm larvae* and the abundance of *Calanus helgolandicus*.

A) Phytoplankton



B) Zooplankton

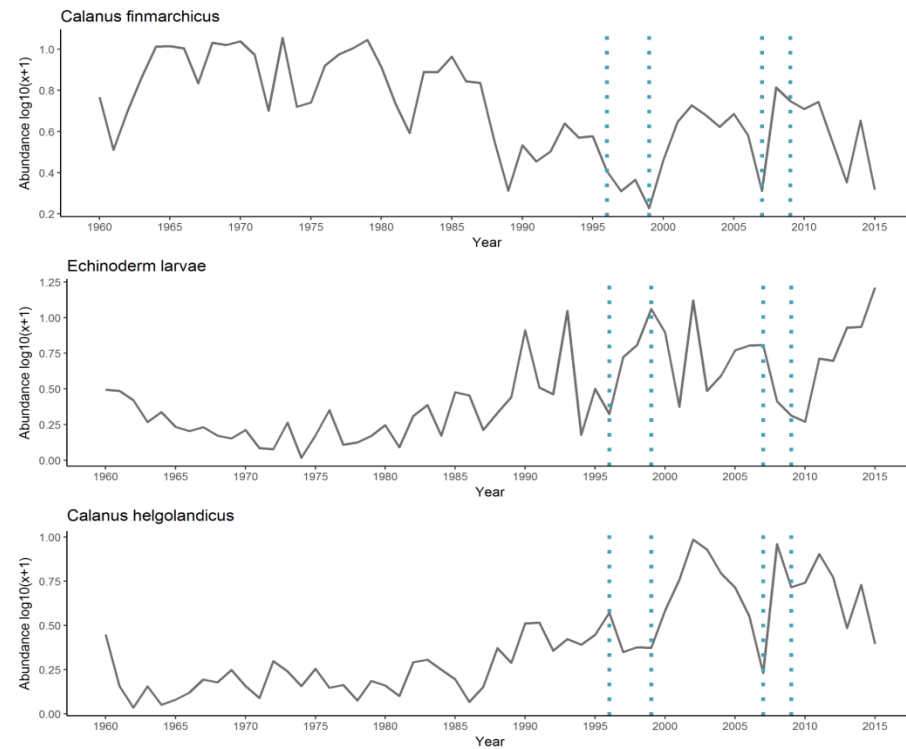


Figure 3.4. Annual abundance of top 3 species with highest Species Contribution to Beta Diversity (SCBD), blue lines represent years with significant LCBD values. A) Phytoplankton in permanently mixed areas, B) zooplankton in permanently stratified areas.

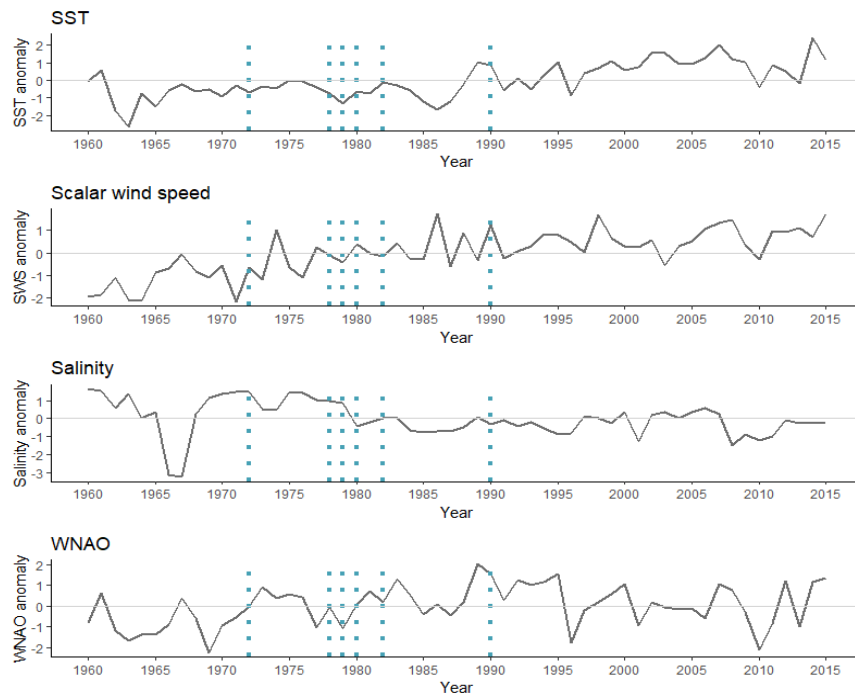
3.4.3.2 *Environmental covariates*

Environmental variables for permanently mixed areas are shown in Figure 3.5A, with the years with significant LCBD values for phytoplankton communities highlighted. The period of significant LCBD values from 1978-1980 identified for phytoplankton communities coincided with a decrease in Sea Surface Temperature and salinity, known as the 'Great Salinity Anomaly' (Dickson et al., 1988). Years with significant LCBD values often appear to coincide with transitions between periods of negative and positive WNAO anomalies. Stepwise multiple regression was used to quantify the environmental determinants of the variation in the local contributions of each year to BD_{Total} . For phytoplankton communities, all variables were retained in the final model after the stepwise AIC procedure, but this model did not significantly explain variation in LCBD indices. I also tested for Granger causality between each environmental variable and annual LCBD indices, to test for lags between environmental variables and LCBD. None of the variables showed significant Granger causality with lags between 1-5 years.

Environmental variables for permanently stratified areas are shown Figure 3.5B, with the years with significant LCBD values for zooplankton communities highlighted.

Between the late 1970s and the year 1990, which had a significant LCBD value, there was an increase in both SST and scalar wind speed, previously attributed to a regime shift that occurred in the North Sea ecosystem (Reid et al., 2015). Stepwise multiple regression showed that SWS was the best predictor of variation in LCBD values for zooplankton, but did not have a statistically significant relationship with LCBD values. In contrast, the Granger causality tests, suggested that SST was the most important variable, at a lag of 1-5 years ($p=0.026$).

A) Phytoplankton



B) Zooplankton

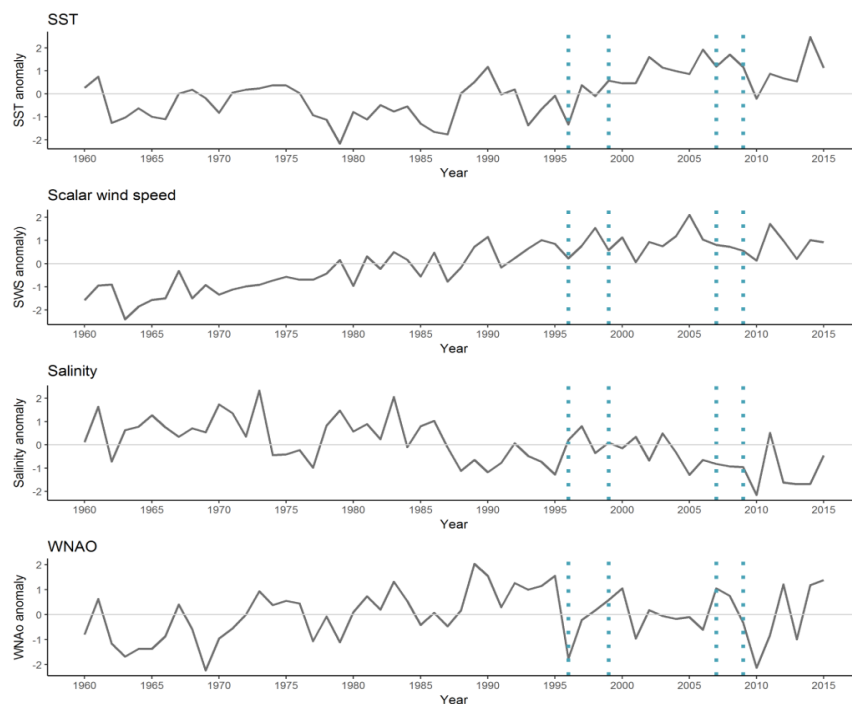


Figure 3.5 Annual anomalies (expressed as standard deviations from mean) of Sea Surface Temperature (SST °C), Scalar Wind Speed (SWS), salinity (PSAL) and Winter North Atlantic Oscillation (WNAO) against long term mean. A) Permanently mixed areas, blue lines represent years with significant LCBD values for phytoplankton. B) Permanently stratified areas, blue lines represent years with significant LCBD values for zooplankton.

3.5 Discussion

3.5.1 Temporal Beta Diversity patterns

Identifying ecologically meaningful change in plankton communities, distinguished from background variability and variation in prevailing conditions, is a key challenge facing the formal assessment of pelagic habitats under policy drivers. Temporal Beta Diversity, or the variability in plankton community composition between points in a time-series, provides a useful framework for quantifying variability structures in plankton community composition through time, and partitioning where in the time-series variability is greatest. Here, I found that BD_{Total} varies between stratification regimes within the OSPAR Greater North Sea region. Due to the latitudinal differences in the core distribution of stratification regimes however, variation in BD_{Total} is likely to be influenced by geographical area and associated specific environmental conditions, as well as just stratification regime. I also found that phytoplankton communities in particular had high BD_{Total} values, implying a proliferation of years with unique community compositions compared to wider community composition. Barton et al. (2015) found high year-to-year variability in plankton assemblages that was greater than variation in physical drivers, causing environmental associations that are present on seasonal scales to break down over interannual and multidecadal scales.

The presence of a previously-identified regime shift could also be seen in the analysis of Local Contributions to Beta Diversity. For example, when examining the full time-series for zooplankton, all the years with significant LCBD indices occurred post-1988. Such directional turnover in zooplankton community composition in response to

temperature warming has been well documented in North Sea zooplankton communities, specifically centred on a regime shift occurring in the mid 1980s, where there was a transition from a colder to a warmer dynamic regime. Results here suggest years post-regime shift are considered unique when compared to before the regime shift occurred. Although some degree of turnover is expected in time-series as a result of random drift and temporal autocorrelation, it is likely that climate warming increases baseline directional turnover rates in zooplankton communities. Similarly, a study of turnover rates in benthic epilithic communities by Hillebrand et al. (2010) suggested that community turnover increases with increasing temperatures, with different temperature regimes resulting in different species compositions and different indicator species.

Furthermore, for zooplankton time-series, the year 1996 had a significant Local Contribution to Beta Diversity when looking at the full time-series and when only looking at data post-1990, and had a significant LCBD for phytoplankton when looking at data post 1990. This year marked the start of a period of rapid increases in SST and Scalar Wind Speed, increase in the abundance of echinoderm larvae, and declines in the abundance of *Calanus finmarchicus*, a copepod species previously widely documented as a key indicator species for North Sea zooplankton response to climate change (Helaouët and Beaugrand, 2007). There were also decreases in *Ceratium fusus* after 1996 and increases in *Thalassiosira* sp. The year 1996 has previously been identified as the beginning of a regime shift in the North Sea, detected in the plankton signal by Beaugrand et al. (2014), which showed a similar magnitude to the more widely documented late-1980s shift. It appears therefore that 1996 represents unique phytoplankton and zooplankton community compositions, as the regime shift starting in 1996 resulted in a changed community composition. This tendency for significant

LCBD indices to 'frame' a specific event was also found by Legendre et al (2017), who showed that LCBD values for mollusc assemblages before nuclear testing events were significant in a long term-time-series, indicating that the intervention of nuclear testing led to the establishment of a community largely different to what it had previously been.

As well as corroborative evidence for previously-identified regime shifts there were other anomalous periods in the time-series identified through partitioning BD_{Total} into Local Contributions to Beta Diversity. For example, a period of significant LCBD indices for phytoplankton communities was found between 1978 and 1980, and was associated with reduced abundances of *Ceratium fusus* and *Ceratium furca*. This period has previously been identified as an anomalous period in the CPR time-series, associated with the 'Great Salinity Anomaly', where a pulse of cold, low salinity water entered the North Sea causing a rapid decrease in SST and salinity (Dickson et al., 1988; Edwards et al., 2002), and associated changes in phytoplankton populations, including a population crash of the warm-water species *Ceratium macroceros*.

3.5.2 Conclusions

It is always a challenge to identify appropriate reference conditions when assessing applied policy indicators, especially when working with multiple datasets of different lengths, or when a long-term time-series experiences a major hydrographic change, such as a regime shift. The question becomes do we select reference conditions representing 'new conditions' or do we use reference conditions representing the whole time-series? Here, inclusion of pre-regime shift data alters whether plankton

community composition in a particular year is statistically unique compared to community composition throughout the remainder of the time-series, with post-1990 community compositions are often only considered unique when compared to pre-1985 data, but are typical of the current time period. It is also likely that temporal scale of reference conditions data will affect the assessment of other pelagic habitat indicators than LCBD indices. For example, the 2017 OSPAR Intermediate Assessment of total zooplankton biomass used wider time-series variability to categorise anomalies of indicator values compared to the long-term mean (OSPAR, 2017b). Although omitting pre-1985 data from an assessment may reduce the range of what is considered an important change in community composition, it may be more realistic to assess for impacts of direct anthropogenic pressures within the current climatic regime (Duarte et al., 2009). In this way, reference periods can be dynamic and adaptive through time in response to ongoing climate change. This shorter reference period however, represents a trade-off between relevant management information, with a potentially reduced sensitivity of analysis.

The identification of unique years within the time-series, through understanding Local Contributions to Beta Diversity, also allows for contextualising reference conditions that are based on a fixed period of time (e.g. a period of 5 years within the time-series). For example, the assessment of changes in the relative abundance of plankton functional groups included in the OSPAR IA2017 assessment used a period of 2004-2009 as reference conditions from which to assess for change in functional group abundances (OSPAR, 2017a). The present analysis suggests that when examining the full time-series, this reference period is representative of wider community composition for phytoplankton, although the year 2007 had a high, but not significant LCBD value with a low abundance of *Ceratium fusus*. For zooplankton, the years 2007

and 2009 had significant LCBD indices, with particularly high SST anomalies and a sharp change in *Calanus helgolandicus* abundance between 2007 and 2009. These potentially atypical plankton communities warrant further investigation as to whether this may skew the results of an indicator assessment.

The patterns in temporal Beta Diversity in plankton community composition found here also have implications for interpreting the relevance of the degree of change in indicator values away from reference conditions. For example, as a result of directional turnover a certain level of change is to be expected between assessment periods, due to both inherent turnover properties and changing prevailing conditions causing unique plankton community compositions. Further work to quantify the expected amount of change in an indicator value between assessment periods could aid in identifying thresholds of indicator change that may indicate perturbation to the community by direct anthropogenic pressures above and beyond underlying directional turnover.

Local Contributions to Beta Diversity indices also have potential as ecosystem indicators, and could provide useful contextual information for assessing Good Environmental Status. Calculating LCBD indices for individual points within the time-series can help identify anomalous periods of plankton community composition that may be linked to abnormal or changed prevailing conditions, such as regime shifts or ocean climate anomalies. Importantly, as new time-points are added to a time series, it is important not just to consider the significance of the LCBD indices of the new time points, but the significance of older time points. This is because these older time-points may retrospectively be assessed as unique when compared to the newer time-

points, suggesting that the newer time points may represent changed community compositions.

It is likely that other indicators of plankton community structure, as well as LCBD indicators, including bulk indicators of biomass and relative abundance of functional groups, may also respond to these anomalies in prevailing conditions (McQuatters-Gollop et al., 2017). Although no significant relationships were found between LCBD indices and prevailing conditions, other than a lagged effect of SST on zooplankton, and key knowledge gaps still exist on the responsiveness of LCBD indices to direct anthropogenic pressures such as nutrient pollution, LCBD indices could have a useful role in interpreting future changes in other plankton indicators. This includes furthering our understanding of whether their changes are a result of changing prevailing conditions, or direct anthropogenic pressures.

Plankton communities are highly dynamic, and the drivers structuring community composition highly complex. Quantifying these variable structures as temporal Beta Diversity as done here is important to be able to interpret anthropogenic perturbations to pelagic habitats from appropriate reference conditions. Temporal Beta Diversity indices make useful indicators of community change in plankton communities, and have strong potential for operational assessment under the Marine Strategy Framework Directive, especially if included as part of a suite of other indicators for a holistic picture of plankton community change.

Chapter 4

Assessing the ability of plankton lifeform groups to indicate the influence of climate change on pelagic habitats in the North Sea

Chapter 4 : Assessing the ability of lifeform groups to indicate the influence of climate change on pelagic habitats

4.1 Introduction

A functional approach is increasingly being taken to understand the responses of ecological communities to environmental change. Functional traits are phenotypic characteristics that can mediate the effect of an individual species on ecosystem functioning (termed 'effect' traits), mediate the response of the individual species to variation in its environment (termed 'response' traits), or both (Hevia et al., 2017). Species with similar functional traits can be aggregated into functional groups, inferring shared effects and responses within the constituent species. Therefore, the use of functional groups to describe communities facilitates linking community change to the consequences for ecosystem processes, as well as to the drivers of the change (Litchman et al., 2010). A functional group approach to describe phytoplankton and zooplankton communities, the base of the marine pelagic ecosystem, is particularly useful as changes in the structure of plankton communities in response to spatial and temporal environmental variation can have consequences for energy flow to higher trophic levels (Drinkwater et al., 2010).

The use of functional group-based approaches has applications for the development of biodiversity indicators for the formal assessment and monitoring of marine ecosystems under policy drivers (Beauchard et al., 2017). As the management of marine ecosystems transitions towards an ecosystem-based approach, there is an increasing

demand for an assessment of the consequences of community change for ecosystem processes and services, as well as the drivers of change, when assessing for change in biodiversity status (Levin et al., 2009). The EU Marine Strategy Framework Directive takes an ecosystem-based approach to the assessment of marine biodiversity, including pelagic habitats (plankton), and the overall target of 'Good Environmental Status' includes the maintenance of ecosystem functioning (Directive 2008/56/EC). Therefore, an indicator based on plankton functional groups has been developed at the OSPAR level to assess the state of pelagic habitats (OSPAR 2017). As per OSPAR methodology, plankton taxa of similar functional type are grouped into broad functional taxonomic groupings, termed 'lifestyles', reducing the complexity of information from that of taxon-level data and simplifying the communication of state changes. The relative abundances of different lifestyles are then monitored in ecologically relevant pairs, conveying information on changes in key aspects of plankton community structure and functioning (Tett et al., 2013). The use of 'effect' and 'response' trait concepts outlined by Hevia et al. (2017), is a useful framework for understanding the scope of the information gained from a change in the relative abundance of a particular lifestyle when assessed as an indicator. Changes in lifestyle groups that are based on shared 'effect' traits, i.e. the constituent taxa within the lifestyle group share a general effect on community functioning, may indicate a change in community functioning, whereas changes in lifestyle groups that are based on shared 'response' traits, i.e. the constituent taxa within the lifestyle group share a general response to an environmental driver, may indicate the influence of that environmental driver on the plankton community.

The lifestyle pairs that were selected by the work of ICG-COBAM for inclusion in OSPAR's 2017 Intermediate Assessment in the Northeast Atlantic have specific

“ecological rationales” given with them, i.e. the changes in marine ecosystem indicated from changes in the relative abundance of the lifeforms (OSPAR, 2017a)(Table 4.1). Some of these ecological rationales are based on changes in the lifeform pair indicating an influence of an ecosystem driver on plankton communities, more specifically an influence of a defined direct anthropogenic pressure. For example, dinoflagellates are known to increase in relative abundance over diatoms as a result of anthropogenic nutrient pollution, due to the ability of dinoflagellates to capitalize on increased nitrogen and phosphorous levels for growth over diatoms, which also require silicate (McQuatters-Gollop et al., 2007a). In order to capture a holistic picture of the structure and state of pelagic habitats, however, the majority of the ecological rationales are based on the consequences of change in the lifeform pair to the wider community and food web. For example, change in the relative abundance of large vs small copepods indicates potential changes in energy flow efficiency to higher trophic levels. Therefore, if retrospectively applying an ‘effect/response’ framework to these ecological rationales, most of the lifeform assessment rationales are based on shared ‘effects’ of constituent species, and fewer directly on shared ‘responses’ (Table 4.1).

Table 4.1. Lifeform pairs selected for assessment under the MSFD at the OSPAR level, along with their ecological rationales, adapted from OSPAR (2017a).

Lifeform 1	Lifeform 2	Ecological Rationale (OSPAR 2017)	'Effect' or 'Response' based rationale?
Diatoms	Dinoflagellates	Dominance by dinoflagellates may be a sign of eutrophication and result in less desirable food webs	Effect and Response
Large phytoplankton	Small phytoplankton	'Size-based indicator of energy flow to higher trophic levels'	Effect
Pelagic diatoms	Tychopelagic diatoms	Benthic disturbance and resuspension events	Response
Large copepods	Small copepods	'Size-based indicator of food-web structure'	Effect
Crustaceans	Gelatinous zooplankton	Indicator of alternative trophic pathways	Effect
Phytoplankton	Non-carnivorous zooplankton	Energy flow and balance between primary produces and secondary consumers'	Effect
Holoplankton	Meroplankton	Indicator of strength of benthic-pelagic coupling	Effect

Linking changes in plankton communities to environmental drivers however, is an important step for MSFD assessments, which require information on the main drivers of biodiversity change, either direct anthropogenic pressures or changes in “prevailing oceanographic conditions” (McQuatters-Gollop, 2012). Determining whether lifeform group membership is a factor regulating the ‘response’ of an individual species to a specific driver, in addition to being a factor determining its ‘effect’ on community processes, aids in determining the scope of information that can be gained from change in the relative abundance of a lifeform group (Hevia et al., 2017). For example, although the relative abundance of large copepods vs small copepods is selected for assessment due to an ‘effect’-based ecological rationale (changes in energy flow

efficiency) (Van Deurs et al., 2015), climate change is thought to favour smaller species (Beaugrand et al., 2010; Daufresne et al., 2009). Therefore, as well as an 'effect' on the ecosystem, changes in the relative abundance of these lifeforms may also indicate an influence of an ecosystem driver (climate change) on plankton communities, if copepod size also determines the 'response' of individuals to climate change. It is important therefore to determine whether the constituent taxa within plankton lifeform groups that are selected for use in the OSPAR assessments share responses to environmental drivers. In this current study therefore, I focus on these previously-selected lifeforms in order to align results directly with the policy process.

Previous studies have shown mixed results for the role of functional type in determining individual plankton species dynamics, depending on environmental context. Whilst Rocha et al. (2011) showed that temperate freshwater plankton species that were functionally similar shared similar dynamics over time, Bode et al. (2015) found that species within an upwelling region of the North East Atlantic responded to environmental variability independently of functional type. Here I focus on understanding the role of functional type (lifeform group membership) in determining the response of individual taxa to Sea Surface Temperature (SST), a key signal of climate change and a leading component of the 'prevailing conditions' which must be accounted for when formally assessing state of the North Sea ecosystem under the MSFD (Frost et al., 2016). SST is a dominant factor structuring the composition and distribution of plankton communities (Richardson, 2008) and also has been shown to covary with wider environmental variables including wind speed (Beaugrand, 2003). Within a defined geographic area, SST can vary due to linkages with atmospheric temperature change, large-scale climate oscillations (Zhai et al., 2013) and variation of incursion of warmer water masses into the area (Reid et al., 2003).

Consequently, the abundance of an individual plankton taxon can increase in an area in response to SST as a result of advection processes bringing the taxon into the area through water mass incursions, regional temperature changes meaning the conditions become more favourable for that taxon, or the result of biogeographic range shifts (Beaugrand, 2004).

Here, I use a Species Archetype modelling approach on a multi-decadal plankton time-series to summarise the main linear responses of North Sea plankton taxa to variation in annual SST (Frost et al., 2016; Richardson, 2008). Here by 'responses' I refer to the trend in abundance associated with the signal of increasing SST. By then examining the distribution of these summarised responses within the pre-defined OSPAR lifeform groups, the current study aims to address the following questions to contribute to the use of lifeform-based indicators:

- 1. Do taxa within lifeform groups respond similarly to temperature change?**
- 2. As well as their use for indicating change in ecosystem processes, can changes in OSPAR lifeform group abundances indicate a temperature-driven influence on the plankton community during ecosystem assessments?**

4.2 Data and Methods

4.2.1 Data sources

4.2.1.1 Continuous Plankton Recorder

The Continuous Plankton Recorder survey has been collecting samples in the North Sea on a routine, consistent basis since 1958. Records of species from a species list

compiled outside of the current study to assess the North Sea at the OSPAR level (OSPAR, 2017a) were extracted from the OSPAR Greater North Sea area (Figure 4.1). Samples were split into two North Sea regions, based on the stratification regimes identified in a model by van Leeuwen et al. (2015) that were used in the OSPAR 2017 Intermediate Assessment for the assessment of change in plankton lifeforms (OSPAR, 2017a). In the current study, areas defined by the model as 'permanently stratified' or 'seasonally stratified' were merged together to define areas of the North Sea that were 'permanently/seasonally stratified'. Areas defined as 'permanently mixed' or 'intermittently stratified' by the model were merged together to define areas of the North Sea that were 'mixed /intermittently stratified' (Figure 4.1). This coarser spatial resolution represented a balance between the need to consider contrasting stratification regimes when examining the responses of species to SST in the North Sea, the alignment of analysis with relevant policy scales, and the retention of a large sample size.

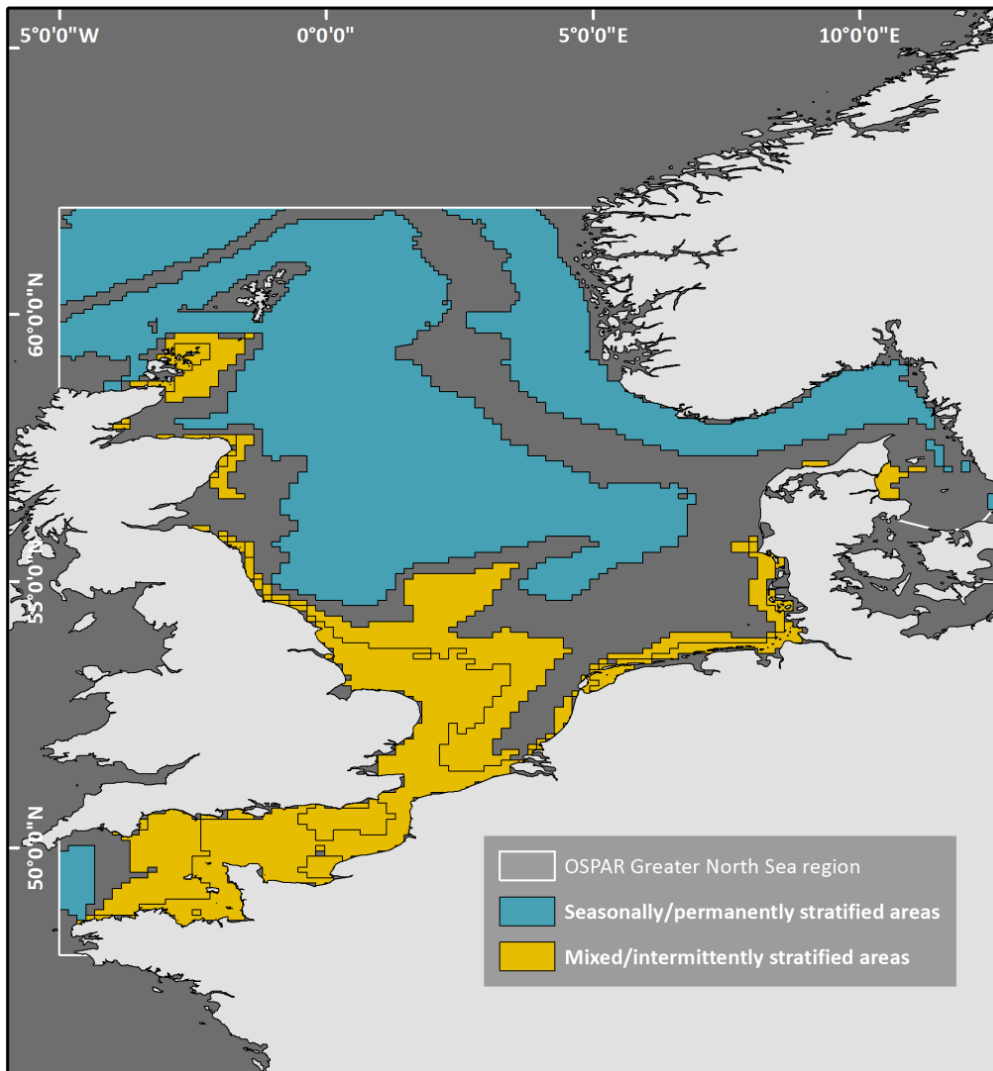


Figure 4.1. 'Permanently/seasonally stratified' areas (blue), or 'Mixed/intermittently stratified' areas (yellow) in the North Sea aggregated from hydrodynamic regions identified by van Leeuwen et al. (2015).

Only species consistently looked for and enumerated, as opposed to identified as 'present' or 'absent, throughout the CPR time-series were included in the analysis. Similarly, only species recorded in over 1% of samples in each area within the time-series were included. This threshold represented a balance between a need to remove rare species which may skew the analysis, and the need to retain a representative species list.

4.2.1.2 Lifeform trait information

Information on functional traits, used to group species into lifeforms, was compiled outside of my thesis research through the work of OSPAR ICG-COBAM and the EcapRHA project (Applying an Ecosystem Approach to (sub) Regional Habitat Assessment) through literature searches (Ostle et al., 2017). These traits were based around plankton functional type, feeding mechanism, size and habitat. In the current study, these traits were added to the representative CPR species list used and, following methodology outlined in Ostle et al. (2017), queries were used to extract the constituent species for each lifeform group, based on specific combinations of traits. For example, the 'tychopelagic diatom' lifeform grouping consists of phytoplankton species that share both functional type trait ('diatom') and habitat ('tychopelagic'). Similarly, the 'large copepod' lifeform grouping consists of zooplankton species that share both functional type trait ('copepod') and size ('large'). CPR data were not used to assess all lifeform groups within the OSPAR Intermediate Assessment, including 'large phytoplankton' and 'small phytoplankton' due to sampling limitations of CPR survey (see Ostle et al. (2017) for selection criteria). Therefore in this current analysis I

only included lifeform groups that were assessed using CPR data during the 2017 OSPAR Intermediate Assessment (OSPAR, 2017a).

4.2.1.3 Sea surface temperature data

Monthly SST data were downloaded for the Greater North Sea area from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) at a 1 degree resolution. Data points were extracted from each stratification region, and the annual mean calculated for each year in the time series (Figure 4.2).

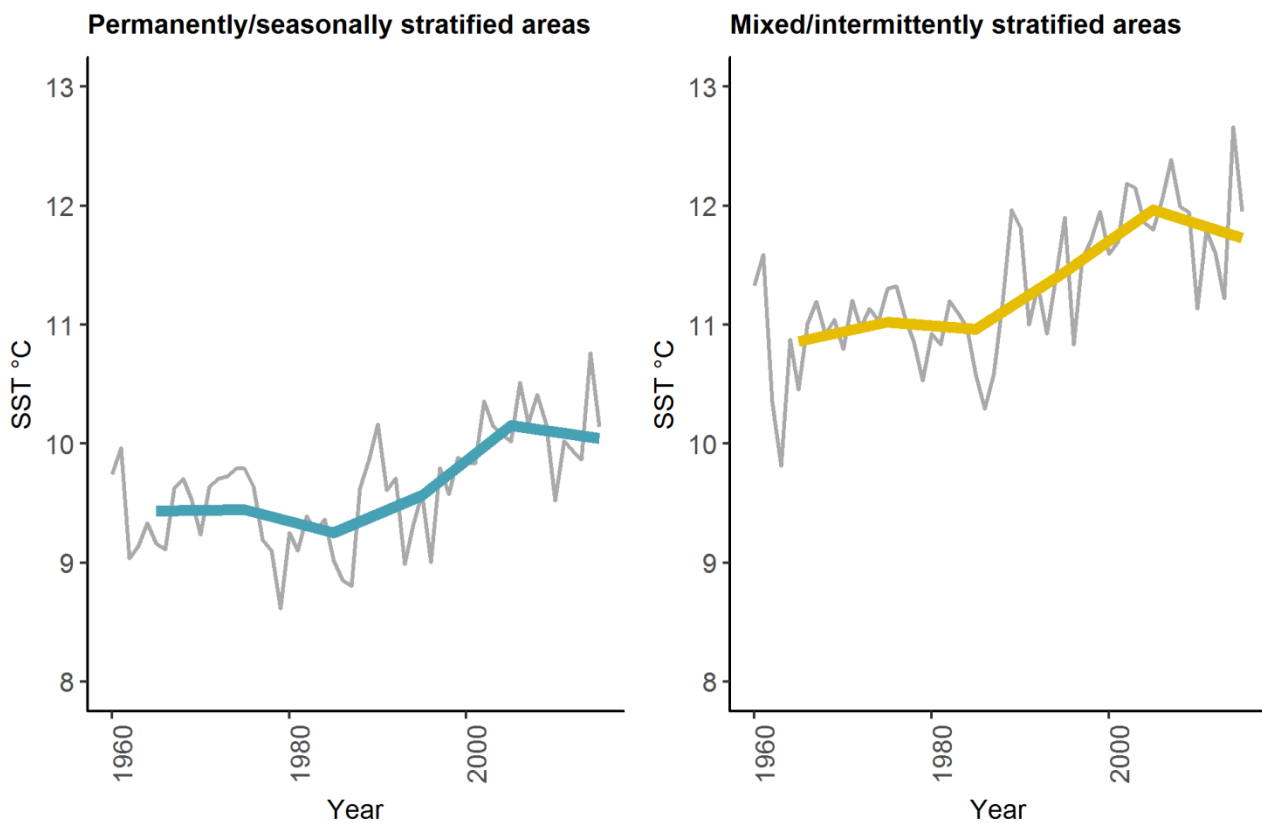


Figure 4.2. Annual Sea Surface Temperature (°C) of the two North Sea areas used in this study. Data taken from the ICOADS dataset. Annual SST is shown in grey, with the decadal mean shown in blue and yellow. Differences in SST between the two areas are likely at least partially explained by differences in latitudes between the core distributions of the stratification regimes within the Greater North Sea OSPAR region.

4.2.2 Data Analysis

4.2.2.1 *Species Archetype Modelling*

The main responses to SST within phytoplankton and zooplankton species were summarised for each aggregated hydrodynamic region using a Species Archetype Modelling approach (SAMs), implemented through the R package 'SpeciesMix' (Dunstan et al., 2013). SAMs use finite mixture models to cluster species based on responses to a predictor variable; here the slope coefficients between SST and abundance. The modelling approach assumes each species comes from one of a defined number of statistically distinct distributions, and the composition of each group and the coefficients of the shared response within each group are estimated simultaneously (Dunstan et al., 2011). The relationship between SST and untransformed mean annual abundance of plankton taxa was modelled using a tweedie distribution with a log-link, due to the proliferation of zeroes in Continuous Plankton Recorder data (all surveyed taxa are 'looked for' in every sample, but are often absent). Models were run allowing 2 to 5 groups when clustering, and the appropriate number of groups was then selected based on minimising the Bayesian Information Criterion (BIC). These groups represent 'Archetypal' responses of phytoplankton and zooplankton species to SST change, thus coarsely summarising the different responses observed.

4.2.2.2 *Examining distribution of Archetypal responses within lifeforms*

Through running the Species Archetype Models, each plankton species was assigned a strength-of-membership (tau) value for each Archetypal response group (with a tau of 0 meaning no affiliation with a group, and a tau of >0.8 suggesting strong affiliation

with a group) (Foster et al., 2015). Archetype groups were retained in the analysis if they contained tau values above 0.5. The proportions of each Archetypal response across all the phytoplankton and zooplankton species included could be calculated. Subsequently, the proportions of each archetypal response within each lifeform group were calculated. To aid comparison, chi-squared tests were calculated to see if differing proportions were statistically significant. These comparisons therefore examined whether different lifeforms were skewed towards a particular Archetypal response to SST. If a lifeform grouping is skewed towards a particular archetype response, it suggests that lifeform group membership is a factor determining the response of individual constituent taxa to SST. On the other hand, if a lifeform grouping is not skewed towards a particular archetype response, it suggests that lifeform group membership is not a factor determining the response of individual plankton taxa.

In addition, I also calculated mean annual abundance of each lifeform group for each area, to compare with the distribution of archetype responses of the individual constituent taxa. The abundances of the constituent taxa of each lifeform group in each sample were summed, before being log transformed. The monthly mean was then calculated, before being aggregated to annual mean. These were then plotted against SST to examine response of lifeform total abundance to SST in each region. The coefficient of these relationships were calculated using generalized least squares regression, with an autocorrelation term added to the model to test for statistical significance.

4.3 Results

4.3.1 Phytoplankton taxa

In both North Sea areas, the variation in phytoplankton responses could be summarized by two archetype groups, representing a positive and a negative response respectively (Table 4.2). The proportions of each archetype group are shown in Figure

Table 4.2 Coefficients and standard errors of the Archetype groups for North Sea phytoplankton.

	A1		A2	
	<i>Coefficient</i>	<i>SE</i>	<i>Coefficient</i>	<i>SE</i>
<i>Permanently /seasonally stratified areas- Phytoplankton</i>	0.71	0.08	-0.205	0.04
<i>Mixed/ intermittently stratified areas- Phytoplankton</i>	-0.31	0.04	0.23	0.04

The proportions of each archetype response within each phytoplankton lifeform group are shown in Figure 4.3 for the Permanently/seasonally stratified areas and in Figure 4.4 for the Mixed/intermittently stratified areas.

These distributions of archetype responses across all the phytoplankton taxa were used to assess whether the distributions within each lifeform group were skewed towards a particular archetype response in each area respectively. In both areas, the dinoflagellate lifeform group had a higher proportion of constituent taxa that were clustered into the negative archetype response than the proportion of the overall

phytoplankton community exhibiting this response. Although not statistically significant with the chi squared tests, a clear majority of the taxa showed a negative response to SST, especially in the mixed/intermittently stratified area. Most of the dinoflagellate species clustered into the negative response archetypes belonged to the genus *Ceratium*, which is recorded particularly well by the CPR due to its robust nature and large size. The overall abundance of dinoflagellates showed a negative relationship with SST in both areas (Permanently/seasonally stratified coef=-0.52, Mixed/intermittently stratified coef= -0.79) although these relationships were not statistically significant when including the autocorrelation term. The skewed proportions of archetype responses within the dinoflagellate lifeform group suggest that whether an individual phytoplankton taxon is a dinoflagellate is a factor mediating its response to SST.

In contrast to dinoflagellates, the constituent taxa within the diatom lifeform grouping showed no large differences in the proportions of different archetype responses compared to phytoplankton overall. These patterns suggest that whether an individual phytoplankton taxon is a diatom is not a factor mediating its response to the increasing SST signal. The total abundance of diatoms did not show a negative relationship with SST as did dinoflagellates, but instead had a slight, but not significant positive relationship. Changes in the relative abundance of dinoflagellates when examined in the dinoflagellates vs diatoms lifeform pair may therefore indicate climate as a driver of plankton community change.

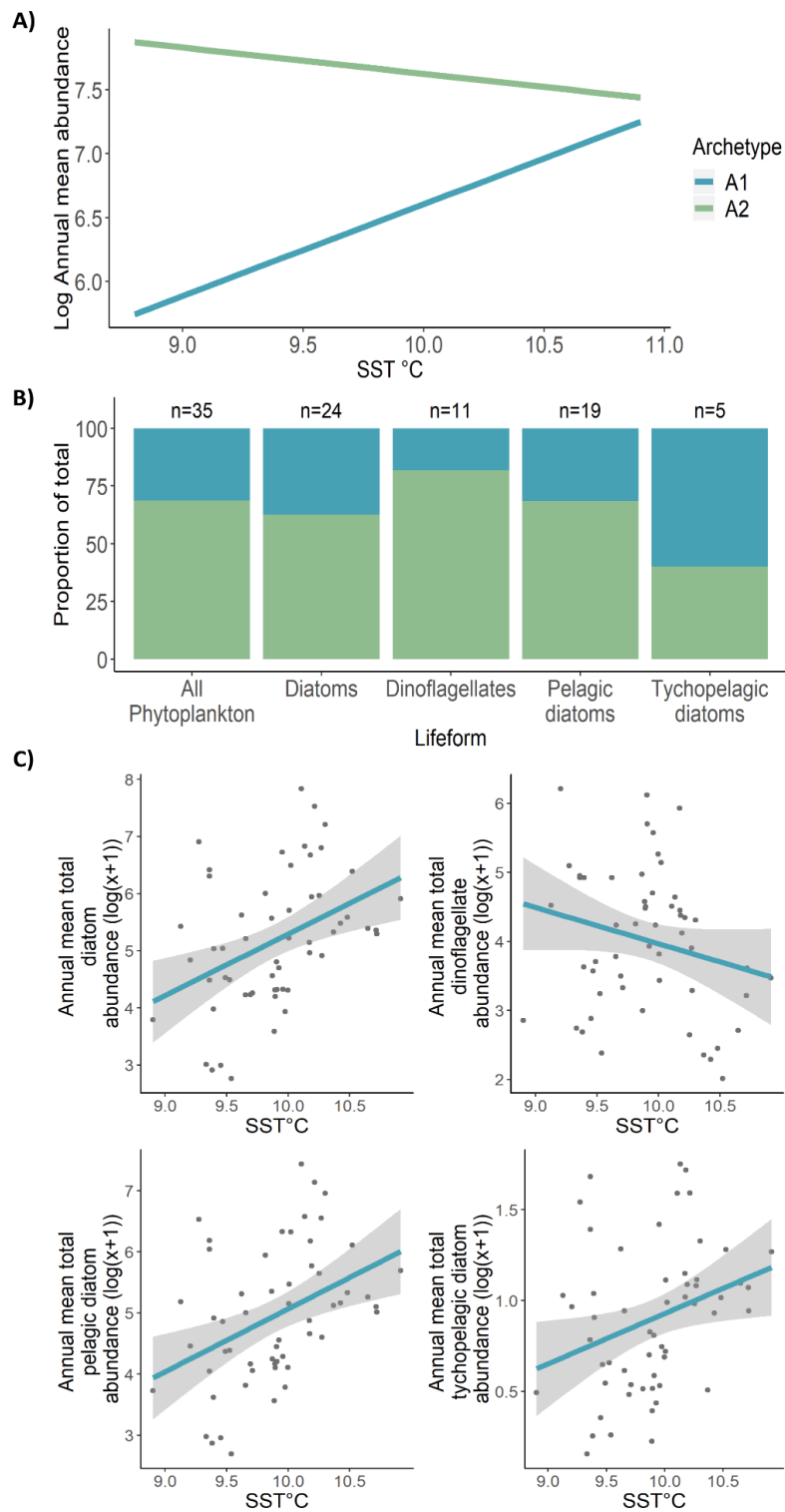


Figure 4.3 Responses of phytoplankton lifeforms to SST within permanently/seasonally stratified areas. A) The Archetypal responses to SST of phytoplankton taxa. Y-intercepts are the average of each species within the Archetype group. B) The proportions of each archetype response within each lifeform species list. C) Responses of mean annual total lifeform abundances to SST (y axes differ).

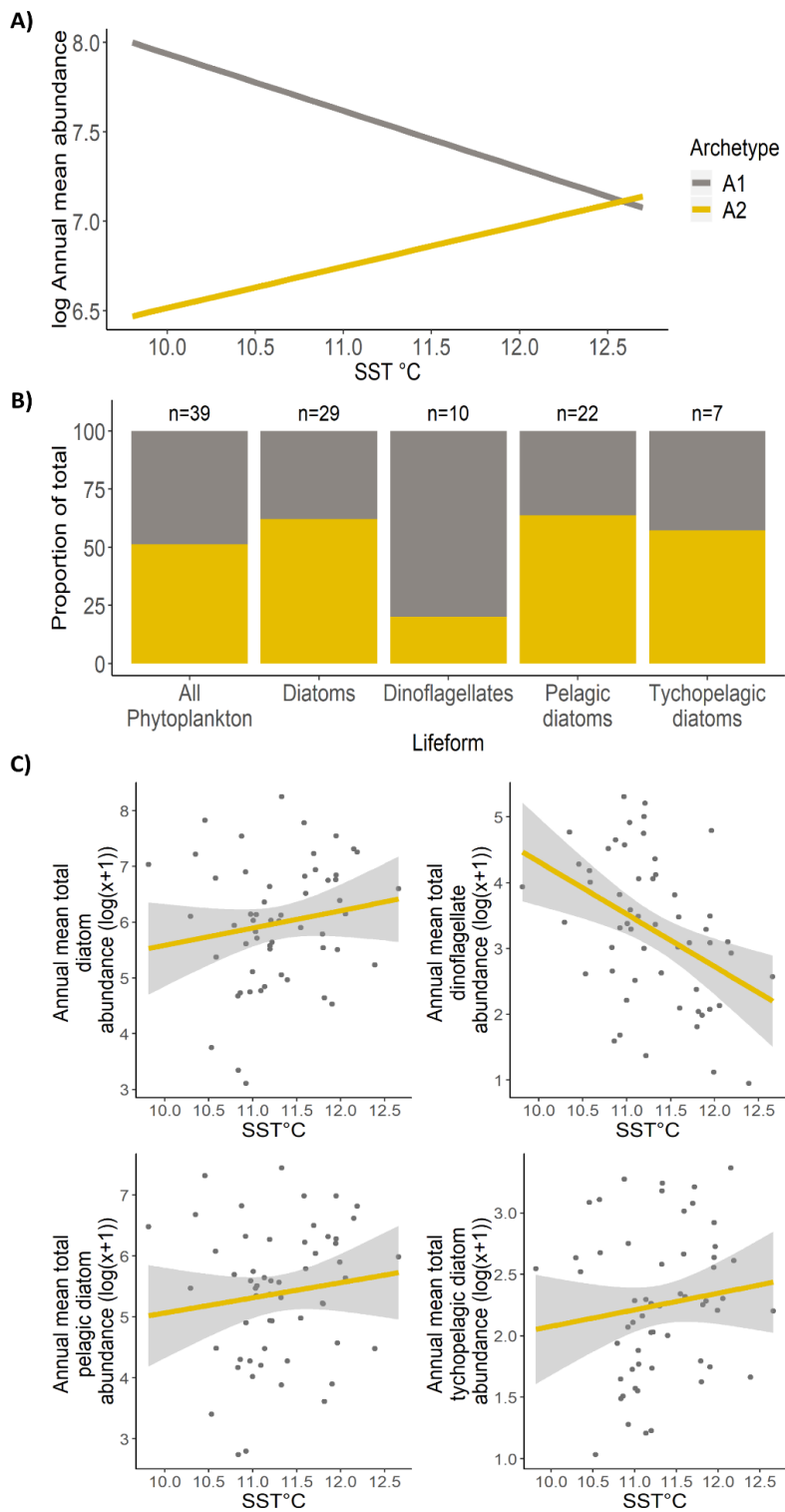


Figure 4.4 Responses of phytoplankton lifeforms to SST within mixed or intermittently stratified areas. A) The Archetypal responses to SST of phytoplankton taxa. Y-intercepts are the average for each species within the Archetype group. B) The proportions of each archetype response within each lifeform species list. C) Responses of mean annual total lifeform abundances to SST (y axes differ).

4.3.2 Zooplankton taxa

In the Permanently/seasonally stratified area, three archetype groups could summarize the variation in zooplankton responses to SST. In the mixed/intermittently stratified area, 4 archetype groups resulted in the lowest BIC, although Archetype 1 consisted only of unidentified *Centropages* species, whereas many *Centropages* species are identified to species level by the CPR survey (Table 4.3). In both areas, one of the Archetype groups represented a negative response to SST. The remaining archetypes represented positive responses to SST.

Table 4.3 Coefficients and Standard Errors of the Archetype groups for North Sea zooplankton. A1 in the Mixed/intermittently stratified area consists of *Centropages* spp. (unidentified) only.

	A1		A2		A3		A4	
	<i>Coefficient</i>	<i>SE</i>	<i>Coefficient</i>	<i>SE</i>	<i>Coefficient</i>	<i>SE</i>	<i>Coefficient</i>	<i>SE</i>
<i>Permanently /seasonally Stratified areas- Zooplankton</i>	1.173	0.071	-0.407	0.05	0.437	0.05		
<i>Mixed /intermittently stratified areas- Zooplankton</i>	2.12	0.512	0.604	0.05	0.07	0.03	-0.44	0.03

In contrast to the phytoplankton lifeform groups, none of the constituent taxa within the different zooplankton lifeform groups seemed skewed towards a particular Archetype response, in either area, confirmed with the chi squared tests (Figure 4.5 and Figure 4.6). There was a mixture of positive and negative responses within each lifeform group, although there was a slightly lower proportion of the negative

archetype group in the large copepods, and a higher proportion of the negative archetype group in small copepods within the Mixed/intermittently stratified area. This lack of skewed proportions suggests that zooplankton lifeform group membership is not a primary factor determining individual responses to SST, and instead the response of individual constituent taxa is governed by other factors than the lifeform groups of which it is a member.

The total abundances of some lifeform groups, however, did show responses to SST. For example, the meroplankton lifeform group showed an increase in response to SST in both areas (Permanently/seasonally stratified area Coef=+0.9, Mixed/intermittently stratified areas, Coef= +0.20), although only the Mixed/intermittently stratified area response was statistically significant when then including an autocorrelation term ($p < 0.05$). Despite these positive relationships for the overall abundance of the meroplankton lifeform, the constituent taxa did not show a skew towards a particular Archetype response, and there was a mixture of archetype responses within the group. Therefore, these changes in total lifeform abundance are likely an emergent pattern based on the dynamics and differing abundances of select taxa, unrelated to the functional groupings themselves, i.e. a meroplanktonic life cycle itself doesn't lend itself to a certain response to SST, but increases in certain individual meroplanktonic taxa lead to the overall lifeform abundance to increase.

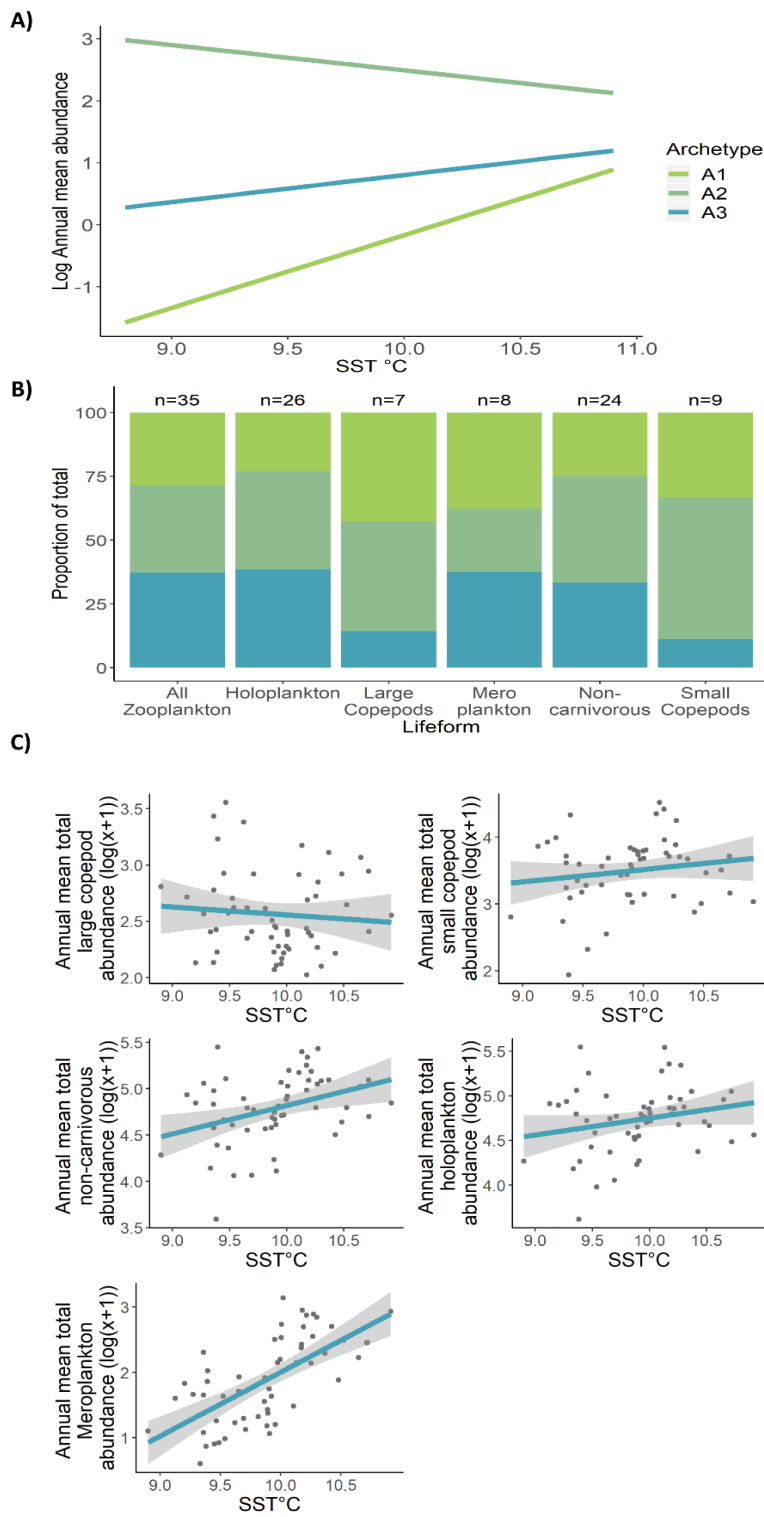


Figure 4.5 Responses of zooplankton lifeforms to SST within permanently or seasonally stratified areas. A) The Archetypal responses to SST of zooplankton taxa. Y-intercepts are the average of each species within the Archetype group. B) The proportions of each archetype response within each lifeform species list. C) Responses of mean annual total lifeform abundances to SST (y axes differ).

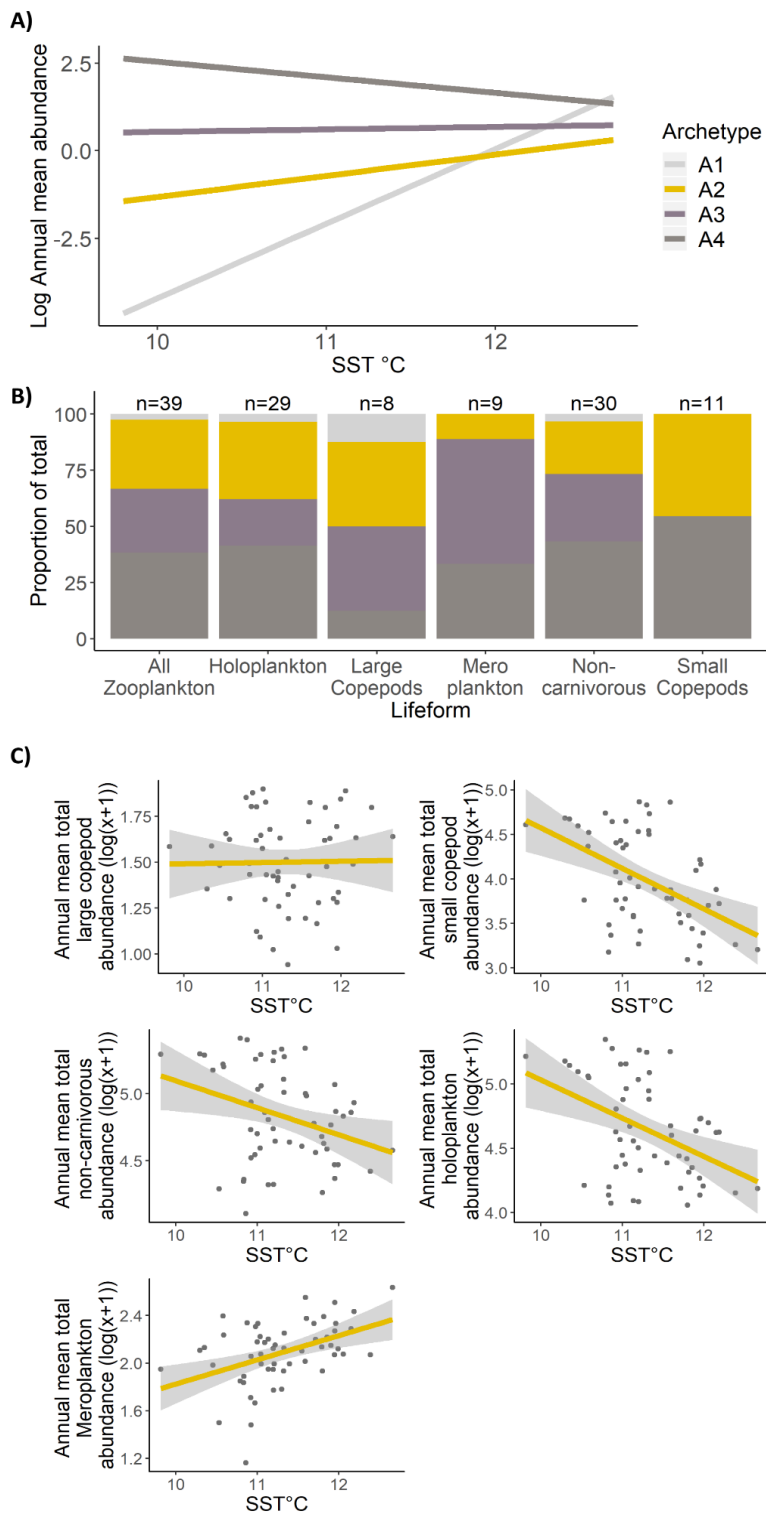


Figure 4.6 Responses of zooplankton lifeforms to SST within mixed/intermittently stratified areas. A) The Archetypal responses to SST of the zooplankton taxa. Y-intercepts are the average of each species within the Archetype group. B) The proportions of each archetype response within each lifeform species list. C) Responses of mean annual total lifeform abundances to SST (y axes differ).

4.4 Discussion

A 'lifeform', approach to describing plankton communities has many practical advantages in communicating change in community structure and functioning. In order to fully understand the scope of information gained through monitoring changes in different lifeforms, an understanding is needed as to whether the traits governing lifeform group membership are factors determining the responses of individual taxa to environmental drivers. From this, it can be determined whether lifeform groupings are based on shared 'responses' to environmental drivers in addition to shared 'effects' on the ecosystem. From the perspective of the use of lifeforms as applied policy indicators, changes in 'response' based lifeforms may indicate an influence of an environmental driver on plankton communities during formal indicator assessments.

Here, I have found that traits associated with the dinoflagellate lifeform group may be a factor influencing the response of individual taxa to SST. The dinoflagellate lifeform group was largely skewed towards an Archetype response showing a negative response to SST change, compared to the distribution of archetype responses of all phytoplankton, especially in the Permanently/seasonally stratified area. The total abundance of dinoflagellates also showed a negative relationship in total abundance with SST, although not significant when accounting for autocorrelation. In contrast, the diatom lifeform group exhibited a more similar distribution of responses as phytoplankton overall and did not show a negative relationship between total abundance and temperature. Hinder et al. (2012) also found that total abundance of dinoflagellates was decreasing in the North Sea as a result of the majority of the species included in their study showing a negative response to SST, interacting with

scalar wind speed. In contrast, they found the total abundance of diatoms did not exhibit a decreasing trend. The results in the present study suggest that the dinoflagellate lifeform group is skewed towards a negative response to SST compared to the whole phytoplankton community, and therefore traits associated with dinoflagellates may be a factor influencing the response of individual taxa to SST. Chivers et al. (2017) found that dinoflagellate species tracked the movement of isotherms more closely than diatom species, and concluded that diatoms display more niche plasticity than dinoflagellates in terms of response to SST. Although the diatom/dinoflagellate lifeform pairing is included in formal assessment due to the ability of the pairing to indicate eutrophic conditions, changes in the pairing may also indicate climate change as a driver of phytoplankton community change.

The dynamics behind changes in the total abundance of zooplankton lifeform groups in contrast, seems to be mainly dependent on the differential responses of individual taxa, and differentiation in responses happens at the taxon level unrelated to the OSPAR lifeform traits. No zooplankton lifeform groupings appeared clearly skewed towards a particular response to SST. The total abundance of zooplankton lifeforms do show responses to SST change however. For example, here we showed an increase in the total abundance of meroplankton in response to SST even though the distribution of responses within the individual constituent meroplankton taxa were not skewed towards a particular Archetype response. In both areas, 'Bivalvia' were clustered into a negative archetype response whereas 'Decapoda' were clustered into a positive archetype response for example. The differing responses of individual zooplankton taxa, and their differing abundances, influence the total abundance of the lifeform. Therefore, zooplankton lifeforms that are selected for assessment to group taxa based on a shared 'effect' on community functioning, do not inherently group taxa by a

shared 'response' to temperature. Changes in the relative proportions of zooplankton lifeforms, including large and small copepods, may therefore indicate changes in community processes, but the lifeforms themselves do not indicate climate change as a driver of zooplankton community change.

Factors other than these broad-scale lifeform groups are likely to be stronger determinants of taxa responses to SST for zooplankton. For example, two congeneric calanoid copepod species *Calanus finmarchicus* and *Calanus helgolandicus* were clustered into different archetypal responses, despite both belonging to the same lifeform groupings. Changes in the abundance of these two species have been observed in the North Sea, with an increasing proportion of *Calanus helgolandicus* compared to *Calanus finmarchicus*, which has declined in abundance in response to climate change, attributed to differing affinities for warmer sea surface temperatures (Helaouët and Beaugrand, 2007). The responses of individual zooplankton taxa to SST seem to be mediated predominantly by biogeographic temperature affinities (Beaugrand et al., 2013; Beaugrand et al., 2002b) rather than by lifeform traits mediating SST response.

Therefore, understanding which individual taxa are contributing to overall lifeform abundance changes can help to confidently indicate and influence of SST on plankton communities during ecosystem assessments, requiring taxonomically resolved data (McQuatters-Gollop et al., 2017). For example, if changes in zooplankton lifeform abundances are found to be predominantly a result of decline in the abundance of *Calanus finmarchicus*, this is a strong indication that climate is driving change in the lifeform indicator. Similarly, Salmaso et al. (2015) stress that plankton functional groups are not meant to be a substitute for the whole extent of information gained

from species level data, and suggest that knowledge of which taxa dominate a functional group is still important to identify specific environmental drivers of community change.

From the perspective of the practical implementation of the Marine Strategy Framework Directive, SST is considered a 'prevailing oceanographic condition' and as an ecosystem driver is outside of the scope of management under the directive. A varied response to SST within lifeform groupings therefore presents a potential further advantage to taking a lifeform approach to indicator assessment. Previous work has suggested that a high 'response diversity' infers stability in ecological communities experiencing changing environmental conditions (Elmqvist et al., 2003). Contrasting dynamics of constituent species within a lifeform group may work to counteract each other, displaying compensatory dynamics (Fischer et al., 2001), for example the varied responses found here within the diatom lifeform group. When aggregating individual taxa into lifeform groups therefore, the variation in total abundance of the lifeform in response to prevailing conditions may be reduced compared to the variation exhibited by individual taxa, helping to distinguish important ecological changes from underlying variability (Lindegren et al., 2016). The sensitivity of dinoflagellates to the increasing SST signal means a challenge remains in assessing the diatom/dinoflagellate pair for signals of direct pressures against a backdrop of changing prevailing conditions (McQuatters-Gollop, 2012).

Further work is needed to establish whether the relative degree to which lifeform groupings are based on shared 'responses' of constituent species found in this study apply to wider environmental drivers in general, or whether the result is driver-specific. Apparent strong positive responses to SST within North Sea regions are often

a result of advection process resulting from warm-water incursion events, and therefore the patterns observed may not hold for other environmental drivers that are also related to climate change. Furthermore, continued research into how different lifeforms respond to direct anthropogenic pressures such as nutrient pollution, in addition to these further climate change variables, will aid in efficiently informing appropriate management measures under the Marine Strategy Framework Directive. Ultimately, although examining plankton communities at a lifeform group level presents many advantages for conveying change in the state of pelagic habitats, taxonomically resolved time-series, at long temporal scales, are necessary for confidently determining the drivers of community change during assessments, not just for the initial construction of lifeform-based indicators.

Chapter 5

Plankton as prevailing conditions: a surveillance role for plankton indicators within the Marine Strategy Framework Directive

Aspects of this chapter have been included in the following:

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.

For this published paper, I came up with the concept and rationale, outlined the new roles presented, researched the relevant examples and completed all of the writing. DJ and AMG provided overall supervision and feedback. SG provided feedback on descriptions of surveillance indicators and checked the description of fish indicators and targets for accuracy.

Chapter 5 : Plankton as prevailing conditions: a surveillance role for plankton indicators within the Marine Strategy Framework Directive

5.1 Introduction

An ecosystem-based approach is increasingly adopted for the management of marine ecosystems (Apitz et al., 2006; Jennings and Rice, 2011). Whilst previous management strategies focused on key species and habitats, they neglected the interactions and linkages between ecosystem components, as well as between ecological and social systems (Levin and Mollmann, 2014; Tett et al., 2013). Ecosystem-based management on the other hand, considers humans as part of the ecosystem, and aims to manage the impact of multiple anthropogenic activities to achieve a healthy ecosystem state with a sustained flow of ecosystem services to humans (Broszeit et al., 2017; Tett et al., 2013). The EU Marine Strategy Framework Directive (MSFD) takes an ecosystem approach to the management of European seas, supported by Integrated Ecosystem Assessments, where indicators are required to synthesize scientific information and formally assess progress towards the overall ecosystem objective of 'Good Environmental Status' (GES) (Levin et al., 2009; Walther and Möllmann, 2013). Out of the 11 qualitative descriptors that comprise the MSFD (Directive 2008/56/EC), the descriptors , 'Biodiversity', 'Food webs' and 'Sea Floor Integrity', describe ecosystem state (Borja et al., 2013).

Indicators that describe the structure and functioning of plankton communities have been developed to formally assess the state of ‘pelagic habitats’ within the MSFD. These include indicators of bulk properties such as primary production as well as indicators of change in plankton functional groups (McQuatters-Gollop et al., 2017). Plankton indicator change may be driven by a multitude of direct anthropogenic pressures, most notably eutrophication resulting from anthropogenic nutrient pollution (McQuatters-Gollop et al., 2009). The assessment of these MSFD plankton indicators, therefore, can directly contribute to the design of the programme of management measures needed to ensure marine ecosystems are in Good Environmental Status under the MSFD, should a change in the plankton indicators be detected during assessment, and linked to direct anthropogenic pressure.

Plankton dynamics, however, are largely driven by climate (Zhai et al., 2013), particularly at the regional scale which is the spatial focus of the MSFD. Consequently, both climate variability and anthropogenic climate change can cause widespread changes in the plankton (Hays et al., 2005) which are likely to manifest through changes in plankton indicators. The MSFD refers to these drivers of change as ‘prevailing conditions’ and mandates that *“the quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions”*. Changes in the plankton driven by climate change and environmental variability, therefore, would be considered in line with Good Environmental Status, with no management impetus through the MSFD.

As a Directive concerning direct, manageable anthropogenic pressures on the marine environment, the development of MSFD biodiversity state indicators for formal assessment initially focused on indicators with clear pressure-state relationships and

associations with defined thresholds and targets. An example of such an indicator is a fish stock size controlled by levels of fishing pressure (Rice and Rochet, 2005; Rochet and Trenkel, 2003). These state indicators can clearly follow an 'Activity'-'Pressure'-'State'-'Response' (APSR) framework of marine management, where a human activity applies a defined pressure on the system. This pressure causes a change in the state of the indicator, which can trigger a management response (Shephard et al., 2015). However, Shephard et al. (2015) argue that a separate class of indicators called 'surveillance indicators', where the links to defined anthropogenic pressures are not well understood and where target setting is difficult, can also contribute to ecosystem assessments under the MSFD. Surveillance indicators do not have a direct influence on the formal assessment of Good Environmental Status, but their 'surveillance' can provide information on wider ecosystem impacts of anthropogenic pressures as well as changing environmental conditions. Therefore, surveillance indicators can also result in triggering management action when pre-defined bounds are passed.

Because plankton are sensitive to changes in climatic and physical oceanographic conditions however, and have been shown to amplify weak climatic signals (Taylor et al., 2002), they can be useful indicators for large scale changes in prevailing conditions. For example, indicators of variability in volume of Atlantic inflow into the North Sea, a key forcing variable for the North Sea ecosystem, can be derived from zooplankton communities (Reid et al., 2003). Furthermore, due to the key role of phytoplankton as primary producers in the marine food web, and the key role of zooplankton as prey for higher trophic levels such as fish, climate-induced changes in plankton themselves may be considered as prevailing conditions for other biodiversity components (Drinkwater et al., 2010). In this way, in addition to their use in directly assessing for Good

Environmental Status, plankton indicators can also be considered surveillance indicators, reflecting change in prevailing conditions that can aid in the interpretation of formal biodiversity indicator assessments. Plankton indicators can therefore have an additional 'surveillance role' even when the plankton indicator changes are not linked to direct anthropogenic pressures.

The surveillance role of plankton indicators is not limited to the formally assessed MSFD plankton indicators however, and can extend to the wider climate change trends identified from time-series datasets that aren't formally assessed within the MSFD. For example a trend for the replacement of *Calanus finmarchicus* by its congeneric warmer-water species *Calanus helgolandicus* was identified in the North Atlantic and is an indicator of climate change (Helaouët and Beaugrand, 2007). Similarly, changes in the phenology of phytoplankton bloom dynamics, linked to the efficiency of energy transfer from phytoplankton to higher trophic levels, have been identified and attributed to climate change (Edwards and Richardson, 2004). These trends are not formally assessed within the MSFD, but are derived from the same time-series datasets as the assessed MSFD plankton indicators, providing useful supplementary information with no additional monitoring effort.

Here, the utility of plankton indicators in the surveillance role of informing on changing prevailing conditions is demonstrated, particularly how this plankton surveillance role can add contextual information to formal state indicator assessments within the MSFD, aiding in assessment interpretation. Specifically, here the contextual information gained from the surveillance of plankton indicators is classified as 'diagnostic', which helps diagnose the drivers of changes within the ecosystem, and

'strategic' which aids in setting targets and management measures for Good Environmental Status.

5.1.1 Plankton surveillance information

The surveillance indicator framework outlined by Shephard et al and described in Chapter 1, provides a tool for integrating changing prevailing conditions into the formal biodiversity assessment process. When applying plankton to this surveillance indicator framework, time-series data can be used for setting surveillance bounds (Probst and Stelzenmüller, 2015; Shephard et al., 2015), for example based on past ranges of indicator values, or using past variability to categorize different magnitudes of change. This is because long term time-series aid in contextualising any indicator changes identified, in terms of the indicated changes in prevailing conditions. An example is the use of time-series data in the detection of regime shifts, such as the 1980s climate-driven regime shift detected in Continuous Plankton Recorder survey data that caused widespread changes in both phytoplankton and zooplankton communities ,coinciding with changes across the wider food web (Gröger et al., 2011; Lindegren et al., 2012; Reid et al., 2015). Time series data can also aid in identifying whether observed changes are the continuation of longer term trends by identifying any existing trajectories of indicator change (Gorokhova et al., 2016).

Often, however, the strength of coupling between hydro-climatic variation, plankton, and other food web components may not be clear and instead obscured by natural variability. Thus, covariation between a plankton indicator and assessed indicators at higher trophic levels would not be sufficient to trigger precautionary management

alone within the framework. Furthermore, the use of correlations to conclude links between environmental variation and higher trophic levels has been criticised (Dickey-Collas et al., 2014). Instead, within the framework, any covariation identified would highlight questions that could be considered when interpreting the results of formal state indicator assessments, often requiring further research and analysis. Examples of how information on prevailing conditions gained through plankton surveillance provides evidence for the interpretation of formal biodiversity indicator assessments are given below.

5.2 Diagnostic role in identifying drivers of change in formally assessed biodiversity indicators

A key challenge in assessing any biodiversity state indicator within the Marine Strategy Framework Directive is in the attribution of observed indicator changes to either direct anthropogenic pressure or prevailing conditions (McQuatters-Gollop, 2012), thus ‘diagnosing’ the cause of indicator change (Figure 5.1) (Hardman-Mountford et al., 2005). Within pelagic habitats, it is established that an understanding of climate-driven plankton trends is essential for disentangling any effect of direct pressures from wider climatic influences (McQuatters-Gollop et al., 2015). For example, an indicator for phytoplankton community structure using functional groups is formally assessed at the OSPAR level (OSPAR, 2017a). This indicator may reveal changes in phytoplankton community structure as a result of human pressures, such as, for example, the effects of anthropogenic nutrient loading altering the proportions of dinoflagellates and diatoms within phytoplankton communities (McQuatters-Gollop et al., 2009). Phytoplankton community structure, however, is also influenced by climate. For

example, the CPR survey reveals multi-decadal range changes in multiple phytoplankton taxa in response to climate change. These responses to climate are not uniform across taxa, with some taxa tracking northward movements of thermoclines closer than others, causing restructuring of phytoplankton communities (Chivers et al., 2017). Understanding the climate contribution to changes in plankton communities, therefore, helps diagnose the drivers of change in the assessed MSFD plankton indicators (Figure 5.2A).

As well as performing this diagnostic role in the interpretation of formally assessed pelagic habitat indicators however, plankton surveillance information can also be useful for interpreting changes in assessed indicators within other habitats and trophic levels. Similarly to plankton, MSFD indicators from these other components may be driven by both direct anthropogenic pressures as well as changes in prevailing conditions, requiring a degree of attribution of the different drivers when interpreting indicator change. Plankton indicator surveillance could inform on changes in prevailing conditions affecting these assessed indicators, and therefore help diagnose when changes are not driven by direct anthropogenic pressures alone. For example, under the MSFD, benthic habitat condition is assessed at the OSPAR level for the 'Biodiversity' and 'Seafloor integrity' descriptors (OSPAR, 2017c). Multi-metric indices are used to compare the condition of benthic habitat communities over intensity gradients of different anthropogenic pressures, resulting from a range of human activities including bottom-trawling and sediment extraction allowing for the determination of the degree to which the pressures causes change in benthic condition (OSPAR, 2017c).

Benthic communities, however, are also impacted by large scale climate variability, and regime shifts detected in plankton communities have coincided with changes in the benthos (Birchenough et al., 2015). Changes in the abundance of the larval stages of different benthic invertebrate groups (meroplankton) in relation to climate have also been detected from plankton time-series surveys (Kirby et al., 2008). Furthermore, particularly in coastal regions, there is often tight benthic-pelagic coupling as phytoplankton production is the main source of organic supply to benthic faunal communities (Griffiths et al., 2017). Phytoplankton bloom dynamics may therefore control benthic community structure by influencing food availability and levels of environmental hypoxia (Zhang et al., 2015). Clare et al. (2017) showed that abrupt shifts in the temporal trends of large and long-lived taxa within a benthic community time-series were attributed to increased detrital input from pelagic primary production. Increasing frequency of Harmful Algal Bloom events as a result of climate change (Edwards et al., 2006; Hallegraeff, 2010) may also influence benthic communities through selectively impacting both larval and post-larval survival of benthic invertebrates (Grall and Chauvaud, 2002) . As the MSFD benthic condition assessment is based on quantifying pressure state relationships, changes in benthic state indicators influenced by changes in prevailing conditions may result in the influence of direct pressures being misinterpreted (Kroncke and Reiss, 2010). The surveillance of plankton indicators including bulk primary productivity and HAB dynamics (Figure 5.2B), can therefore aid in the interpretation of the assessment of benthic habitat condition.

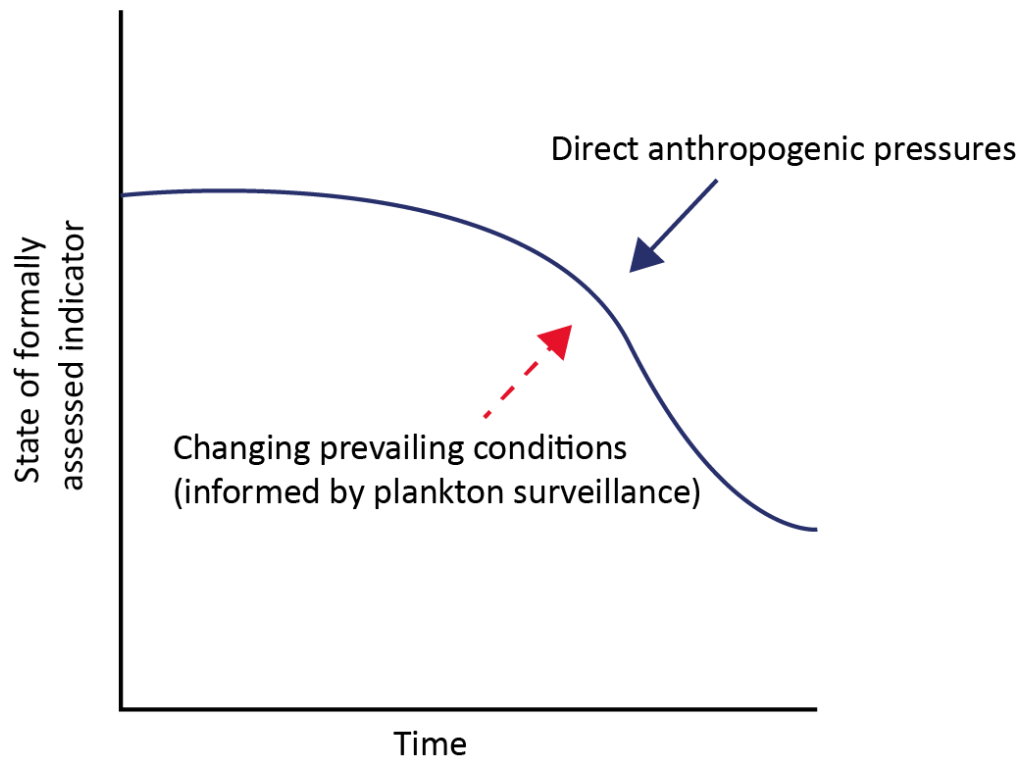


Figure 5.1 Schematic diagram of the diagnostic role for plankton surveillance information. Change in the state of a formally assessed biodiversity state indicator can be influenced by both direct anthropogenic pressures and prevailing conditions. Plankton surveillance can aid in understanding the relative influence of prevailing conditions.

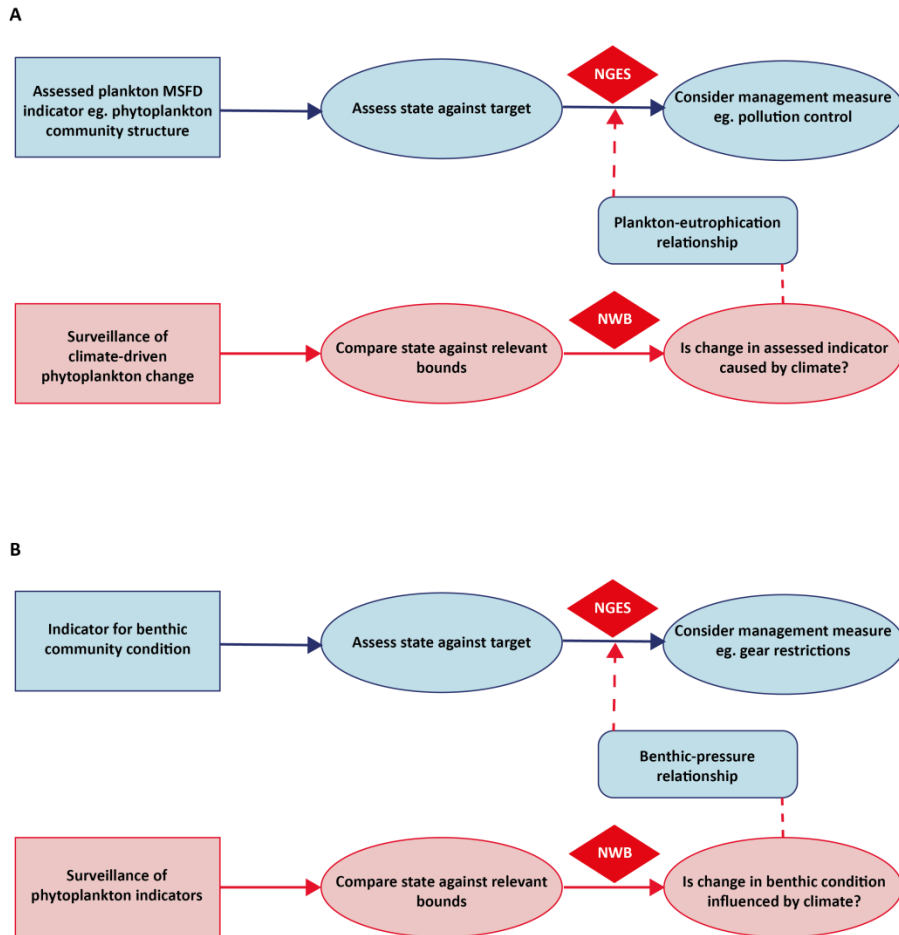


Figure 5.2 Examples of the diagnostic role of plankton surveillance information in MSFD implementation A) The role of plankton surveillance information in diagnosing drivers of change in pelagic habitat MSFD indicators. Here, range shift indicators (bottom, red) trigger research targeted at the pressure-state relationship between phytoplankton GES indicator and eutrophication pressure (top, blue)- ‘Is change in plankton GES indicator driven by climate induced range shifts?’ B) The potential role of plankton surveillance information in diagnosing the drivers of change in assessed indicators within other habitats and ecosystem components. Here, surveillance of phytoplankton indicators (red), trigger research targeted at the benthic pressure-state relationship, and therefore assessment of GES, between benthic community composition and anthropogenic benthic disturbance (blue)- ‘Is change in benthic condition indicator influenced by climate?’.

5.3 Strategic role in influencing targets and management measures for formally assessed biodiversity indicators

In addition to diagnosing the drivers of change in MSFD biodiversity indicators during formal assessments, plankton surveillance information could contribute to the determination of GES targets (Figure 5.3). For example, an indicator for recovery in the population abundance of sensitive fish species has been developed for formal assessment at the OSPAR level (OSPAR, 2017g). However, the influence of changing prevailing oceanographic conditions on population growth is required to determine the scope for population recovery (OSPAR, 2017g). Changes in plankton indicators can track trends in physical oceanographic conditions that may affect recovery, and changes in plankton community composition and phenology may affect fish recruitment independently of the size of the spawning stock biomass (Lowerre - Barbieri et al., 2016). For example, directly after the 1980s plankton regime shift North Sea cod populations fell to historically low levels and showed weak signs of recovery (Lindegren et al., 2010). Furthermore, a regime shift that occurred in the North Sea in the early 2000s was suggested as the leading candidate mechanism to explain the low herring recruitment observed between 2002 and 2007, with plankton shifts providing more explanatory power than the effects of physical variables alone (Payne et al., 2009). Although the linking of fish recruitment dynamics to environmental variability is challenging (Pepin, 2015), surveillance of plankton indicators provides information on any influence of plankton on fish recovery potential (Platt et al., 2007).

The method for assessing GES in respect to fish population recovery is outlined by (Greenstreet et al., 2012). First, targets for a given indicator are set at the individual species level, based on the indicator metric falling in the upper 25 percentile of all values in the species' reference period. These species-level indicator assessments are then aggregated to the community level by comparing the number of different species achieving their target for the given indicator. Therefore, changes in prevailing conditions that affect the recovery potential of stocks, despite a reduction in anthropogenic pressure, may mean the GES targets may no longer be realistic. Instead, the permitted range in which individual species metrics can fall may need to be increased, or the number of species required to be in GES at the community level may need to be reduced (Probst et al., 2013). In this way, plankton indicator surveillance can contribute to the setting of realistic targets for the assessment of fish state indicators (Kenny et al., 2009) (Figure 5.4A).

As well as affecting the feasibility of reaching a specified state target, changes in prevailing conditions detected through plankton surveillance may alter the sensitivity of an ecosystem component to a specified anthropogenic pressure, thus affecting the amount of pressure that will cause an assessed biodiversity indicator to move away from Good Environmental Status (Figure 5.3). For example, indicators of seabird population size and breeding success are formally assessed at the OSPAR level within the MSFD (OSPAR, 2017d, e) and are useful indicators of the food web repercussions of direct pressures targeted at the lower levels of the food web, such as fishing pressure on forage fish prey (Rombouts et al., 2013; Tam et al., 2017). For effective ecosystem-based management, management of forage fish exploitation must account for the need to sustain top predators and as forage fish biomass and productivity is highly

variable, the setting of acceptable fishing levels must remain adaptive (Cook et al., 2014; Dickey-Collas et al., 2013). With a reduction in the recruitment success of key forage fish species such as sandeel predicted under climate change (Arnott and Ruxton, 2002), reducing fishing pressure on forage fish through precautionary management measures may be needed to maintain Good Environmental Status of seabirds under future climate conditions (Carroll et al., 2015).

Forage fish abundance and growth has been linked to phytoplankton production (Eliassen et al., 2011) and zooplankton community composition through changes in the distribution of copepods indicating both changes in physical oceanographic conditions and influencing recruitment and growth (Clausen et al., 2017; Frederiksen et al., 2013). There can also be direct trophic links between zooplankton and seabirds, especially in the non-breeding season (Jessopp et al., 2013; Reiertsen et al., 2014). In these ways, climate-driven plankton shifts may place an additional 'unmanageable' pressure on seabirds, influencing the outcome of seabird state indicator assessments, and could therefore indicate relevant prevailing conditions when setting management measures (Figure 5.4B). Within MSFD assessment cycles, management of direct pressures could be altered to take into account trends in climatic (non-manageable) drivers (Frost et al., 2016), informed by plankton surveillance. In this way, although the drivers of climate induced changes cannot be addressed by the MSFD, adaptive management of direct pressures could increase the likelihood of an indicator remaining in Good Environmental Status in relation to manageable pressures, as well as help increase the resilience of the ecosystem component to climate change (Fuentes et al., 2016; Hulme, 2005; Morecroft et al., 2012).

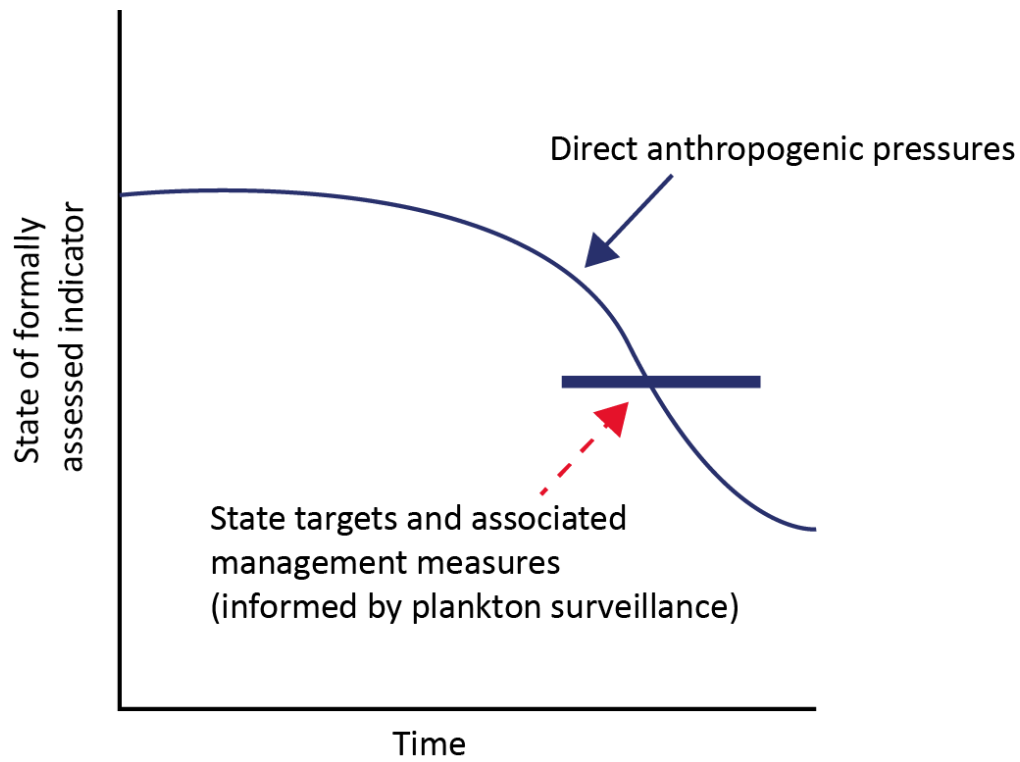


Figure 5.3 Schematic diagram of the 'strategic' role for plankton surveillance information. Targets, and associated management measures, for a formally assessed state indicator can be adapted to changing prevailing conditions. Plankton surveillance information can inform appropriate target setting and management measures.

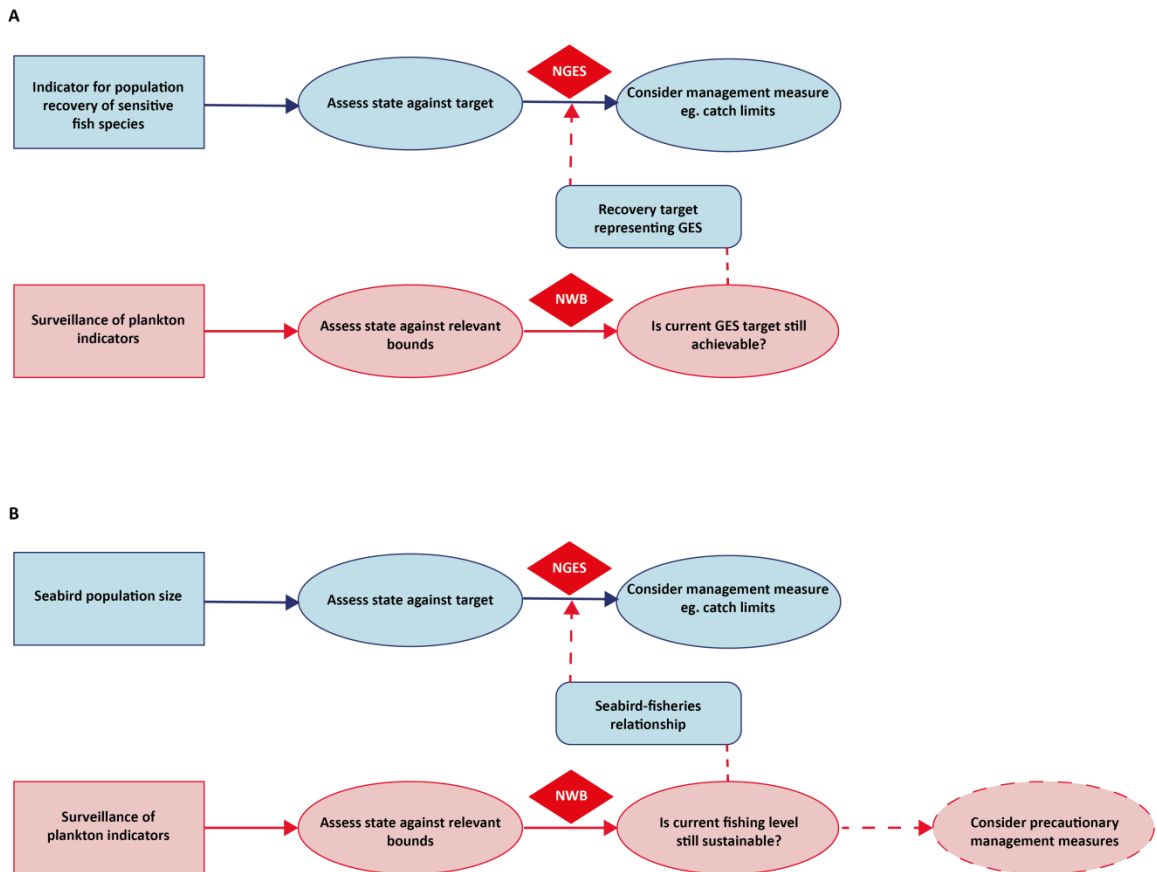


Figure 5.4 Examples of the strategic role of plankton surveillance information in MSFD implementation . A) The potential role of plankton surveillance information in setting targets for other components and descriptors. Here, plankton indicator surveillance (red) triggers research around the target representing GES for the recovery of sensitive fish communities (blue)- ‘Is the current GES target still achievable under the new climate conditions?’ .This research could lead to the adjustment of GES state targets. B) The potential role of plankton surveillance information in influencing the programme of measures. Here, plankton indicator changes linked to prevailing conditions (bottom, red) trigger research targeted at the pressure-state relationship between forage fish fisheries and seabird breeding success (top, blue)- ‘Is the current threshold level of fishing still sustainable, considering the changed prey landscape?’ This research could lead to more precautionary management measures being implemented.

5.4 Summary and conclusions

In this chapter, I have illustrated a surveillance role of plankton indicators within the Marine Strategy Framework Directive in addition to their primary role in formally assessing pelagic habitats for influences of direct anthropogenic pressures. Plankton indicators are useful early-warning indicators of physical hydro-climatic changes and can therefore inform on changes in the underlying prevailing conditions in which MSFD biodiversity indicators are formally assessed. Furthermore, changes in plankton can be important prevailing conditions to consider themselves. The importance of including biotic ecosystem drivers, such as changes in plankton, within marine monitoring programmes has been acknowledged by the Framework for Ocean Observing (FOO) with the development of 'ecosystem Essential Ocean Variables (eEOVs)', which are defined biological or ecological quantities derived from field observations (Constable et al., 2016). The surveillance indicator Shephard et al. (2015) concept is a useful tool in translating this established monitoring need into the MSFD implementation process.

This surveillance of plankton indicators provides two, newly-defined, types of contextual information for the assessment of biodiversity within the MSFD.

'Diagnostic' plankton surveillance information can help disentangle the influence of direct anthropogenic pressure from the influence of prevailing conditions, both within pelagic habitats, and within other habitats and ecosystem components. On the other hand, plankton surveillance information can have a 'strategic' role by indicating when the climate influence on the ecosystem may mean targets and management measures need to be altered. Due to the highly variable nature of coupling between changes in the plankton and changes in the wider marine ecosystem, both diagnostic and

strategic roles of plankton surveillance information are based on the triggering of targeted research questions for consideration during assessments, following the observation of a change in plankton indicators and the detection of trends, thereby making an important evidence contribution to allow the implementation of the MSFD to be adaptive under climate change (Hughes et al., 2005).

Currently, changes in plankton communities linked to climate are considered as being aligned with Good Environmental Status, as the changes are linked to natural variations or exogenous pressures. Limiting the application of these climate-driven indicator changes in this way however, is not using monitoring effort efficiently, when plankton indicators are also useful in a wider surveillance role. Progressing this surveillance role for plankton indicators requires further work on understanding ecosystem interactions between plankton and other formally assessed biodiversity components, as well as the consequences of changes in climatic and oceanographic conditions on both plankton indicators and the wider foodweb. This in turn requires further collaboration between scientists working on these different components. Ultimately, the maintenance of long-term plankton time series therefore has multiple applications for ecosystem-based management of European seas within the Marine Strategy Framework Directive.

Chapter 6

General Discussion

This chapter provides a general discussion of the results of the analyses within this thesis. These results are evaluated in reference to the main aims of the thesis. Policy recommendations are subsequently presented, to incorporate the results of this thesis into the biodiversity assessment process under the Marine Strategy Framework Directive.

Chapter 6 : General Discussion

6.1 Introduction

Assessing and managing the overall status of marine biodiversity under ecosystem-based management frameworks is scientifically challenging. A literature review mapping these challenges and knowledge gaps in Chapter 1, using pelagic habitat assessments as an example, highlighted that climate change, and the concept of 'integration', are challenges facing all 'layers' of biodiversity management under the MSFD. These challenges and knowledge gaps are symptomatic of scaling up from more local scale, single pressure focused management such as the EU Water Framework Directive, to regional scale management of multiple anthropogenic activities. Under the MSFD, evidence needs to be combined to be able to set the political agenda for ecosystem-based management of regional seas in Europe, and monitor progress towards high-level environmental targets. Although managing the drivers of climate change is outside the scope of the MSFD, understanding the impacts of these changing 'prevailing conditions' on the North Sea ecosystem is needed to ensure these regional scale management plans can adapt to ongoing environmental change.

In addition, in Chapter 1, a number of challenges and knowledge gaps facing the assessment of pelagic habitats at this level of regional scale governance were highlighted. Due to the key influence of prevailing conditions on structuring plankton communities, continued understanding of these influences is needed to be able to confidently assess for Good Environmental Status in pelagic habitats and maximise the contribution of plankton indicators to the information provided by integrated

ecosystem assessments. During this discussion Chapter, the overall aims of this thesis are first evaluated in relation to the results of analyses within. Subsequently, recommendations for policy are made in relation to the use of long-temporal scale plankton data in the development of marine strategies, framed around the assessment and reporting of OSPAR PH1/FW5 indicator (Changes in phytoplankton and zooplankton communities) in the North Sea as a case study.

6.2 Aim 1- The setting of appropriate reference periods in the context of changing prevailing conditions

The role of long temporal scale plankton data in the formal assessment of pelagic habitats under ecosystem-based policy frameworks is unclear, specifically in the use of historical data in the setting of reference conditions. An important distinction should be made when using any data from a time-period in the past between **'threshold'** data, which provide a level which triggers management responses if the system moves away from the past state, **'restorative'** data, which provide a target for restoration efforts, and **'contextual'** data, which provide information on ecological change over long temporal scales. Due to the important influence of climate in driving the dynamics of plankton communities, a stable temporal baseline against which plankton indicators are assessed may be difficult to define for the North Sea. For example, Chapter 2 suggested that community composition differed from the early 1900s to the beginning of the CPR temporal coverage (1960s), coinciding with warming Sea Surface

Temperature, indicating that the community in the 1960s was a snapshot of community state over the last century, and does not necessarily represent a stable baseline.

Specifically, the occurrence of climate regime shifts makes selecting a period of time to represent reference conditions challenging. For example Chapter 3 found that years assessed as having significant Local Contributions to Beta Diversity were dependent on whether data from different climate regimes were included in the reference period used. This is because inclusion of data from before the 1980s regime shift altered the threshold of what is assessed as a significant change in community composition. From a restorative perspective, Duarte et al. (2009) found that climate change alters the feasibility of returning to pre-eutrophication conditions, likening using past state in a restorative context as attempting to 'return to Neverland'.

This is a different perspective from the classical concept of shifting baseline syndrome outlined by (Pauly, 1995), where shifting baselines leads to a lack of environmental ambition when setting targets. Instead here, because the baseline has been shifted by prevailing conditions, using historical data as reference conditions may represent an unrealistic and unattainable state. For pelagic habitats in the North Sea therefore, in order to 'escape Neverland', it may be more appropriate to use contemporary data, within the current climate regime, as a 'threshold' reference period. This threshold data would be used as a level which flags a change in the plankton community, triggering further analysis (Dickey-Collas et al., 2017; Scherer et al., 2016). As per chapter 3, this contemporary reference period should be evaluated as to whether it is representative of community structure across a wider time period. Subsequently, and crucially, longer temporal scale plankton data can be used as 'contextual' data, aiding

in interpreting the outcome of pelagic habitat assessments by informing on the drivers of change over longer time scales. By using long temporal scale data in this contextual way, the assessment process can adapt to ongoing environmental change, whilst also avoiding shifting baselines syndrome by not losing important information on the influence of prevailing conditions (Figure 6.1)

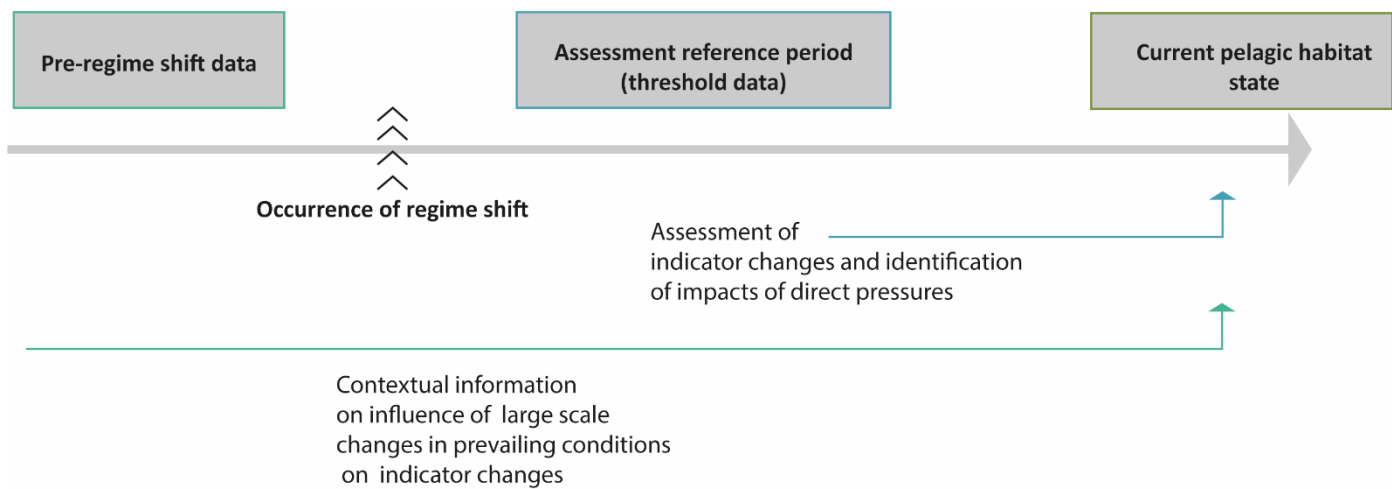


Figure 6.1. Suggested potential incorporation of climate regimes into the pelagic habitat assessment process in the North Sea. Long temporal scale data should be used as ‘contextual data’ to inform on the influence of changing prevailing conditions, helping to avoid shifting baselines syndrome, but contemporary data should be used as the assessment reference period.

6.3 Aim 2- The responses of policy indicators to changing prevailing conditions

Using long temporal scale data to provide this contextual information on the responses of plankton indicators is an important step for MSFD indicator development (Frost et

al., 2016), which I contributed to with this thesis. For example, the relative abundance of key plankton lifeform groups (broad-scale functional groups) is a pelagic habitat indicator under OSPAR assessments (OSPAR, 2017a). Chapter 4 found corroborative evidence for the sensitivity of dinoflagellates as a lifeform group to changing prevailing conditions, finding that the constituent taxa within the dinoflagellate group were skewed towards a negative response to Sea Surface Temperature (SST). Although changes in the relative abundance of dinoflagellates compared to diatoms is used as an indicator for eutrophic conditions, changes in the relative abundance of dinoflagellates compared to diatoms may also indicate prevailing conditions as an influence on pelagic habitats. This also means that the diatom/dinoflagellate lifeform pair may change with future changes in prevailing conditions. In contrast, for zooplankton groups, it was found that constituent taxa within lifeform groups follow more similar proportions of responses to SST as when looking at the zooplankton community as a whole. This means that differentiation in responses to SST change happens at the individual taxon level, rather than the lifeform level, and therefore in order to confidently link indicator change to drivers of change during ecosystem assessments, it is important to identify the key taxa contributing to lifeform change requiring fine taxonomic resolution data.

For example, in Chapter 2, by further increasing the temporal coverage of our understanding of North Sea plankton community change, corroborative evidence of the sensitivity of certain zooplankton taxa to temperature was found, which can aid indicator interpretation. The copepod *Centropages typicus* showed a significant contribution to zooplankton community response to SST over the extended dataset, with the data suggesting a continuing increase in occurrence frequency since the early 1900s. Similarly, in Chapter 3, variation in the abundance of the cold water copepod

Calanus finmarchicus had a high Species Contribution to Beta Diversity. Therefore, if changes in zooplankton lifeform groups during an ecosystem assessment are found, identifying which individual taxa contribute to the indicator change can help determine whether the indicator is being driven by changing prevailing conditions.

The responses of phytoplankton and zooplankton communities to changing prevailing conditions were found to differ throughout the analyses. It is important to understand and compare the dynamics of these two components of pelagic habitats as the MSFD assesses for the first time indicators of both phytoplankton and zooplankton community structure under its biodiversity and food web descriptors, whereas the Water Framework Directive focuses on phytoplankton indicators for water quality assessments. For example, in Chapter 2, zooplankton communities showed larger directional response to SST change over the historical time-period than phytoplankton communities, which showed subtler trajectories of change. This response of zooplankton was corroborated by results from Chapter 3, which showed clear directional structure within the temporal beta diversity for zooplankton structured around the 1980s regime shift. Therefore, during an ecosystem assessment, zooplankton indicators may be expected to show changes result of both inherent turnover properties and changing prevailing conditions, requiring flexibility when interpreting whether an indicator change represents an ecologically meaningful change in pelagic habitat state.

6.4 Aim 3- Using plankton indicators as surveillance indicators to monitor and inform on changing prevailing conditions

The primary aim of understanding the influence of changing prevailing conditions on plankton indicators is to be able to disentangle these changes from perturbations resulting from direct anthropogenic pressures. Finding shifts in pelagic habitat structure through time due to climate change, such as suggested in Chapter 2, however, is still important information for managing regional seas. The method for incorporating climate-driven changes in plankton into the policy process, nevertheless, is not clear. As the MSFD focuses on direct anthropogenic pressures that are manageable at the regional scale, if a change in plankton communities linked to climate is detected during assessments, these changes don't contribute to plankton communities missing their target of 'Good Environmental Status'. These definitions of GES targets and 'prevailing conditions' ensure targets are realistic and achievable, and management measures are implemented efficiently. The question then arises, however, a change in plankton communities linked to prevailing conditions is identified during an ecosystem assessment, how can this information be best used?

This is where the concept of 'surveillance indicators' comes in. Surveillance indicators are indicators that do not have clear, quantifiable relationships with direct pressures, but can still inform on wider influences of human activities or underlying environmental change. A strong understanding of these underlying changes in prevailing environmental conditions is needed to effectively assess and manage marine biodiversity under the MSFD, and to inform on an effective and adaptive programme of management measures.

Chapter 5 illustrates that plankton can play a key 'surveillance role' in marine ecosystem assessments by informing on changing 'prevailing conditions (Figure 6.2). First, a 'diagnostic role' for this plankton surveillance information is outlined, which aids in understanding the relative influence of prevailing conditions over direct pressures on the ecosystem. For example, the OSPAR pelagic habitat indicator 'PH3L Changes in plankton diversity', which includes time-series of Local Contributions to Beta Diversity indices (LCBD), provides useful surveillance information. Although this indicator was difficult to statistically link to variation in climatic and oceanographic variables, variation in LCBD values coincided with previously-identified ocean climate anomalies and regime shifts. These atypical prevailing conditions and plankton communities may also affect wider ecosystem components, such as fish and seabirds, warranting consideration when interpreting outcomes of biodiversity assessments for these higher trophic levels. Secondly, a 'strategic' role for plankton indicators is outlined, which aids in setting targets and management measures that are adaptive to climate change. For higher trophic levels, for example, current management measures may no longer be sufficient if there are wider ecosystem shifts as a result of climate change. For example, more stringent management measures for seabirds may be needed to counteract the pressures caused by climate change. Using plankton as surveillance indicators therefore aids in the challenge highlighted in Chapter 1 of integrating results of the assessments of different biodiversity components.

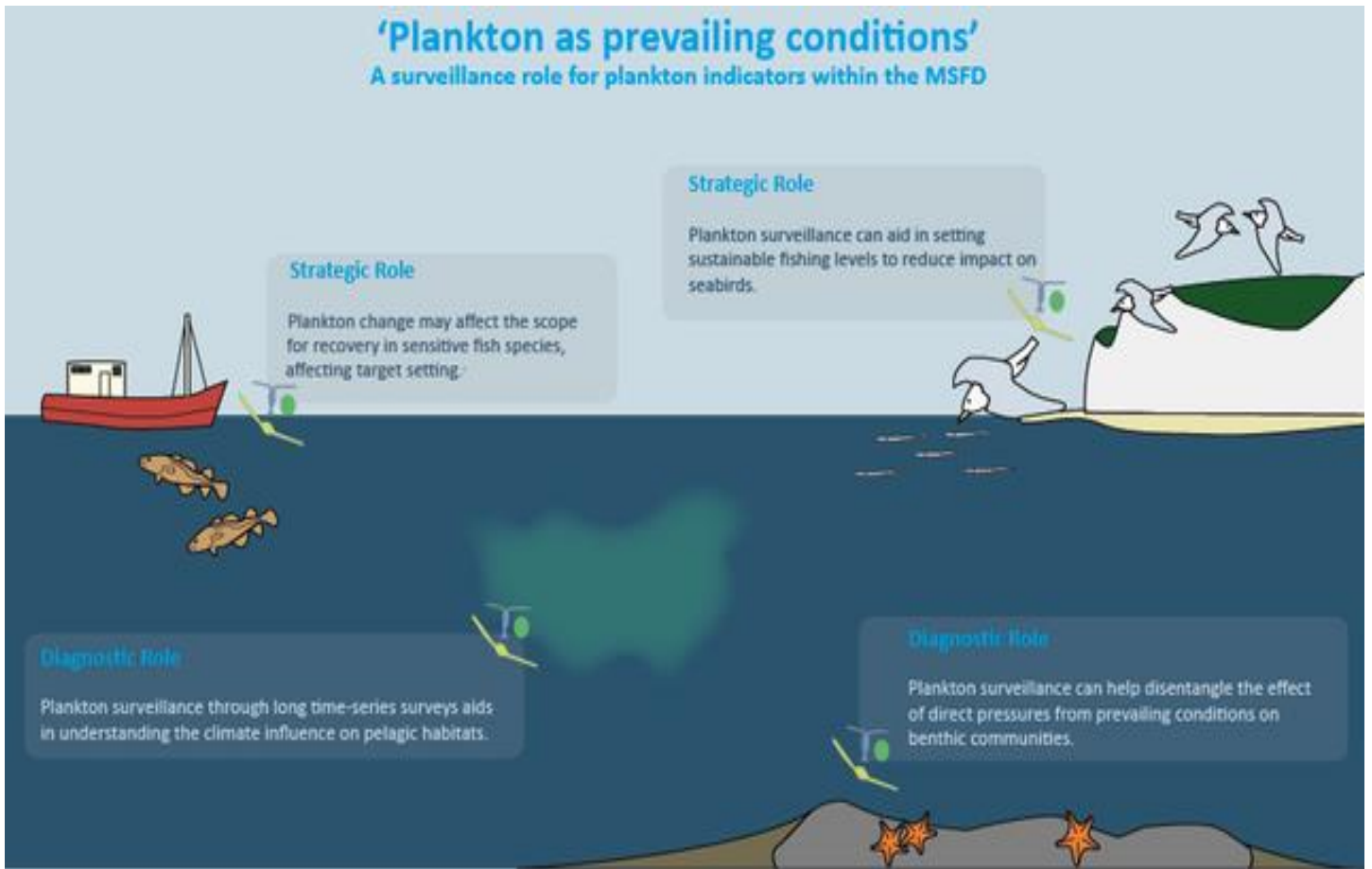


Figure 6.2 'Plankton as prevailing conditions'- examples from Chapter 5 of the diagnostic and strategic roles of plankton surveillance information can provide for the assessment and management of biodiversity under the MSFD.

6.5 Policy recommendations- a progressed workflow for assessment of OSPAR pelagic habitats indicator PH1/FW5 (Change in phytoplankton and zooplankton communities) in the North Sea

PH1/FW5, 'Change in phytoplankton and zooplankton communities', is an OSPAR-wide biodiversity indicator for pelagic habitats under OSPAR's biodiversity assessments for the North East Atlantic, and is based on changes in the relative abundance of key plankton lifeform pairs. The method employed to detect change in these lifeform pairs, is described in Chapter 1. Samples from the assessment period are compared against a 'comparison period', to detect if a change has occurred. The length of data used as a comparison period is undecided, and the role of long temporal scale plankton data in the operational assessment of PH1/FW5 is unclear. Below, a progressed workflow for PH1/FW5 assessments is outlined and shown in Figure 6.3.

This workflow can be broken down into the collation and management of disparate data sources, the detection and interpretation of change in plankton lifeforms, and then the reporting of change against GES targets. For each stage policy recommendations are made based on the results of this thesis, and are summarised in Figure 6.3.

6.5.1 Data collation and management

Policy recommendation:

- **Develop a master list of shared common taxa between surveys that is representative of the core plankton community.**

Regional scale indicator assessments require data to be used across disparate sampling programmes. For example, the OSPAR Intermediate Assessment 2017 of change in plankton lifeform groups combined data from both continuous and station-based plankton surveys across the North East Atlantic region (OSPAR, 2017a). An ‘extreme’ example of dataset disparity was illustrated in Chapter 2, where data from the ICES historical plankton database was compared with the Continuous Plankton Recorder dataset, requiring integration of the taxonomic data. Chapter 2 concluded that using a master list of taxa that are common to both datasets and which are assessed to be reliably sampled across survey types was representative of wider community dynamics in response to environmental change. Similarly, the plankton lifeform indicator could be based on a shared taxa list across sampling programmes, to ensure consistency, and crucially making it simpler and cheaper to assess across disparate plankton surveys. The use of the lifeform approach inherently alleviates issues of varying taxonomic resolution that were also addressed during the integration process in Chapter 2.

6.5.2 Flagging and interpreting change in plankton lifeforms

Policy recommendations:

- **Use a contemporary reference period as a threshold to flag change in lifeform pairs**
- **Identify taxa contributing to zooplankton lifeform change**
- **Use long temporal scale data to provide context on drivers of change**

Changes in the relative abundance of plankton lifeform pairs at the OSPAR regional sea scale are quantified via a state-space approach (OSPAR, 2017a; Tett et al., 2008).

Described in Chapter 1, the method involves plotting the relative abundance of the key lifeform pairs within a reference periods onto a 'state-space' plot. Subsequent assessment periods can then be overlain on this reference period to quantify change.

During the OSPAR 2017 Intermediate Assessment, the time period 2004-2009 was used as the reference conditions to assess for changes in the relative abundance of the different lifeform pairs (OSPAR, 2017a). This contemporary reference period was therefore used as 'threshold' data to understand whether a change in pelagic habitat state had occurred. The full assessment of GES however was incomplete as the drivers of these changes were not fully quantified. In future, by using long-temporal scale plankton data as 'contextual' data the drivers of change can be further investigated.

Figure 6.3 A proposed assessment workflow for PH1/FW5, based on results of this thesis, including the use of long temporal scale plankton data to provide context on the drivers of change.

Figure 6.3 outlines how this process can be operationalized into the formal indicator assessment process through outlining a proposed assessment workflow. For

zooplankton particularly, identifying the taxa causing the changes in lifeforms, and plotting their trajectories over time, can further aid in identifying the drivers of change, facilitating a more complete assessment of Good Environmental Status. A similar approach to assessment reporting is given by the International Group for Marine Ecological Time Series who produce status reports based on summarised long-term trends in ecological time-series (O'Brien et al., 2017). By applying this approach for PH1 assessments, i.e. presenting the wider-time series alongside the comparison to the threshold reference period can aid in understanding the influence of prevailing conditions, and evaluating Good Environmental Status.

6.5.3 Reporting on GES using change in plankton lifeform pairs

Policy recommendations:

- **Although outside the definition of GES, climate change-driven trends in plankton lifeforms should be reported during ecosystem assessments and can be used as surveillance indicators**
- **Develop lifeform pairs that are specifically responsive to climate change to provide additional surveillance information used for tracking changes in prevailing conditions**

Although changes in plankton lifeforms linked to prevailing conditions are outside the definition of Good Environmental Status, and outside the scope of management interventions under the MSFD, climate change trends in plankton lifeforms are still important for implementing ecosystem based management. In particular, as changes in plankton lifeform pairs imply a consequence on ecosystem functioning, changes in lifeforms should still be reported even if not linked to a direct anthropogenic pressure.

Used as surveillance indicators, these lifeform changes can provide contextual information when integrating different biodiversity components together.

Plankton lifeforms can be based on 'effect' and 'response' based functional traits, with abundance changes in lifeforms that are based on 'response' traits indicating an influence of an environmental driver on plankton communities. To progress the surveillance role of plankton indicators in the Marine Strategy Framework Directive, new lifeform pairs could be developed that directly respond to climate variability. Chapter 4 concluded that currently none of the zooplankton lifeform groups were inherently indicators of climate change by themselves, as the climate response of individual zooplankton taxa were mixed within the different lifeform groupings. Instead, it was concluded that biogeographic range seemed to be a greater factor influencing temperature response than current OSPAR lifeform group membership. Therefore, in order to inform on climate drivers specifically, new lifeform pairs could be selected based on biogeographic groupings to specifically detect climate influences on pelagic habitats. For example Beaugrand et al. (2002a) divided calanoid copepods into different assemblages based on spatial distribution, and suggest using changes in the number of species in each assemblage as an indicator of biogeographical shifts (Beaugrand, 2005). A similar principle could apply to the concept of key lifeform pairings used in the OSPAR assessments, and this is an important area for potential future indicator research and development. For example, a pairing of 'warm-temperate' vs 'cold-temperate' copepods could be developed. Lifeforms in this pairing would therefore be grouped based on 'response' to temperature, and changes in this lifeform pair could supply useful surveillance information on changes in prevailing conditions to ecosystem assessments.

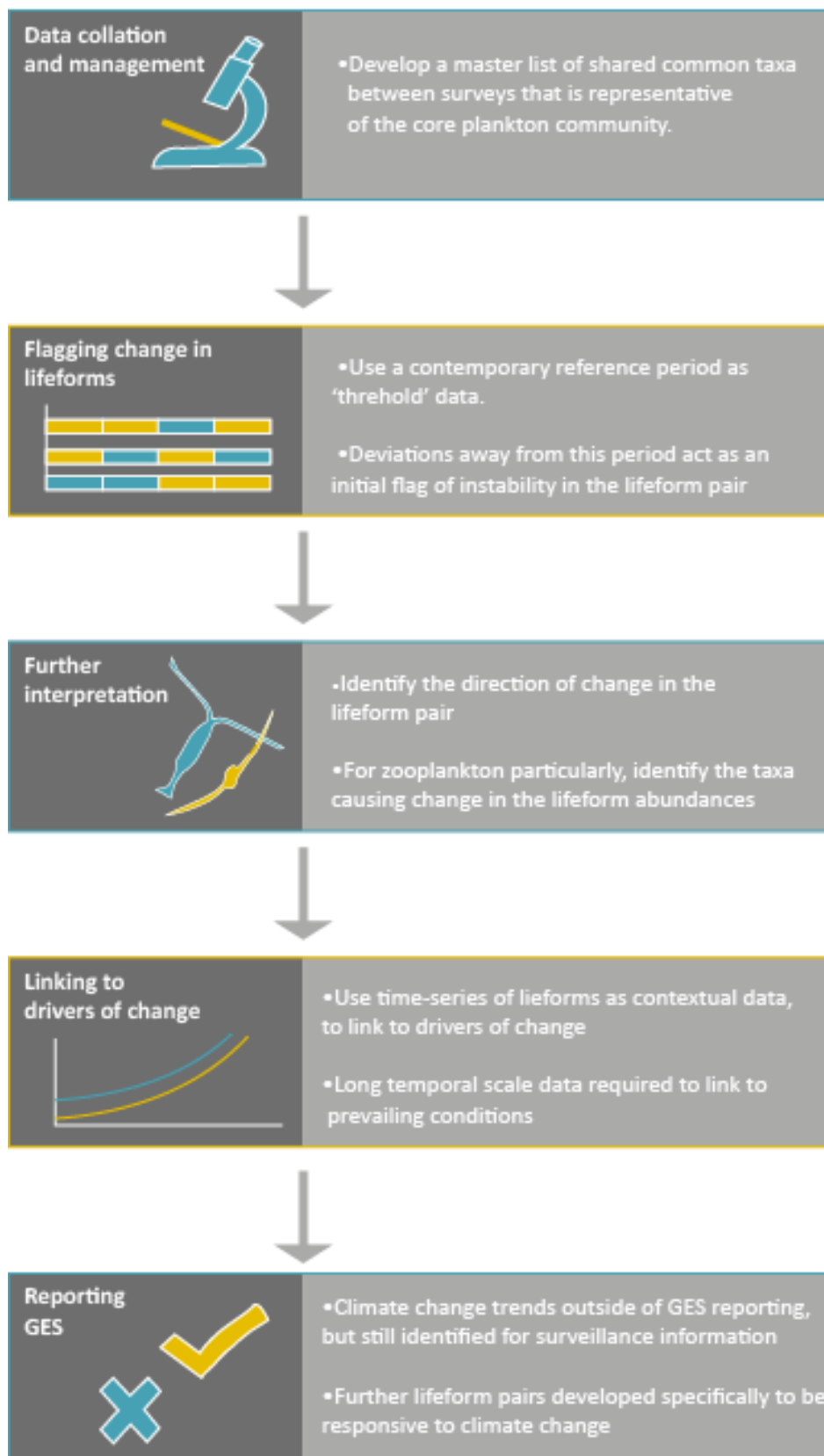


Figure 6.3 A proposed assessment workflow for PH1/FW5, based on results of this thesis, including the use of long temporal scale plankton data to provide context on the drivers of change.

6.6 Concluding remarks

The implementation of the Marine Strategy Framework Directive in the North East Atlantic is at a crossroads, as both initial and intermediate assessments of Good Environmental Status have been undertaken at both the member-state and OSPAR levels. A key test for the effectiveness of the MSFD in guiding the implementation of an ecosystem-based approach to management is in whether future programmes of measures are added-to or altered in response to the outcomes of the ecosystem assessment process. Furthermore, a second key test for the effectiveness of the MSFD is whether biodiversity components, and the pressures facing biodiversity, are managed in an integrated manner or continue to be managed separately. The adaptive nature of the MSFD, however, means that the ecosystem assessment process can continually be improved, with new information incorporated, leading to an improved regional-scale programme of measures.

Ultimately, long temporal scale plankton data are needed to make robust assessments of the status of pelagic habitats through confidently linking plankton indicator change to the drivers of change. Furthermore, surveillance information on changing prevailing conditions provided through long-term plankton monitoring can be incorporated into future ecosystem assessments. Although, importantly, this surveillance role for plankton indicators would be secondary to the primary role of plankton indicators which is to detect the impacts of direct anthropogenic pressures such as eutrophication, the importance of this surveillance information, and indicators for climate driven change, should not be undervalued in the implementation of effective ecosystem-based management.

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