

The Continuous Plankton Recorder survey: how can long-term phytoplankton datasets contribute to the assessment of Good Environmental Status?

Abigail McQuatters-Gollop^{a*}, Martin Edwards^{a,b}, Pierre Helaouët^a, David G. Johns^a, Nicholas J.P. Owens^{a,b}, Dionysios E. Raitsos^c, Declan Schroeder^d, Jennifer Skinner^a, and Rowena F. Stern^a

a Sir Alister Hardy Foundation for Ocean Science (SAHFOS), The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK.

b Marine Institute, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom

c Plymouth Marine Laboratory (PML), Prospect Place, The Hoe, Plymouth PL1 3DH, UK

d Marine Biological Association (MBA), The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK.

* Corresponding author:

Phone: +44 (0)1752 633233

E-mail address: abiqua@sahfos.ac.uk (A. McQuatters-Gollop)

Abstract

Phytoplankton are crucial to marine ecosystem functioning and are important indicators of environmental change. Phytoplankton data are also essential for informing management and policy, particularly in supporting the new generation of marine legislative drivers, which take a holistic ecosystem approach to management. The Marine Strategy Framework Directive (MSFD) seeks to achieve Good Environmental Status (GES) of European seas through the implementation of such a management approach. This is a regional scale directive which recognises the importance of plankton communities in marine ecosystems; plankton data at the appropriate spatial, temporal and taxonomic scales are therefore required for implementation. The Continuous Plankton Recorder (CPR) survey is a multidecadal, North Atlantic-basin scale programme which routinely records approximately 300 phytoplankton taxa. Because of these attributes, the survey plays a key role in the implementation of the MSFD and the assessment of GES in the Northeast Atlantic region. This paper addresses the role of the CPR's phytoplankton time-series in delivering GES through the development and informing of MSFD indicators, the setting of targets against a background of climate change and the provision of supporting information used to interpret change in non-plankton indicators. We also discuss CPR data in the context of other phytoplankton data types that may contribute to GES as well as explore future possibilities for the use of new and innovative applications of CPR phytoplankton datasets in delivering GES. Efforts must be made to preserve long-term time series, such as the CPR, which supply vital ecological information used to inform evidence-based environmental policy.

Keywords: phytoplankton, time-series, ocean policy, Continuous Plankton Recorder, climate changes

Introduction

Phytoplankton are the sea's major marine primary producers, generating 50% of the world's oxygen and playing an important role in ocean carbon cycling (Falkowski et al., 2004). Plankton therefore

comprise the base of the marine food web, and alterations to their composition and abundance often have repercussions on higher trophic levels, including those of economic importance, such as fish (Platt et al., 2003; Richardson and Schoeman, 2004). Phytoplankton are also particularly good indicators of marine environmental change (Hays et al., 2005). They are seldom commercially exploited, most individuals are short-lived so populations are only minimally influenced by persistence of individuals from previous years, and they respond rapidly to changes in their environment through range alterations (Hays et al., 2005). Phytoplankton responses to environmental change occur at a variety of spatio-temporal and taxonomic scales, from ephemeral blooms of a single species in a local area to regional-scale decadal changes in community composition.

Phytoplankton datasets which are 20 – 30 years in length, spatially extensive and taxonomically detailed are increasingly important in informing the new generation of policy mechanisms which seeks to manage the marine ecosystem holistically. The European Union's Marine Strategy Framework Directive (MSFD) aims to achieve Good Environmental Status (GES) of European seas by 2020 through implementation of an ecosystem approach to marine management. The Directive requires the development of regional sea scale indicators, encompassing both near-shore and off-shore waters, which must be monitored towards environmental targets. Both the Directive and the supporting Commission Decision explicitly acknowledge the ecological importance of achieving GES for multiple aspects of the phytoplankton, including phytoplankton species, communities, functional groups, and biomass (European Commission, 2008, 2010). Under the MSFD, GES must be achieved for 11 qualitative descriptors of the marine ecosystem. Phytoplankton data are required to inform two of these descriptors which are undergoing collective implementation (Descriptor 1: Biodiversity, Descriptor 4: Food webs). Along with Descriptor 6: Seafloor integrity, these three descriptors are collectively known as the 'biodiversity' descriptors as they represent facets of ecosystem state. Phytoplankton data are also required for supporting Descriptor 5: Eutrophication, which is a 'pressure' descriptor undergoing implementation through a slightly different process; for this reason Descriptor 5 is not a focus of this work.

In Europe, the majority of phytoplankton monitoring programmes which collect species-level data is coastal and usually associated with a local laboratory or observatory (e.g. Southward et al., 2005; Wiltshire et al., 2010; Zingone et al., 2010 and other papers in this issue), leaving non-coastal areas critically undersampled (Edwards et al., 2010; Koslow and Couture, 2013). Similarly, phytoplankton datasets possessing the minimum 30-40 year time-series, required to determine multidecadal climate-driven trends (Henson et al., 2010), are also scarce. Not surprisingly, plankton monitoring programmes, which are multidecadal, taxonomically detailed and regularly sample the open ocean at a wide spatial scale, are the rarest (Edwards et al., 2010; Koslow and Couture, 2013).

The Continuous Plankton Recorder (CPR) survey, managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in the UK, routinely monitors the open sea environment, providing a comprehensive picture of epipelagic plankton communities at the regional scale. Approximately 500,000 plankton samples have been collected in the surface waters of the North Atlantic basin on a monthly basis since 1931 (Fig. 1). The collection and taxonomic analysis of CPR samples have been carried out using a consistent methodological approach since 1958 (1948 for the CPR's Phytoplankton Colour Index - PCI), making the CPR survey the longest continuous dataset of its kind in the world (Edwards and Richardson, 2004). CPR taxonomists routinely identify and enumerate

Comment [AMG1]: Other papers in this special issue

over 300 phytoplankton taxa collected by the survey, which has resulted in an 80+ year dataset of comprehensive taxonomic depth. Research using CPR data has advanced the understanding of phytoplankton spatio-temporal dynamics by examining their responses to both natural and anthropogenic components of climate variability, and their links to anthropogenic pressures. CPR data have also contributed to the development of applied indicators that routinely inform UK, European and basin-scale policy and management mechanisms (Edwards et al., 2010; McQuatters-Gollop, 2012). Because of the spatio-temporal scope and taxonomic breadth of the time-series, CPR phytoplankton data are integral to the assessment and delivery of Good Environmental Status through the MSFD.

This paper addresses the role of the CPR's phytoplankton time-series in delivering GES through the development and informing of MSFD indicators, the setting of targets against a background of climate change and the provision of supporting information used to interpret change in non-biodiversity indicators. We also discuss CPR data in the context of other phytoplankton data types that may contribute to GES as well as explore future possibilities for the use of new and innovative applications of CPR phytoplankton datasets in delivering GES.

The CPR's methodology: a balance between taxonomic detail and sampling constraints

Taxonomic information provides a crucial understanding of the most basic component of biodiversity: which organisms are present in a region or ecosystem? Fundamental knowledge of phytoplankton taxonomy is necessary to assess diversity, understand plankton community dynamics, gain insights into phytoplankton responses to climate change, detect non-indigenous species, and identify emerging scientific and policy issues. This type of detailed, species level phytoplankton community composition information can only be obtained through analysis by trained taxonomists. Unlike modern analysis techniques (such as automated visual identification, flow cytometry, satellite remote sensing, or fluorometry) which can, for the most part, only discriminate coarse phytoplankton groups, taxonomists can distinguish a wide variety of species relatively efficiently, generating information needed to investigate diversity in complex marine systems. At the wide spatial and multiple decadal scales monitored by the CPR, detailed taxonomic information forms the foundation to understand spatio-temporal changes in global distributions of species and alterations to their community composition (e.g., Beaugrand et al., 2002; Burrows et al., 2014). For a detailed review of the CPR's general methodology and history, which is outside the current remit, please see Batten et al. (2003), Reid et al. (2003) and Richardson et al. (2006).

The CPR most effectively samples phytoplankton which are robust and large in size, particularly diatoms and armoured dinoflagellates; small or delicate phytoplankton taxa are less adequately captured by the CPR for two key reasons. Firstly, the mesh size of the CPR sample silk is relatively large (270 μm) compared to most nets designed for collecting phytoplankton which have a mesh size of < 50 μm . As a fisheries ecologist, Alister Hardy originally conceived the CPR as a way to monitor the key food source for larval fish: zooplankton. The mesh size of 270 μm was chosen in order to capture zooplankton yet still provide an indication of phytoplankton bloom conditions without clogging (Hardy, 1939); the CPR was not originally designed as a phytoplankton monitoring tool. Secondly, the sampling method itself can be destructive, with plankton retained on a continuously moving band of filtering silk, which is then wrapped around a storage spool (Batten et al., 2003).

Despite these challenges, over 300 North Atlantic phytoplankton taxa are regularly identified, most to species level, and enumerated in CPR samples.

Due to the time demands required to analyse large numbers of CPR samples by light microscopy, there is often insufficient time to identify all taxa to as fine a resolution as scientifically feasible. Consequently, certain groups are simply recorded to genera. The nature of an established time-series over an extended period of time, however, results in a large base of expertise which allows responsive expansion of taxonomic scope with little additional effort. With just a small investment in time and training, the identification to the species level of certain relevant taxa can be implemented. For example, throughout the CPR's history *Dinophysis* was identified only to genus level. In response to increasing interest in harmful algal bloom (HAB) species, since 2004 the twelve most frequently occurring *Dinophysis* species have been identified and recorded to the species level; *Dinophysis* also continues to be recorded at its coarser genus level in order to maintain the original time-series. Similarly, recent concern about ocean acidification has led to increased interest regarding coccolithophores, a calcareous phytoplankton taxa. Prior to 2014 coccolithophores were simply recorded to a coarse taxonomic resolution (class: Coccolithophyceae). Since 2014, eight distinct taxa are now routinely recorded within this group, while the taxa continues to be recorded at the coarse level in order to maintain the historically consistent time-series (Johns and Brice, 2014). The CPR dataset has the flexibility to maintain its historic time-series yet can expand taxonomically to meet policy needs: this may become important during the forthcoming stages of the MSFD implementation process.

As with taxonomic detail, a balance is also required between the number of analysed samples needed to maintain the CPR's extensive spatial coverage and the identification and enumeration of all phytoplankton individuals on each sample. Each CPR sample consists of a piece of silk measuring 15 cm by 10.5 cm (an area of approximate 157 cm²) and representing 10 nautical miles of tow (approximately 3 m³ of water). The size of each sample means that it is not feasible to identify and count all individual cells, particularly during periods of elevated phytoplankton biomass. To maintain the high number of samples analysed by the survey, phytoplankton cells are instead recorded as either present or absent across 20 microscopic fields of view spanning each CPR sample. CPR phytoplankton abundance is therefore a semi-quantitative estimate (i.e. the species is recorded once per field independently of the number of cells in a field). The proportion of cells captured by the silk is a good indicator of the major changes in abundance, distribution, and community composition of the phytoplankton, and is consistent and comparable over time (Robinson, 1970).

In addition to its taxonomic time-series, the survey also records an indicator of phytoplankton biomass, the Phytoplankton Colour Index (PCI). The PCI is a visual estimate of phytoplankton biomass, recorded using a consistent methodology since 1948. The PCI is essentially a measure of the 'greenness' of the CPR's sample collection silk, caused by chlorophyll staining (Batten et al., 2003). As the values are categorical (0 (no green), 1 (very pale green), 2 (pale green), 6.5 (green)) the PCI is a semi quantitative estimate of phytoplankton biomass; however, PCI has been successfully intercalibrated and correlated with independent measurements of both *in situ* fluorometric (Raitsos et al., 2013) and satellite-derived (Raitsos et al., 2005) chlorophyll estimates. In both cases, a highly significant relationship was found between PCI and chlorophyll, while there was a distinct differentiation (95% confidence limits) in mean chlorophyll among PCI categories. These results enabled the retrospective calculation of chlorophyll for CPR samples, creating a quantitative time-

series from 1948 (Raitso et al., 2005). For further technical detail regarding PCI see Batten et al. (2003). While the PCI is not fully quantitative, it is a consistent, multi-decadal time-series estimate of phytoplankton biomass at an expansive spatial scale, thus enabling a robust interpretation of results.

The CPR survey samples most of the North Atlantic on a monthly basis, with sampling predominantly occurring in transects crossing shelf and open sea waters. The survey is able to consistently sample offshore regions due to its cooperation with 'ships of opportunity' (SOOPs), commercial vessels such as cargo ships and ferries, which tow CPRs on their normal operating routes. The relationship between the CPR survey and the merchant navy enables oceanic sample collection via CPR for a fraction of the cost of traditional ocean plankton sampling which includes expensive equipment, scientist salaries and research vessel costs. SOOPs normally cross ocean regions rather than track along coastlines; for the CPR survey this means a deficit in more commonly sampled coastal regions but routine sample collection in the traditionally less accessible offshore marine regions. Because not all ships travel consistent routes every month, CPR sampling effort is also uneven. Despite this, the survey sampled 140,208 nautical miles of sea in 2014, generating over 10,000 plankton samples and providing data to inform MSFD indicators at the corresponding regional scale.

CPR data in the context of other phytoplankton data

In addition to the CPR, other methods such as fixed point station sampling (Wiltshire et al., 2010), automated optical imaging identification (Álvarez et al., 2011; Jakobsen and Carstensen, 2011), remote sensing (Sathyendranath et al., 2014), fluorometry (Li et al., 2006), and flow cytometry (Li et al., 2006) are also used to monitor phytoplankton in the Northeast Atlantic. As with the CPR, these methods have strengths and weaknesses which enable them to monitor aspects of the plankton community with varying levels of effectiveness and inform policy indicators to differing degrees.

Due to the patchiness of the plankton distribution, an individual phytoplankton sample is unlikely to be representative of the community of a larger water mass. Although regional chlorophyll data are collected via satellites, and ferry boxes measure biomass along continuous tracts, the CPR is the only regional scale species-level plankton sampling survey in European seas. The CPR can therefore provide an overview of MSFD-scale regional phytoplankton dynamics, with, as mentioned previously, a focus on non-coastal waters. In contrast, fixed point sampling stations usually collect discrete measurements of near-coastal areas and primarily reflect local scale changes. When data from fixed point sampling stations are employed alongside those collected by the CPR, the CPR provides an important broader context against which to interpret changes observed at coastal and more locally-representative fixed point stations. The use of fixed point and CPR datasets in tandem, therefore, affords the formation of a more spatially robust picture of phytoplankton community distribution in European seas in line with the regional scale of the MSFD.

Most phytoplankton datasets are shorter than the 30-40 year time-series required to identify multidecadal climate-driven trends (Henson et al., 2010). Phytoplankton time-series based on traditional light microscopy methods of analysis are generally longer in length than those depending on newer technologies such as automated optical imaging identification, remote sensing, fluorometry, and flow cytometry. The Helgoland Roads fixed point plankton time-series in the German Bight, for example, commenced in 1962, making it nearly as long as the CPR's time-series (Wiltshire et al., 2010). Helgoland and the CPR are exceptional as most European phytoplankton time-series are considerably shorter (Edwards et al., 2010). Samples at fixed point stations are often

collected bi-weekly, weekly or even daily, revealing detailed changes in phytoplankton variability. In contrast, CPR data are best used at the monthly temporal resolution needed to monitor seasonal and annual changes required for indicator development.

Phytoplankton datasets with a detailed taxonomic resolution are key to informing the MSFD's biodiversity indicators. Like the CPR, samples collected at fixed point stations are analysed to species level. Consistent and reliable speciation is not currently possible with newer technologies such as flow cytometry, fluorometry, HPLC pigment analysis, remote sensing and automated visual identification, which can be used to provide functional group or bulk indicators, but contain no underlying species information. While the CPR best samples large and robust phytoplankton, the sampling methods used at fixed point stations allow identification and enumeration of fragile and small phytoplankton taxa, although sampling and analysis methodologies vary between fixed point monitoring programmes. Due to its unique sampling method, data collected with the CPR are not directly comparable to those from fixed point sampling stations, even for taxa which are well sampled in both instances. In other words, data from the two types of sampling cannot be directly combined into a single time-series but instead must be used in parallel; this is a research gap that must be filled in order to increase the policy usefulness of both types of phytoplankton data.

Setting targets against a background of climate change

The MSFD focuses only on changes caused by manageable anthropogenic pressures. Climate change is a long-term issue outside the scope of the MSFD and is referred to as a 'prevailing condition' in the Directive. This means that climate change impacts should be considered when defining a vision for GES and when setting targets, but the Directive itself is not intended to mitigate climate change (McQuatters-Gollop, 2012). In the North Atlantic, phytoplankton community responses to climate drivers have included alterations to species distributions and abundances, changes in overall phytoplankton biomass and growing season length, and changes in the ecosystem functioning and productivity (Beaugrand et al., 2002; Edwards et al., 2002; Edwards et al., 2001a; Edwards and Richardson, 2004; McQuatters-Gollop et al., 2011). An understanding of prevailing conditions is therefore essential for identifying climate change impacts and thus for interpreting which ecosystem changes are anthropogenically-triggered, and can therefore be managed through the MSFD.

The CPR survey's focus on open ocean plankton sampling provides a spatial context against which data from infrequent research cruises or coastal fixed point sampling stations may be interpreted. Because offshore waters are less likely to be impacted by land-based anthropogenic pressures than coastal waters, the wider geographic perspective of the CPR can help facilitate separation of plankton responses to climate from those driven by direct anthropogenic pressures. For example, during the 1970s, 1980s and 1990s, data from fixed point stations in some coastal regions of the North Sea revealed changes in the plankton community that included increased phytoplankton biomass, increased flagellate abundance and elevated numbers of harmful algal bloom taxa which were attributed to anthropogenic eutrophication (Cadee, 1986; de Jonge et al., 1996; Hickel et al., 1993). Examination of offshore CPR data revealed that the changes occurring in coastal waters were also observed in the less anthropogenically-impacted non-coastal North Sea (Edwards et al., 2006; McQuatters-Gollop et al., 2007b), indicating that regional scale phytoplankton dynamics were being driven not by anthropogenic nutrient input but by large-scale climatic forcing. This suggests that climate is the prevailing driver of phytoplankton dynamics throughout the North Sea, even in

nutrient-rich coastal waters (McQuatters-Gollop et al., 2007b; McQuatters-Gollop and Vermaat, 2011). The ability to apportion drivers of change to phytoplankton dynamics is needed for constructing GES targets as well as for informing the MSFD's programme of management measures for achieving GES.

Because the Northeast Atlantic phytoplankton community has experienced climate-driven changes, defining phytoplankton targets for GES is not as easy as simply selecting a historical state to which to aspire. In the case of target-setting for MSFD indicators, the CPR's multidecadal time-series provides context between contemporary and historical plankton community states. For example, in the 1980s the Northeast Atlantic experienced a regime shift, a step-wise set of rapid changes in the structure and functioning of the marine ecosystem; the most notable aspect of the regime shift was a region-wide increase in phytoplankton biomass (Fig. 2; Beaugrand, 2004; McQuatters-Gollop et al., 2011; Reid et al., 1998). Since the regime shift, the North Sea has been in a warm-temperate state characterised by relatively high levels of phytoplankton biomass and increased abundance of warmer-water plankton taxa; these changes were climate driven and not due to nutrient loading (Beaugrand, 2004; McQuatters-Gollop et al., 2007b; McQuatters-Gollop and Vermaat, 2011). Because the North Sea plankton community is now considerably different from its pre-regime shift counterpart, it makes sense to set phytoplankton targets in line with the current, rather than the previous, regime. By considering the temporal context revealed by a long time-series, environmental targets can be selected which are both ecologically meaningful (i.e. they represent GES) and realistic (i.e. the targets reflect a vision of GES which acknowledges climate variability and past ecosystem use).

Developing and informing biodiversity indicators of GES

The Oslo-Paris Convention (OSPAR) is the Regional Seas Commission responsible for delivery of the biodiversity-relevant MSFD indicators and targets in the Northeast Atlantic region. The CPR programme is the only plankton survey with a pan-northern European spatial coverage, spanning political boundaries and supporting indicator assessment at the regional sea scale required by the Directive. CPR data are therefore integral to both the development process and subsequent informing of each of the three regional scale plankton indicators. Two of the indicators (plankton biomass and the plankton biodiversity index) are biodiversity indicators (Descriptor 1 in the MSFD), while the plankton lifeform index is both a biodiversity and food web (Descriptor 4 in the MSFD) indicator. The indicators presented here are intended to be used together as an indicator suite as they each represent a different aspect of phytoplankton community change. As the indicators are currently in development, it is not the purpose of this paper to provide technical detail regarding each indicator; this will be published elsewhere when development is complete. The focus is instead on the role of the CPR's phytoplankton time-series in informing the indicators.

Plankton lifeform index

The plankton lifeform index is comprised of time-series of pairs of plankton functional groups, or lifeforms, and has similarities with the UK's MSFD plankton indicator approach (Gowen et al., 2011; Gowen et al., 2013; McQuatters-Gollop et al., 2014). The lifeform approach groups plankton taxa into ecologically-relevant lifeform pairs, changes in the relative abundances of which are linked to manageable anthropogenic pressures. Single-species plankton indicators are relatively easy to interpret if the species is abundant but interpretation of the dynamics of less-common species is

Comment [AMG2]: Editor: Please also add 'Gowen et al, this issue'

more complex (Beaugrand, 2005). This is because variability in single species time-series may be primarily attributable to factors such as environmental variation, misidentification or miscounting of organisms, or sample contamination, masking the identification of anthropogenically-driven change (Beaugrand, 2005; de Jonge, 2007). Indicators based on lifeforms are also more easily intercomparable between datasets than those which are species-based as the effects of extreme variation of a single taxon are relatively less important (Beaugrand, 2005; McQuatters-Gollop et al., 2014).

The CPR taxonomically-detailed phytoplankton time-series is central to the development of OSPAR's plankton lifeform indicator because each lifeform consists of multiple taxa performing a similar functional role. Taxon-specific biological traits were used to group CPR taxa into lifeforms (Table 1). If a change is detected in a particular lifeform, further investigation into the abundance of the lifeform's component taxa is possible through the exploration of the underlying taxonomic data. Once the method is suitably refined using CPR data, its application will be expanded to other phytoplankton datasets in the OSPAR area. Though data from the CPR and fixed point sampling stations cannot be combined into a single time-series, relative changes in time-series can be compared and assessed, providing a robust picture of the regional phytoplankton community.

Table 1: Lifeform pairs which are undergoing testing for suitability as indicators. Only pairs with phytoplankton-relevant lifeform components are listed. Shifts in the relative abundance of the lifeforms provide an indication of ecological change.

Lifeform pair	Ecological rationale for pair selection
Diatoms and dinoflagellates	Dominance by dinoflagellates may be an indicator of eutrophication and result in less desirable food webs
Large (>20µm) and small (<20 µm) phytoplankton	Size-based indicator of the efficiency of energy flow to higher trophic levels
Diatoms and non-heterotrophic dinoflagellates	Shift in primary producers may indicate eutrophication
Harmful algal bloom (HAB) dinoflagellates and non-HAB dinoflagellates	Shift in phytoplankton community towards/away from dinoflagellate HAB taxa
Non-carnivorous zooplankton and phytoplankton	Indicator of energy flow and balance between primary producers and primary consumers
Pelagic diatoms and tychopleagic diatoms	Indicator of benthic disturbance and frequency of resuspension events

Phytoplankton biomass

Phytoplankton biomass is frequently used as an indicator of phytoplankton productivity and is often also used as an indicator of eutrophication as phytoplankton are among the first ecosystem components to respond to nutrient loading. Climate variability, however, is also a driver of change of

North Atlantic phytoplankton biomass, as mentioned previously. The MSFD's phytoplankton biomass indicator is in development using chlorophyll data from fixed point sampling stations; once the indicator is further developed it will be applied to data from the CPR's PCI. As with the plankton lifeform indicator, time-series constructed from the PCI cannot be directly compared to those populated with chlorophyll data. However, relative changes in the two types of datasets can be compared. Though not explicitly a food web indicator, it is anticipated that the phytoplankton biomass indicator will also support the food web indicator regarding productivity (production per unit biomass) of key species or trophic groups (European Commission, 2010), which is also in development.

Plankton biodiversity index

Diversity indices such as species richness, evenness or dominance can identify subtle ecosystem changes by reflecting modifications in the structure of the assemblages or the abundance of certain species (Beaugrand, 2005). These changes may not be evident using the lifeforms or biomass indicators. Although diversity indices may detect change, they can be difficult to interpret as they attempt to capture ecosystem state in a single variable (Beaugrand, 2005). High resolution taxonomic data obtained via light microscopy are needed to inform biodiversity indices. Several indices representing phytoplankton biodiversity are currently undergoing testing with data from fixed point stations. The next phase of testing will see the indices applied to CPR phytoplankton data at the regional scale.

Informing non-biodiversity indicators of GES

In addition to the development and application of plankton indicators for the delivery of the MSFD's biodiversity descriptors, CPR data regarding phytoplankton community composition can potentially be used to inform indicators supporting non-biodiversity descriptors. Datasets which will support indicator interpretation and assessment likely will be required later in the process, after the current development phase. The following examples, however, illustrate where CPR data may support this work.

Descriptor 2 of the MSFD focuses on non-indigenous (NIS) species. Descriptor 2 is a pressure rather than a state descriptor; however, CPR data can support the assessment of plankton NIS in the Northeast Atlantic MSFD region. A thorough understanding of the species composition of a marine region over an extended time period is necessary in order to recognise and track the spread of NIS. Because much of the North Atlantic has been monitored by the CPR survey for multiple decades, occurrences of non-indigenous taxa are relatively easy to identify. Over the course of the survey, several phytoplankton taxa have been discovered in areas where they were previously absent – *Mediopyxis* spp. (Kraberg et al., 2012), *Coscinodiscus wailesii* (Boalch and Harbour, 1977; Edwards et al., 2001a), and *Neodenticula seminae* (Reid et al., 2007). For a number of these taxa, vectors of introduction (e.g. ballast water and climate-driven range expansion) have been identified, linkages which would otherwise be difficult to ascertain without a multidecadal time-series.

As with the NIS descriptor, Descriptor 5 is a pressure descriptor, in this case concerning the minimisation of eutrophication effects, including anthropogenically-induced harmful algal blooms (HABs). In many cases HABs are a natural phenomenon driven by hydro-climatic variability; however, increased occurrence or abundance of some HAB taxa has also been associated with anthropogenic

eutrophication (Anderson et al., 2002). Multidecadal abundance changes have been documented for multiple Northeast Atlantic HAB taxa; these changes have been linked to regional climate change (Edwards et al., 2006; Hinder et al., 2012). Separating anthropogenically-driven HAB events from those resulting from climate variability is a key management challenge. The CPR's spatio-temporal scope can provide a regional multidecadal overview of HAB species dynamics which can help interpret the wider drivers of change overlying the occurrence of localised near-shore HABs, which are more likely to result from local nutrient loading.

Expanding the policy contribution of the CPR's phytoplankton time-series

Much of the diversity in pelagic environments is from pico (<2 µm) and nano-sized (<20 µm) organisms that the CPR sampling system, like most plankton nets, is not designed to capture. Consequently, a portion of the phytoplankton community is not used to support policy indicators. Analysis of CPR samples using modern genetic techniques reveals that the silks do indeed retain a vast amount of unexplored nano and pico-sized, and even bacterial (Vezzulli et al., 2012), microbial diversity, which is different to that seen by traditional taxonomic analysis (Fig. 3). These molecular techniques aim to fill the gap existing in both the portion of the phytoplankton community sampled by the CPR and our scientific knowledge of the spatio-temporal distributions of these organisms.

In addition to the application of genetic techniques to traditional CPR silk samples, the range of microbial organisms sampled by the CPR has been further extended with the addition of an automated sampling device (the Water and Microplankton Sampler, or WaMS; Stern et al., in press). Samples from WaMS have revealed a new range of nano- and pico-sized phytoplankton taxa, including tiny chlorophyta (<2 µm) and delicate chrysophyta, as well as organisms which are currently unknown (Fig 4). As microbial time-series lengthen, these data may be used to inform regional MSFD plankton indicators, illuminating a more complete view of the phytoplankton community and a more thorough understanding of its population dynamics.

The use of CPR phytoplankton data in conjunction with remotely-sensed data has also enriched the policy application of both datasets (Henson et al., 2009; McQuatters-Gollop et al., 2007b; Raitsos et al., 2014). Recent work using CPR data with satellite data has advanced the capability to detect phytoplankton functional groups from space (Sathyendranath et al., 2014). An expansive coccolithophore bloom in the subarctic North Atlantic in 1998, was detected via analysis of remote sensing data. Data from the CPR were used to identify the species comprising the bloom, *E. huxleyi*, as well as other co-occurring phyto and zooplankton taxa, while the remote sensing time-series allowed detailed observation of the bloom's formation, spatial expanse and decline (Raitsos et al., 2006). Further modelling work using a combination of CPR, satellite and environmental data has enabled the prediction of phytoplankton functional groups under different environmental conditions in the North Atlantic Ocean (Raitsos et al., 2011). The synergistic use of these two datasets progresses the identification of phytoplankton taxa from space (one of the most challenging targets of satellite oceanography), while also increasing the predicative capacity of models to inform and support MSFD indicators.

Much of the pioneering work on ocean acidification effects, for example, has focussed on coccolithophores. Little information, however, is available regarding the impacts that ocean acidification is having, or might have, on coccolithophores outside of a controlled environment or on the occurrence of this taxa *in situ* in the North Atlantic. Most investigations into the subject have

taken place in short-term laboratory, or mesocosm, experiments, and have focussed on the physiological effects of pH change (Iglesias-Rodriguez et al., 2008; Riebesell et al., 2000; Zondervan et al., 2001). Contrary to expectations, CPR data show an increase in the occurrence of coccolithophores in the North Sea (Beare et al., 2013) and North Atlantic (Beaugrand et al., 2013) during the past six decades. Interestingly, neither study found a significant relationship between coccolithophore occurrence and pH, suggesting instead that the current primary driver of North Atlantic calcifying plankton appears to be sea temperature warming (Beare et al., 2013; Beaugrand et al., 2013). Ocean acidification, and other such emerging issues, may present serious threats to marine organisms in coming decades. The CPR, by providing an important context for laboratory experiments, offers a crucial baseline against which to measure such future changes.

The value of the CPR time-series continues to increase with time because the dataset can be retrospectively investigated with reference to issues of emerging political or scientific importance. The extensive archive of CPR samples, extending back to the 1960s, provides opportunities to fill yet-to-be-recognised policy needs. The CPR archive and data have been used to powerful effect in concert with satellite data (e.g. Raitsos et al., 2014) and microbial techniques (Stern et al., in press), uses beyond the imagination of Alister Hardy when he introduced the CPR. These examples serve to demonstrate that the archive will remain a resource for equally unimaginable future new technological innovations and scientific interrogation.

The CPR survey will continue to evolve to address emerging policy needs and scientific questions by embracing new developments in technology. 'Lab on chip' technologies are currently in development and could conceivably be developed to monitor the phytoplankton and zooplankton through deployment on CPRs (see for example, Psaltis et al., 2006). Similarly, taxonomic micro-array technologies offer an exciting new approach for rapid identification of plankton (Kegel et al., 2013); indeed their utility has been shown recently for selected North Sea phytoplankton (Wollschläger et al., 2014). However, these innovative techniques are essentially only research tools and it will take time before they are developed sufficiently to be used to inform policy as part of the routine CPR survey.

Despite the survey's expansive research base, the CPR phytoplankton dataset has been explored less thoroughly than its zooplankton time-series. In depth studies have investigated the ecological niches of individual zooplankton species (Helaouët and Beaugrand, 2009; Helaouët et al., 2011), examined the role of various zooplankton taxa in marine food webs (Beaugrand et al., 2008; Beaugrand and Kirby, 2010; Kirby and Beaugrand, 2009; Witt et al., 2007) and performed a spatio-temporal analysis of calanoid copepod biogeographical shifts (Beaugrand et al., 2002; Helaouët et al., 2013). Similar tools have yet to be applied to the phytoplankton community. With a few exceptions (phytoplankton biomass (Edwards et al., 2001b), calcifying phytoplankton (Beaugrand et al., 2013), *Neoceratium* spp. (Beaugrand et al., 2010), *Coscinodiscus wailesii* (Edwards et al., 2001a), *Neoceratium arcticum* (Johns et al., 2001), HAB taxa (Edwards et al., 2006; Hinder et al., 2012)) there is also a paucity in the mapping of phytoplankton groups and taxa, particularly individual species, at interannual time scales. Even diatoms and dinoflagellates, the two main functional groups, lack a series of decadal maps, although their intra-annual spatial distributions have been reported (McQuatters-Gollop et al., 2007a). This information is sorely needed to interpret changes and patterns observed both in the course of investigative research and policy monitoring.

Regardless of its recognised importance as both a freely available source of data for collaborative research projects and a key dataset supporting policy (Brander et al., 2003; Edwards et al., 2010; Field et al., 2013; McQuatters-Gollop, 2012), sustained funding of the CPR survey presents a challenge. This is not a new problem or one unique to the CPR; there is a recognised scarcity of long-term ecological datasets, particularly in non-coastal regions, driven by a lack of funding (Edwards et al., 2010; Koslow and Couture, 2013). The principal reasons for the termination of established monitoring programmes are also historically consistent and near-ubiquitous - funding is limited and a time lag exists between data collection and scientific yield (Duarte et al., 1992). Like many other sustained observational time-series that support decision making, the CPR survey is only partially publicly funded. Supplementary funding, pieced together from disparate income sources, is required to fill this gap; this piecemeal approach is both risky and resource intensive. Although sometimes viewed as a plodding accountancy exercise, long-term time series such as the CPR need to be recognised for their service in supplying vital ecological information and to ensure their continued contribution to evidence-based environmental policy.

Acknowledgements

The authors would like to extend our gratitude to the CPR survey's supporters. We must thank, in particular, past and present CPR plankton taxonomists as well as the merchant navy which voluntarily tows CPRs – both are integral to this unique dataset. A.M.G. is gratefully supported by a NERC Knowledge Exchange Fellowship as well as SCOR 137: Working Group on Global Coastal Phytoplankton Time-series.

Figure captions

Fig 1: North Atlantic Continuous Plankton Recorder (CPR) samples collected between 1958 and 2013. Each point represents one sample.

Fig 2. Decadal change in North Atlantic Phytoplankton Colour Index (PCI) by CPR standard area. Since the 1950s the PCI has shown a clear increase in phytoplankton biomass throughout much of the North Atlantic basin. Standard area boxes with no data appear blue in colour.

Fig 3: A small subset of taxa from a 2003 North Sea CPR sample obtained using 454 sequencing technology. Chlorophyta, Cryptophyta, fungi and most heterokonts found here are unidentifiable during traditional light microscopy examination of CPR samples. Taxa in bold were found in the sample; all others are reference taxa.

Fig. 4: Microbial eukaryotic phylogeny of the large ribosomal subunit DNA marker from a November 2011 English Channel sample using the CPR's Water and Microplankton Sampler (WaMS). Taxa in bold were found in the WaMS sample; all others are reference taxa. All taxa collected here, except red algae (Bangiophytes), are micro to pico-sized eukaryotes, less-consistently retained by traditional CPR sampling and therefore provide a unique and complementary dataset. Such surveys highlight the role of microbial heterotrophs, such as fungi, illustrated here. This sample also contained DNA from red algae, an unusual offshore finding for a rocky shore macrophyte that may represent fragmented dead material or gametes.

Fig 1

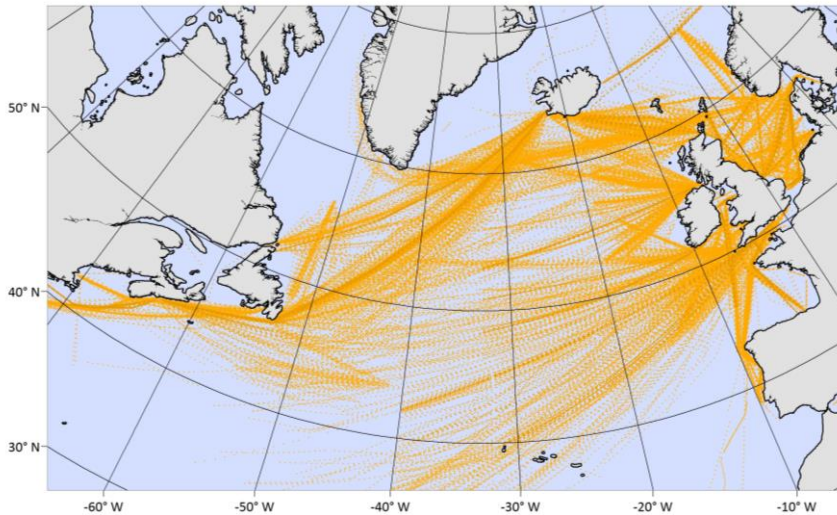


Fig 2

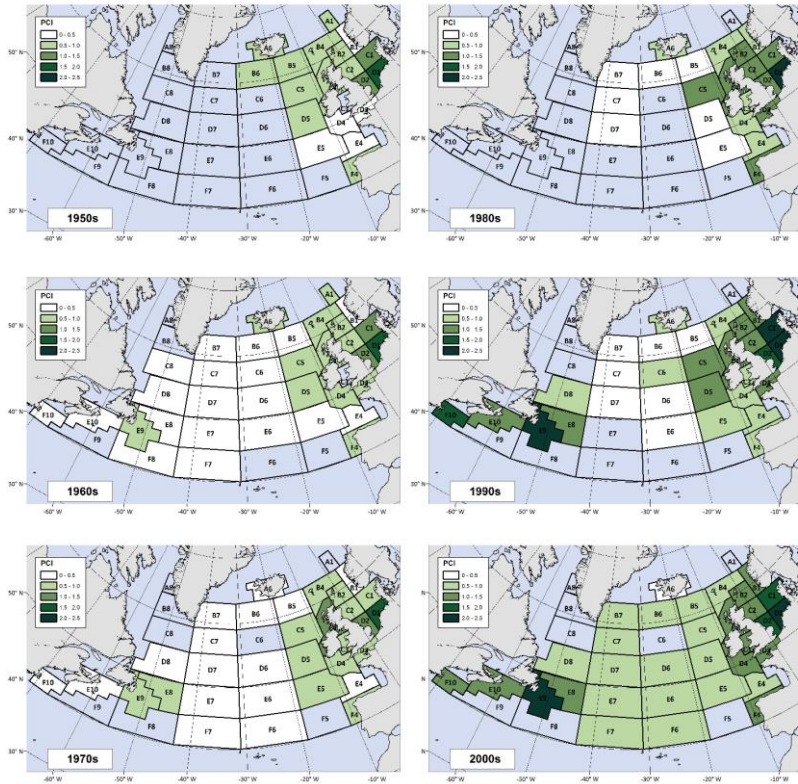


Fig 3

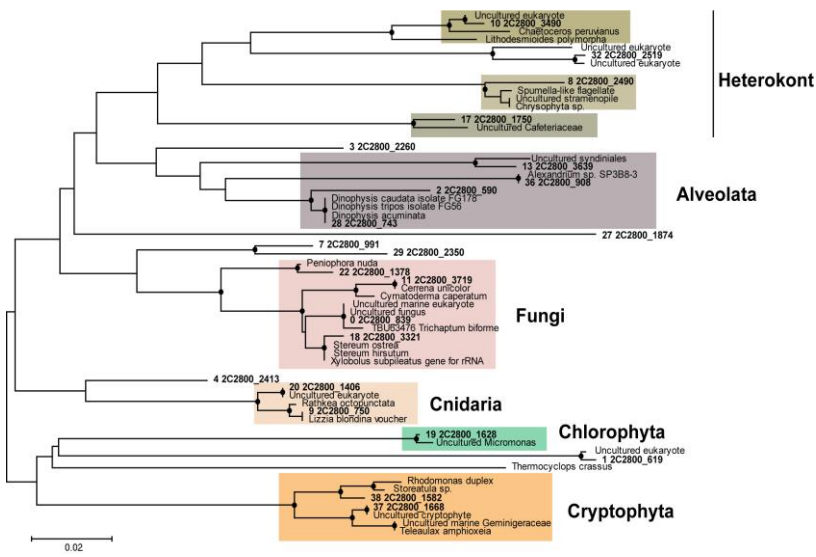
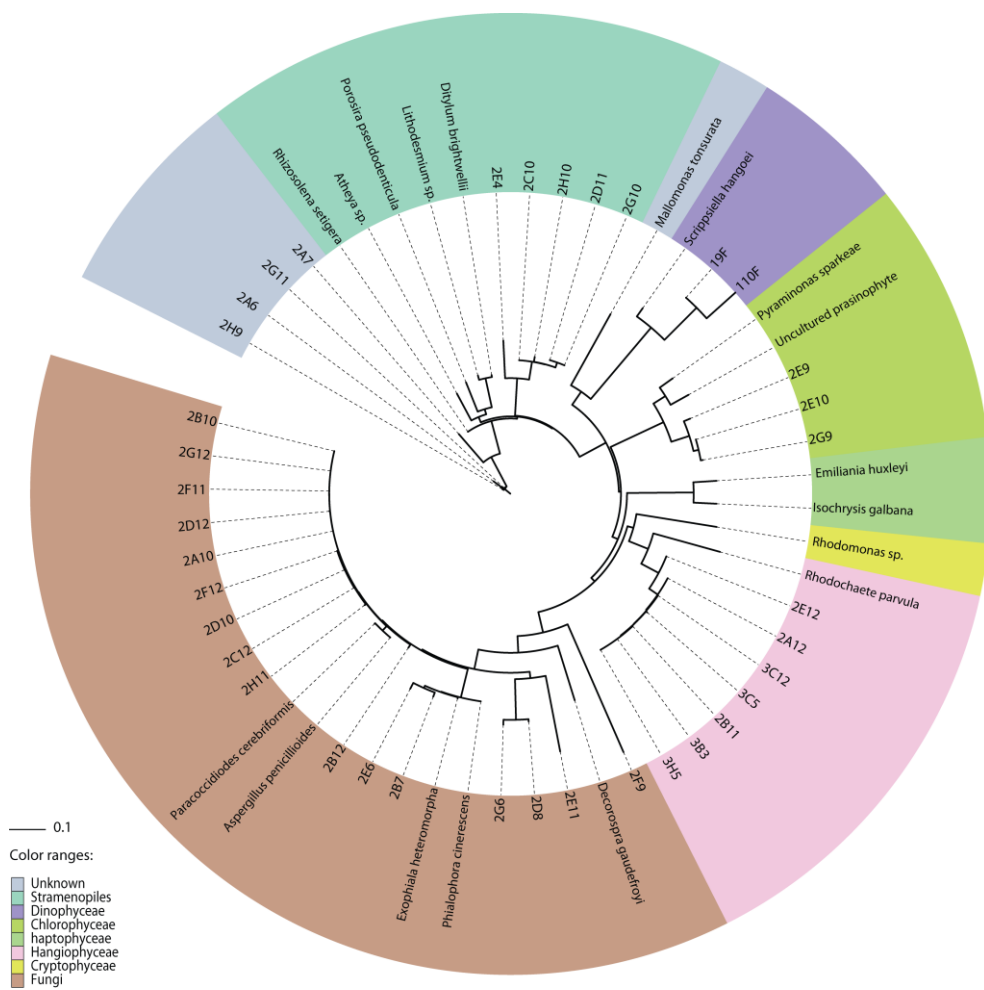


Fig 4



References

- Álvarez, E., López-Urrutia, Á., Nogueira, E., Fraga, S., 2011. How to effectively sample the plankton size spectrum? A case study using FlowCAM. *Journal of Plankton Research* 33, 1119-1133.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25, 704-726.
- Batten, S.D., Clark, R., Flinkman, J., Hays, G., John, E., John, A.W.G., Jonas, T., Lindley, J.A., Stevens, D.P., Walne, A., 2003. CPR sampling: the technical background, materials and methods, consistency and comparability. *Progress in Oceanography* 58, 193-215.
- Beare, D., McQuatters-Gollop, A., van der Hammen, T., Machiels, M., Teoh, S.J., Hall-Spencer, J., 2013. Long-term trends in calcifying plankton and pH in the North Sea. *PLOS ONE* 8, e61175.
- Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60, 245-262.
- Beaugrand, G., 2005. Monitoring pelagic ecosystems using plankton indicators. *Ices Journal of Marine Science* 62, 333-338.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibanez, F., 2008. Causes and prediction of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters* 11, 1157-1168.
- Beaugrand, G., Edwards, M., Legendre, L., 2010. Marine biodiversity, ecosystem functioning and carbon cycles. *Proceedings of the National Academy of Sciences, USA* 107, 10120-10124.
- Beaugrand, G., Kirby, R.R., 2010. Climate, plankton and cod. *Global Change Biology* 16, 1268-1280.
- Beaugrand, G., McQuatters-Gollop, A., Edwards, M., Goberville, E., 2013. Long-term responses of North Atlantic calcifying plankton to climate change. *Nature Climate Change* 3, 263-267.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692-1694.
- Boalch, G.T., Harbour, D.S., 1977. Unusual diatom off the coast of south-west England and its effect on fishing. *Nature* 269, 687-688.
- Brander, K.M., Dickson, R.R., Edwards, M., 2003. Use of Continuous Plankton Recorder information in support of marine management: applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. *Progress in Oceanography* 58, 175-191.
- Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Sydeman, W.J., Ferrier, S., Williams, K.J., Poloczanska, E.S., 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* 507, 492-495.
- Cadee, G.C., 1986. Increased phytoplankton primary production in the Marsdiep area (western Dutch Wadden Sea). *Netherlands Journal of Sea Research* 29, 285 - 290.
- de Jonge, V.N., 2007. Toward the application of ecological concepts in EU coastal water management. *Marine Pollution Bulletin* 55, 407-414.
- de Jonge, V.N., Bakker, J.F., van Stralen, M., 1996. Recent changes in the contributions of river Rhine and North Sea to the eutrophication of the western Dutch Wadden Sea. *Aquatic Ecology* 30, 27-39.
- Duarte, C.M., Cebrian, J., Marbá, N., 1992. Uncertainty of detecting sea change. *Nature* 356, 190.
- Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A., Richardson, A.J., 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends in Ecology & Evolution* 25, 602-610.
- Edwards, M., Beaugrand, G., Reid, P.C., Rowden, A.A., Jones, M.B., 2002. Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series* 239, 1-10.
- Edwards, M., John, A.W.G., Johns, D.G., Reid, P.C., 2001a. Case-history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 81, 207-211.

- Edwards, M., Johns, D.G., Leterme, S.C., Svendsen, E., Richardson, A.J., 2006. Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnology and Oceanography* 51, 820-829.
- Edwards, M., Reid, P.C., Planque, B., 2001b. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960-1995). *ICES Journal of Marine Science* 58, 39-49.
- Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881-884.
- European Commission, 2008. Marine Strategy Framework Directive 2008/56/EC, European Commission.
- European Commission, 2010. Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters 2010/477/EU, European Commission.
- Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor, F.J.R., 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305, 354-360.
- Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L., 2013. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change: Impacts, Adaptation, and Vulnerability, in: IPCC (Ed.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Gowen, R.J., McQuatters-Gollop, A., Tett, P., Best, M., Bresnan, E., Castellani, C., Cook, K., Forster, R., Scherer, C., McKinney, A., 2011. The Development of UK Pelagic (Plankton) Indicators and Targets for the MSFD. Advice to Defra, Belfast, UK, p. 41 pp.
- Gowen, R.J., Tett, P., McQuatters-Gollop, A., Forster, R., Scherer, C., Bresnan, E., Cook, K., Atkinson, A., Best, M., Baptie, M., Keeble, S., McCullough, G., 2013. Part One of the UK Marine Strategy for the Marine Strategy Framework Directive: Plankton indicators: Development of the Life-form and State-Space Method. Report to Defra, Belfast, p. 27 pp.
- Hardy, A.C., 1939. Ecological investigations with the Continuous Plankton Recorder: object, plan and methods. *Hull Bulletins of Marine Ecology* 1, 1-57.
- Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. *Trends in Ecology & Evolution* 20, 337-344.
- Helaouët, P., Beaugrand, G., 2009. Physiology, ecological niches and species distribution. *Ecosystems* 12, 1235-1245.
- Helaouët, P., Beaugrand, G., Edwards, M., 2013. Understanding long-term changes in species abundance using a niche-based approach. *PLoS ONE* 8, e79186.
- Helaouët, P., Beaugrand, G., Reid, P.C., 2011. Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Progress in Oceanography* 56, 217-228.
- Henson, S., Sarmiento, J., Dunne, J., Bopp, L., Lima, I., Doney, S., John, J., Beaulieu, C., 2010. Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. *Biogeosciences* 7, 621-640.
- Henson, S.A., Raitsos, D., Dunne, J.P., McQuatters-Gollop, A., 2009. Decadal variability in biogeochemical models: Comparison with a 50-year ocean colour dataset. *Geophysical Research Letters* 36, L21601.
- Hickel, W., Mangelsdorf, P., Berg, J., 1993. The human impact in the German Bight - eutrophication during 3 decades (1962-1991). *Helgol. Meeresunters.* 47, 243-263.
- Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change* 2.
- Iglesias-Rodriguez, M.D., Halloran, P.R., Rickaby, R.E.M., Hall, I.R., Colmenero-Hidalgo, E., Gittins, J.R., Green, D.R.H., Tyrrell, T., Gibbs, S.J., von Dassow, P., Rehm, E., Armbrust, E.V., Boessenkool, K.P., 2008. Phytoplankton calcification in a high-CO₂ world. *Science* 320, 336-340.

Jakobsen, H.H., Carstensen, J., 2011. FlowCAM: Sizing cells and understanding the impact of size distributions on biovolume of planktonic community structure. *Aquatic Microbial Ecology* 65, 75-87.

Johns, D.G., Brice, G., (Eds), 2014. SAHFOS Annual Report 2013. SAHFOS, UK, p. 64.

Johns, D.G., Edwards, M., Batten, S.D., 2001. Arctic boreal plankton species in the North West Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 2121-2124.

Kegel, J.U., Del Amo, Y., Costes, L., Medlin, L.K., 2013. Testing a microarray to detect and monitor toxic microalgae in Arcachon Bay in France. *Microarrays* 2, 1-23.

Kirby, R.R., Beaugrand, G., 2009. Trophic amplification of climate warming. *Proceedings of the Royal Society B-Biological Sciences* 276, 4095-4103.

Koslow, J.A., Couture, J., 2013. Ocean sciences: Follow the fish. *Nature online* 502, 163-164.

Kraberg, A.C., Carstens, K., Peters, S., Tilly, K., Wiltshire, K.H., 2012. The diatom *Mediopyxis helysia* Kühn, Hargreaves & Halliger 2006 at Helgoland Roads: a success story? *Helgoland Marine Research* 66, 63-468.

Li, W.K.W., Harrison, W.G., Head, E.J.H., 2006. Coherent assembly of phytoplankton communities in diverse temperate ocean ecosystems. *Proceedings of the Royal Society B-Biological Sciences* 273, 1953-1960.

McQuatters-Gollop, A., 2012. Challenges for implementing the Marine Strategy Framework Directive in a climate of macroecological change. *Philosophical Transactions of the Royal Society* 370, 5636-5655.

McQuatters-Gollop, A., Artigas, F., Aubert, A., Johansen, M., Rombouts, I., 2014. Update report from the OSPAR ICG-COBAM pelagic habitats expert group: Report from 2014 pelagic habitats workshop. Report to OSPAR ICG-COBAM, p. 10.

McQuatters-Gollop, A., Raitsos, D.E., Edwards, M., Attrill, M.J., 2007a. Spatial patterns of diatoms and dinoflagellate seasonal cycles in the North - East Atlantic Ocean. *Marine Ecology Progress Series* 339, 301-306.

McQuatters-Gollop, A., Raitsos, D.E., Edwards, M., Pradhan, Y., Mee, L.D., Lavender, S.J., Attrill, M.J., 2007b. A long-term chlorophyll dataset reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient levels. *Limnology and Oceanography* 52, 635-648.

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

McQuatters-Gollop, A., Vermaat, J.E., 2011. Covariance among North Sea ecosystem state indicators during the past 50 years - contrasts between coastal and open waters. *Journal of Sea Research* 65, 294-292.

Platt, T., Fuentes-Yaco, C., Frank, K.T., 2003. Marine ecology: Spring algal bloom and larval fish survival. *Nature* 423, 398-399.

Psaltis, D., Quake, S.R., Yang, C., 2006. Developing optofluidic technology through the fusion of microfluidics and optics. *Nature* 442, 381-386.

Raitsos, D.E., Lavender, S.J., Maravelias, C.D., Haralabous, J., McQuatters-Gollop, A., Edwards, M., Reid, P.C., 2011. Macroscale factors affecting diatom abundance: a synergistic use of Continuous Plankton Recorder and satellite remote sensing data. *International Journal of Remote Sensing* 32, 2081-2094.

Raitsos, D.E., Lavender, S.J., Pradhan, Y., Tyrrell, T., Reid, P.C., Edwards, M., 2006. Coccolithophore bloom size variation in response to the regional environment of the subarctic North Atlantic. *Limnology and Oceanography* 51, 2122-2130.

Raitsos, D.E., Pradhan, Y., Lavender, S., Hoteit, I., McQuatters-Gollop, A., Reid, P.C., Richardson, A., 2014. From silk to satellite: half a century of ocean colour anomalies in the Northeast Atlantic. *Global Change Biology*.

Raitsos, D.E., Reid, P.C., Lavender, S.J., Edwards, M., Richardson, A.J., 2005. Extending the SeaWiFS chlorophyll data set back 50 years in the northeast Atlantic. *Geophys. Res. Lett.* 32, LO6603.

Raitsos, D.E., Walne, A., Lavender, S.J., Licandro, P., Reid, P.C., Edwards, M., 2013. A 60-year ocean colour data set from the continuous plankton recorder. *Journal of Plankton Research* 35, 158-164.

Reid, P.C., Colebrook, J.M., Matthews, J.B.L., Aiken, J., 2003. The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Progress in Oceanography* 58, 117-173.

Reid, P.C., Edwards, M., Hunt, H.G., Warner, A.J., 1998. Phytoplankton change in the North Atlantic. *Nature* 391, 546.

Reid, P.C., Johns, D.G., Edwards, M., Starr, M., Poulin, M., Snoeijs, P., 2007. A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800,000 years. *Global Change Biology* 13, 1910-1921.

Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305, 1609-1612.

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

Riebesell, U., Zondervan, I., Rost, B., Tortell, P.D., Zeebe, R.E., Morel, F.M.M., 2000. Reduced calcification of marine plankton in response to increased atmospheric CO₂. *Nature* 407, 364-367.

Robinson, G.A., 1970. Continuous Plankton Records: variation in the seasonal cycle of phytoplankton in the north Atlantic. *Bulletins of Marine Ecology* 6, 333-345.

Sathyendranath, S., Aiken, J., Alvain, S., Barlow, R., Bouman, H., Bracher, A., Brewin, R., Bricaud, A., Brown, C.W., Ciotti, A.M., Clementson, L.A., Craig, S.E., Devred, E., Hardman-Mountford, N., Hirata, T., Hu, C., Kostadinov, T.S., Lavender, S., Loisel, H., Moore, T.S., Morales, J., Mouw, C.B., Nair, A., Raitsos, D., Roesler, C., Shutler, J.D., Sosik, H.M., Soto, I., Stuart, V., Subramaniam, A., Uitz, J., 2014. Phytoplankton functional types from space, Reports of the International Ocean-Colour Coordinating Group (IOCCG). International Ocean-Colour Coordinating Group, Dartmouth, Nova Scotia, p. 156.

Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W., Hawkins, S.J., 2005. Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology* 47, 1-105.

Stern, R.F., Picard, K.T., Hamilton, K.M., Walne, A., Tarran, G., Mills, D., McQuatters-Gollop, A., Edwards, M., in press. An automated water sampler from Ships of Opportunity detects new boundaries of marine microbial biodiversity *Progress in Oceanography*.

Vezzulli, L., Brettar, I., Pezzati, E., Reid, P.C., Colwell, R.R., Hofle, M.G., Pruzzo, C., 2012. Long-term effects of ocean warming on the prokaryotic community: evidence from the vibrios. *The ISME Journal* 6, 21-30.

Wiltshire, K.H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H.D., Freund, J., Gebühr, C., Gerdtts, G., Stockmann, K., Wichels, A., . 2010. Helgoland roads: 45 years of change in the North Sea. *Estuaries and Coasts* 33, 295-310.

Witt, M.J., Broderick, A.C., Johns, D.J., Martin, C., Penrose, R., Hoogmoed, M.S., Godley, B.J., 2007. Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Marine Ecology Progress Series* 337, 231-244.

Wollschläger, J., Nicolaus, A., Wiltshire, K.H., Metfies, K., 2014. Assessment of North Sea phytoplankton via molecular sensing: a method evaluation. *Journal of Plankton Research* 36, 695-708.

Zingone, A., Dubroca, L., Iudicone, D., Margiotta, F., Corato, F., d'Alcalà, M.R., Saggiomo, V., Sarno, D., 2010. Coastal phytoplankton do not rest in winter. *Estuaries and Coasts* 33, 342-361.

Zondervan, I., Zeebe, R.E., Rost, B., Riebesell, U., 2001. Decreasing marine biogenic calcification: A negative feedback on rising atmospheric pCO₂. *Global Biogeochemical Cycles* 15, 507-516.