

Should phytoplankton be a key consideration for marine management?

Jacqueline F. Tweddle^{a,*}, Matthew Gubbins^b, Beth E. Scott^a

^a School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Ave, Aberdeen AB24 2TZ, UK

^b Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK



ARTICLE INFO

Keywords:

Primary producers
Phytoplankton
Marine management
Marine spatial planning
Ecosystem services
Patchiness

ABSTRACT

Phytoplankton are an extremely important component of the functioning of ecosystems and climate regulation. Because concentrations of phytoplankton are highly patchy in both space and time, it is proposed that more consideration concerning the potential impact from human developments and activities on the service provision afforded by phytoplankton should be accounted for in marine management processes. The multiple species of primary producers provide important provisioning and regulating ecosystem services (ES) and form the basis of marine food-webs, supporting production of higher trophic levels (a provisioning ES), and act as a sink of CO₂ (a climate regulation ES). Spatial and temporal patchiness in the production of phytoplankton can be related to patchiness in the provision of these ES. Patches of naturally high phytoplankton productivity should be afforded consideration within processes to assess environmental status, within marine spatial planning (including marine protected areas) and within sectoral licensing, with marine planning and licensing acting at scales most in harmony with scales of phytoplankton heterogeneity (meters to tens of kilometres). In this study, consideration of phytoplankton in marine management decision making has been reviewed. This paper suggests that potential impacts of maritime developments and activities on the natural patchiness of phytoplankton communities be included in management deliberations, and mitigation be considered. This affords opportunities for researchers to engage with management authorities to support ecosystems-based management. Doing so will assist in maintaining or achieving good environmental status and support further, reliant, ES.

1. Introduction

Marine management must be based on fundamental principles of ecological function in marine ecosystems. As such, it is here proposed that marine phytoplankton, as known ecosystem service (ES – supply the benefits people obtain from ecosystems) providers, with importance to climate cycle and ecosystem functions, and with spatially and temporally distinct distributions, should be considered within marine management decision making. In particular, the potential impact by human developments and activities on the ES provision afforded by phytoplankton should be accounted for in marine management processes, in order to maintain provision of utilized ES.

Within this paper, the importance of phytoplankton is first explored, and the need to account for spatial and temporal variability when considering phytoplankton. This variability results in the creation of “patches” at a variety of scales of both phytoplankton and the reliant ES they support. The implications for ES such as trophic linkages and carbon drawdown, and in considering climate change impacts, are discussed within the context of the most immediate anthropogenic drivers of pressures on the marine environment and phytoplankton.

Following this, mechanisms are considered which could incorporate this information on phytoplankton dynamics and patchiness into marine management, within the constraints of existing legislation, policies and management processes, to improve environmental standards (regional to basin scale), marine spatial planning (local to regional scale, including use of marine protected areas) and sectoral licensing (at the scale of individual developments). Thus, knowledge and understanding about primary productivity and phytoplankton can be used to assist in ecosystem-based sustainable management of our oceans.

2. Marine phytoplankton

Marine pelagic phytoplankton are primary producers, and their photosynthesizing is a supporting ES required to maintain other supporting, provisioning and regulating services [1]. Phytoplanktonic primary production is the source of approximately 50% of atmospheric O₂ [2]. Phytoplankton also provide important climate regulation ES. For example, some species of phytoplankton produce emissions of dimethylsulfoniopropionate (DMSP) [3], a precursor to dimethyl sulfide (DMS), a condensation nucleus for cloud formation. Phytoplankton are

* Corresponding author at: School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Ave, Aberdeen AB24 2TZ, UK.
E-mail address: jftweddle@abdn.ac.uk (J.F. Tweddle).

also, importantly, major contributors to the drawdown of CO₂ from the air to the oceans, and to carbon sequestration within sediments and the deep ocean [4,5]. 20–35% of worldwide CO₂ emissions are sequestered annually by phytoplankton [6]. The spatial distribution of phytoplankton (both of species and total concentrations) is of interest with respect to the global carbon budget [7–9] and CO₂ flux into the ocean [10,11]. Phytoplankton also form the basis of most marine food-webs, supporting production of higher trophic levels. They provide a source of food for pelagic herbivores, including larval fish, [12–14], and support commercial fisheries [15,16], contributing to food production ES. Spatial variability in primary productivity and ensuing phytoplankton concentrations can influence distributions of higher trophic levels, such as seabirds and marine mammals [17,18].

3. The importance of scale and variability in space

Spatial scale is an important aspect when considering the marine environment, with the oceans exhibiting high spatial variability in physical, chemical and biological parameters at a variety of scales: e.g. vertical gradients in light levels [19], horizontal and vertical gradients in temperature & salinity [20] turbulent mixing [21], nutrient concentrations [20,22,23], phytoplankton concentrations and primary productivity [9], and predator-prey species distributions [17,24]. These studies show higher variability at numerous temporal and spatial scales than has been assumed in the past. Due to advances in technology, such as greater resolution in remote sensing, the proliferation of underwater gliders and the ability to produce accurate 3-D hydrographic simulation models at scales less than 100 m (e.g. the Finite Volume Community Ocean Model, FVCOM, [25]), scientists are now capable of looking at sub-mesoscale (here defined as from meters to tens of kilometres in size) patterns and processes. These abilities are increasing our capability for understanding the impact sub-mesoscale variability has on larger scale estimates of ES, for example, annual rates of primary productivity, CO₂ drawdown, or potential fish biomass within a region. The new capabilities are also increasing our ability to successfully monitor and investigate the physical to biological linkages in marine ecosystems, and are rapidly improving our ability to manage and mitigate human activities impacting at the sub-mesoscale. These capabilities allow us to monitor phytoplankton and primary productivity at these smaller scales, which was previously too expensive, and, within our management processes, not perceived as sensitive to pressures from the maritime activities being managed.

The spatial distributions of phytoplankton and rates of primary productivity (hereafter referred to in combination as phytoplankton parameters) are generally subject to bottom-up control, due to the tight coupling between marine physics and biology [26]. The balance of light and nutrients available to phytoplankton determine their success. In spring, the balance between light and nutrient availability defines the timing, location and strength of a spring bloom [27–30] in temperate regions. During stratified periods, increased turbulent mixing within the marine environment leads to an associated increase in primary productivity within the pycnocline, through the provision of fresh nutrients [31,32]. Phytoplankton are reliant upon nutrient supply, with an increased supply of nutrients supporting increased primary production, if light levels are not limiting. The physical processes driving nutrient supplies can be large in scale, e.g. upwelling [33] or mixing at the shelf break [34,35], but relatively small sub-mesoscale areas can be of disproportionate importance, for example, tidal mixing fronts [36], and over submarine banks [23,37,38]. In many regions physical processes result in vertical variability in phytoplankton patchiness, for example increased phytoplankton concentrations within the seasonal thermocline of temperate shelf seas [13,23,39], which can vary temporally with variations in the physical drivers, such as tides or seasonal changes in heat exchange between atmosphere and ocean. Many of the physical processes creating mixing are predictable in space and time, and produce predictable patches of increased phytoplankton concentrations.

However, climate change driven increased water depth with associated tidal current velocity modification and potential alterations to wind speeds will result in spatial and temporal changes to areas of stratification, and to mixing rates, nutrient supplies and primary productivity. These potential changes should be kept in mind within marine management processes, so as to effectively and adaptably plan toward, and manage for, future conditions. However, to do so, better understanding and increased predictive capabilities of these potential changes is required, to deliver reliable, high quality information to support such management processes.

Shelf seas support a disproportionate amount of oceanic primary production, with typical annual rates 2–5 times greater than open ocean rates, and supporting 15–30% of total primary production although accounting for less than 10% of the ocean's area [40,41]. The primary productivity of shelf seas supports a diverse food web, including supporting over 90% of the world's fisheries catch [42]. As a consequence of this higher primary productivity, shelf seas are an important contributor to climate regulation ES, as a sink for CO₂ [43–48]. Shelf seas are also where the majority of human activities occur [49], and new and expanding developments are proposed (e.g. offshore oil & gas, wind, wave and tidal renewables, aquaculture, dredging for aggregates and dumping of spoils), and are therefore where consideration of phytoplankton within marine management may be most necessary due to the increased potential of overlap between high productivity patches and maritime developments.

Remotely sensed satellite data clearly shows sub-mesoscale variability in surface chlorophyll distributions (e.g. Fig. 1; chlorophyll concentrations, [Chl], are used as a proxy for phytoplankton biomass), including in shelf seas. Towed instrument surveys have also displayed kilometre scale variability in phytoplankton concentrations within the thermocline of seasonally stratified shelf seas (Fig. 1) [32,38]. It is important to note these phytoplankton spatial distributions and intensities can also vary dramatically with time, ranging from multi-year cycles [30], interannual variability [50], and seasonal variations [51], to over spring-neap tidal cycles [52]. This new understanding of the spatial and temporal variability in phytoplankton parameters must be considered and accounted for when considering marine management, as explored in Section 4.

4. Patchy (ecosystem) service coverage

The combination of spatial and temporal variability in phytoplankton parameters leads to a high level of patchiness that has consequential effects at the ecosystem level. Spatial and temporal patchiness in phytoplankton parameters leads to spatial and temporal patchiness in CO₂ drawdown from the atmosphere [53,54], which is of great relevance to global carbon balancing and spatial effects of climate change. Spatially, CO₂ flux variability linked to variations in phytoplankton concentrations have been observed at the 100 s km scale [53], and at the sub-mesoscale kilometre scale [55]. A large temporal variation observed in CO₂ flux is associated with the seasonally increased primary production of the temperate regions' spring bloom [55,56]. [55] also showed a shorter temporal cycle via the spring-neap tidal signal in CO₂ fluxes, and attributed this to changes in phytoplankton concentrations and primary production.

Patchiness in primary production can also be 'passed on' through the trophic levels - patchiness at the sub-mesoscale has been identified in phytoplankton concentrations [57], and linked up multiple trophic levels to top predators [17,58–61]. There is evidence that increased [Chl] can be used as an indicator of areas of importance to top predators [17,18]. However, the processes behind this association are yet to be fully explained; whether the relationship is simply driven bottom up by physical processes, or by complex behaviour interactions, or both [38]. The correlation between patchiness in phytoplankton parameters and patchiness in the spatial distributions of higher trophic levels suggests these locations are limited (both in space and time) foraging

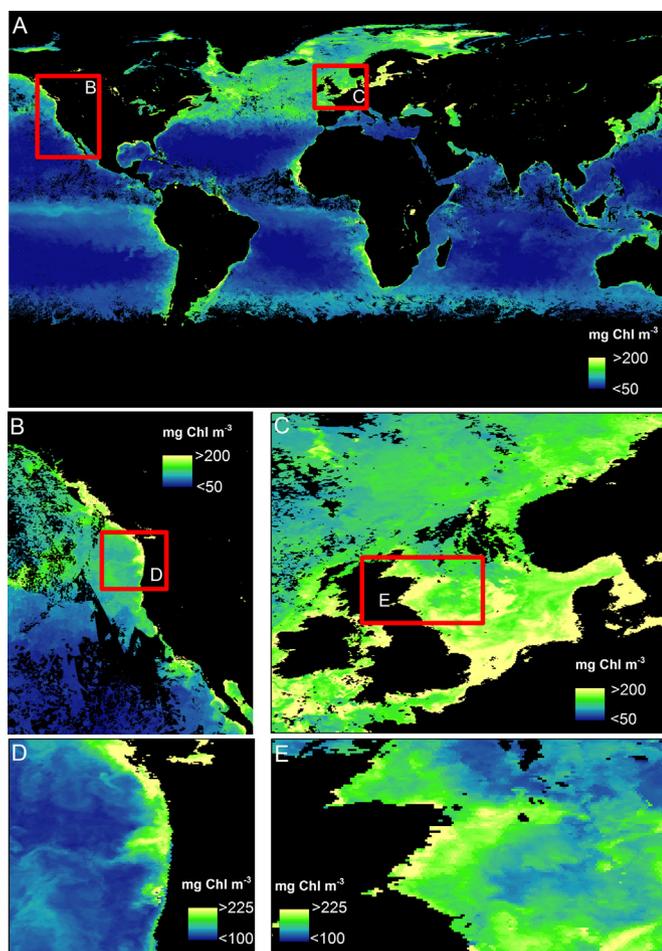


Fig. 1. Spatial scales of patchiness in phytoplankton. MODIS Aqua remotely sensed monthly Chlorophyll *a* concentrations (mg m^{-3}), at 4 km resolution, for August 2016, processed using the OCI algorithm. Green indicates higher concentrations than blue, land and clouds are black. Moving from a global picture (A) to regional (B and C) and then local scales (D and E) highlights the various spatial scales of variability of chlorophyll in surface waters. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Ocean Color Data; 2016. NASA OB.DAAC, Greenbelt, MD, USA. Accessed on 17/09/2016. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

areas. Even without these behavioural links, the vulnerability of these mobile species to human induced pressures is patchy, related to the patchiness of lower trophic levels and, ultimately, to patchiness in phytoplankton parameters, through trophic linkages. Therefore, it is essential that effective marine management must take account of where and how patchiness occurs, so that management measures, for example in MPAs, also protect target species by considering the resources they rely on.

Human maritime developments and activities are most likely to occur in, and therefore impact on, shelf seas, i.e. relatively close to land [49]. Additionally, developments will have largest direct environmental and ecological impacts, including potentially on phytoplankton parameters through decreasing or increasing rates of primary productivity, and disrupting natural phytoplankton distributions and abundances, at the sub-mesoscale, due to their (generally) meter (e.g. wind turbine, aquaculture) – kilometre (e.g. pipelines, fishing) spatial footprints. Many of the entities society benefits from or values (for example, ES such as primary production and fisheries, and top predators such as seabirds and marine mammals) show great variability in distributions at the sub-mesoscale. Additionally, the cumulative impact of many developments may extend to significant local, regional or

global impacts. Modelling work has shown phytoplankton concentrations may be affected by the presence of offshore wind farms [62,63], but how, or if, these changes are significant in terms of CO_2 fluxes or animal populations is currently unknown, and further research would need to be carried out. The ES derived from phytoplankton patches, be it food provision or tourism, can be affected at broad scales if localized vulnerabilities are not taken into account in marine management.

Information on the importance of sub-mesoscale phytoplankton parameter patches to the ecosystem and ES will be invaluable to marine management and planning. For example, applications include potential marine protected area (MPA) creation, in particular towards mobile species utilizing marine space where there are increased phytoplankton concentrations, and to sustainable resource use such as commercial fisheries. Understanding the ecosystem processes creating and supporting valued services in particular areas is necessary to properly protect and/or manage such services and to allow assessment of whether patches of naturally increased phytoplankton parameters require some degree of consideration or protection to maintain provision of ES, as well as what mitigation measures would allow development or use with lower impacts.

5. Integrating consideration of phytoplankton into marine management

Effective marine management and planning provides us with clean, healthy, safe, productive and biologically diverse seas, and can be achieved by applying an ecosystem based management approach. This Ecosystems Approach is “a resource planning and management approach that integrates the connections between land, air and water and all living things, including people, their activities and institutions” [64]. In order to incorporate marine phytoplankton parameters, legislators, policy makers, marine managers, and stakeholders must recognize the important role marine phytoplankton play in a healthy ecosystem and in the provision of ES. Where consideration of phytoplankton parameters should occur within management processes will depend on the process, and applicable existing international, national and local legislation, policies and management processes. Here consideration of phytoplankton parameters in relation to environmental status, marine spatial planning, MPAs and sectoral marine licensing are discussed in turn and in Table 1.

5.1. Environmental status

The maintenance or recovery of marine ecosystems to a certain status is implemented in policy in many maritime nations. The European Union (EU) has used legislative Directives to initiate a move towards ecological considerations within the marine management of its member countries, with the Water and Marine Strategy Framework Directives (WFD - Directive 2000/60/EC, and MSFD - Directive 2008/56/EC, respectively) legislating for coastal and marine environmental standards. Marine phytoplankton are considered both within the WFD and MSFD. The regions over which ecological/environmental status are reported under the WFD and MSFD are large areas, one MSFD region covering, for example, the North East Atlantic, with the Greater North Sea as a sub-region. WFD applies to surface waters out to 1 or 3 nautical miles from shore (depending on specific quality elements and member state). These scales of reporting do not take account of the meso- and submesoscale heterogeneity of phytoplankton communities, nor is this variability necessarily accounted for in assessments. For example, around Scotland, the Scottish Coastal Observatory [65], a network of monitoring stations, undertakes monitoring for MSFD reporting. However, each station is considered to be representative of a larger area, and does not take account of meso- and submesoscale phytoplankton patchiness within that area. This assumption of homogeneity could result in misrepresentation of environmental status with regards to, for example eutrophication. For this reason, remote sensing, with its near

Table 1
 Suggestions for integration of primary production and phytoplankton into marine management processes. When consideration is made of primary production and phytoplankton in marine management processes will be constrained by existing legislation, policies and management processes.

	When in process	Potential Issues	Suggestions for implementation	Examples of future science support required
Environmental Status	<ul style="list-style-type: none"> – Setting baseline standards – Monitoring and assessment 	<ul style="list-style-type: none"> – Legislative and policy support – Cost of (long term) monitoring – International guidelines exist for monitoring phytoplankton and primary productivity (e.g. OSPAR^a, ICES TIMES^b), however, questions still exist around, for example, water sampling versus remote sensing – Where / when to monitor, due to natural patchiness over a variety of scales 	<ul style="list-style-type: none"> – Wider use of indicator types developed by OSPAR 	<ul style="list-style-type: none"> – Assessing baselines (with a need for long term datasets) – Establishing indicators – Understanding ecology of e.g. harmful algal blooms – Understanding impacts of climate change, particularly on shifting baselines – Improve algorithms for remote sensing of ocean color and fluorescence
Marine Spatial Management: <i>Marine Spatial Planning</i>	<ul style="list-style-type: none"> – Evidence base – Consultation with stakeholders 	<ul style="list-style-type: none"> – Collection of sufficient data, especially sub-surface – Knowledge of ES supported in area – Education required on importance of primary productivity and phytoplankton 	<ul style="list-style-type: none"> – Using tools (e.g. [2]) to educate stakeholders, and bring primary productivity into stakeholder engagement and consultation – Identify areas of predictable high local primary productivity within a plan area and identify overlaps or interactions with human activities – Work with stakeholders to support the development of any relevant policies, objectives and spatial considerations to be adopted – No recommendation of developments within regions of predictable high local primary productivity – Requiring developers to take certain measures within such areas (e.g. particular placement of turbines within a wind farm to avoid localized regions of predictable high primary productivity) – Using areas of high productivity as indicators of ecological interest [3] – Protect, e.g. topographic, features which drive high productivity in an area^c 	<ul style="list-style-type: none"> – Ability to map areas of high primary productivity (throughout the water column) – Understanding of the importance of predictable local productivity to wider marine systems and further ecosystem services – Understanding of how maritime activities impact on primary production and linked ES
Marine Spatial Management: <i>Marine Protected Areas</i>	<ul style="list-style-type: none"> – Evidence base – Site selection – Establishing protection measures 	<ul style="list-style-type: none"> – Collection of sufficient data – Education required on importance of primary productivity and phytoplankton 	<ul style="list-style-type: none"> – Protect, e.g. topographic, features which drive high productivity in an area^c – Consideration of the carbon footprint of a marine renewable energy development, with impact on primary production balanced against contribution to climate change mitigation. – Array design, e.g. placement of individual turbines within an offshore wind farm, to take account of natural areas of high primary productivity to minimize impact. 	<ul style="list-style-type: none"> – Ability to map areas of high primary productivity (throughout the water column) – Understanding of how patches link to features (species and habitats) of conservation importance – Develop carbon footprint calculation tools for maritime activities, as for terrestrial, e.g. Cool Farm Tool (http://www.coolfarmlib.org) – Mitigation measures for maritime developments
Maritime Licensing	<ul style="list-style-type: none"> – SEA – EIA – Site design (e.g. wind farm array layout) – Required monitoring as a license condition 	<ul style="list-style-type: none"> – Collection of sufficient data – Understanding impacts – Cumulative effects – Education required on importance of primary productivity and phytoplankton 	<ul style="list-style-type: none"> – Consideration of the carbon footprint of a marine renewable energy development, with impact on primary production balanced against contribution to climate change mitigation. – Array design, e.g. placement of individual turbines within an offshore wind farm, to take account of natural areas of high primary productivity to minimize impact. 	<ul style="list-style-type: none"> – Ability to map areas of high primary productivity (throughout the water column) – Understanding of how patches link to features (species and habitats) of conservation importance – Develop carbon footprint calculation tools for maritime activities, as for terrestrial, e.g. Cool Farm Tool (http://www.coolfarmlib.org) – Mitigation measures for maritime developments

^a <https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/fish-and-food-webs/phytoplankton-production/> and <https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/zooplankton-communities/>.

^b <http://www.ices.dk/publications/our-publications/Pages/ICES-Techniques-in-Marine-Environmental-Sciences.aspx>.

^c <http://www.gov.scot/Topics/marine-environment/mpanetwork/developing/DesignationOrders/FOFDOOrder>.

synoptic spatial coverage of large areas, is being explored in monitoring phytoplankton abundances.

The WFD considers phytoplankton parameters such as abundance and community composition in assessing Good Ecological Status. Under the MSFD, some EU states and Regional Seas Conventions (e.g. the United Kingdom and OSPAR) are considering phytoplankton in assessing Good Environmental Status (GES). The MSFD does not explicitly acknowledge the role phytoplankton in the provision of many ES, such as regulating carbon and nutrient cycles and other biogeochemical cycles [66]. However, community composition is being used as an indicator of biological diversity (MSFD Descriptor 1: Biodiversity), and includes phytoplankton [67], for example in using a lifeform approach [68], biomass and biodiversity indices [67]. In some member states, e.g. the UK, and within OSPAR, the lifeform approach, including consideration of phytoplankton, are also considered as elements of marine food webs, as indicators under MSFD Descriptor 4: Food Webs [67].

GES will also require ensuring phytoplankton populations do not exceed reference values, i.e. as indicators of high nutrient loading (MSFD Descriptor 5: Eutrophication), which can lead to hypoxic (low oxygen concentration) events and undesirable disturbance (e.g. [69]), and, in some seas, harmful algal blooms (HABs; [70]). In some member states, e.g. the United Kingdom, phytoplankton are also considered in reporting on GES under MSFD Descriptor 2 (non-indigenous species). In the UK, two non-native phytoplankton species (*Alexandrium catenella* and *Pseudochattonella verruculosa*) are being actively surveyed for. One species (*Heterosigma akashiwo*), already present, is actively monitored, through WFD monitoring schemes, and if a non-native phytoplankton species not on the surveillance list was discovered, it would be reported as with any other non-native species [71].

In the United States, the Federal Government of the United States of America enacted Acts such as the National Environmental Policy Act in 1969 (NEPA - 42 U.S.C. §4321 et seq. (1969)) and Marine Protection, Research, and Sanctuaries Act of 1972 (MPRSA or Ocean Dumping Act - 16 USC § 1431 et seq. and 33 USC § 1401 et seq. (1988)) to maintain the marine environment, and individual states have also enacted monitoring schemes (see <https://www.epa.gov/nutrient-policy-data/states-monitoring-programs-and-information> for a listing of all 31 state programs). However, phytoplankton related monitoring is generally for HAB species, to reduce potential impacts on human health, in particular through consumption of contaminated, toxic shellfish. In the USA, the Harmful Algal Bloom and Hypoxia Research and Control Act of 1998 (HABHRCA 1998 – Public Law 105–383 § 601 et seq.) and subsequent Amendment Acts of 2004 (HABHRCA 2004 – Public Law 108–456) and 2014 (HABHRCA 2004 – Public Law 113–124) ensures monitoring of phytoplankton species and concentrations. Other countries have non-legislative monitoring for HAB species to inform food safety, human and ocean health, and aquaculture management interests, e.g. UK, Norway, and Chile.

Efforts have been made in many countries to control discharges, both point and non-point, which can cause eutrophication. For example, many states within the United States have legislated for phosphate level regulations in detergents, and at a federal level the Clean Water Act (33 U.S.C. §1251 et seq. (1972)) legislates for pollution control more generally. The EU has also legislated for nitrate and phosphate discharges, through the WFD, Nitrates Directive (Directive 91/676/EEC) and Urban Waste-water Directive (Directive 91/271/EEC), as have many other countries around the world.

Thus, phytoplankton and primary productivity are currently considered within environmental status, but often as indicators of unwanted environmental change (such as eutrophication), with limited consideration of maintaining phytoplankton communities (with the exception of the UK and OSPAR). Further efforts must be made to consider impacts on healthy phytoplankton communities, at spatial and temporal scales which acknowledge scales of natural variability, and areas of healthy, naturally higher productivity (Table 1). In order for this to change, there needs to be a better understanding of what

constitutes a healthy phytoplankton community (e.g. [65,66]) contributing to a range of ES, and the attributes associated with such a community utilized in marine management. The spatially heterogeneous nature of phytoplankton parameter distributions must also be recognized so that management can address issues at the right spatial scale. This will require consideration of the physical environment creating the conditions (“habitat”) for the phytoplankton, as it is this which determines, for example, natural patches of high productivity, and is therefore of importance to supported ES. This is in contrast to the approach taken by the MSFD, where phytoplankton are an aspect of habitats themselves. Additionally, the effects of climate change induced shifts of baselines must be kept in mind [73], and more research is required in this subject to support the use of phytoplankton parameters in maintaining environmental standards and status.

5.2. Marine Spatial Management

Marine Spatial Planning (MSP) is a method for realizing sustainable management of our marine environment. MSP is “a public process of analysing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic, and social objectives that usually have been specified through a political process” [74]. As with terrestrial systems, consideration of marine and maritime ES (such as primary production) along with market-priced goods within MSP will lead to greater overall value for the area being managed [75].

Those involved in the planning processes include the planners themselves and stakeholders; stakeholders being those with an interest (“stake”) in the area under consideration. Stakeholder engagement has an important role in MSP processes [76], and is now a legal requirement within the EU (under the Maritime Spatial Planning Directive - Directive 2014/89/EU). In order for the objective consideration of phytoplankton parameters by both planners and stakeholders, everyone should be aware of the crucial role phytoplankton play in marine ecosystems and in supporting important ES, and of the spatially varying distribution of marine phytoplankton (Table 1). Various processes are being developed (e.g. [70,72]) which can be used to educate stakeholders on the importance of ES such as primary production. Tools, such as these processes, which place phytoplankton parameters into the context of stakeholders’ values, highlight the links between primary production and the ES and derived benefits important to individual stakeholders, for example fishers learning how phytoplankton ultimately support fish stocks and the fishing industry.

Consideration of phytoplankton parameters within MSP could occur at several stages in the planning process. The policy aspects of MSP should be developed in close consultation with stakeholders, and this consultation is recommended to occur after or in conjunction with the application of the previously mentioned knowledge exchange or educational tools (e.g. [70,72]). Recognition of the importance of phytoplankton parameters, which are linked to both the physical and biological aspects within a plan’s spatial data, is imperative. Information should be made available to inform marine planners of potential sensitivities and interactions with maritime activities, and data available on spatial and temporal variability in phytoplankton parameters, to support the development of any relevant policies, objectives and spatial considerations to be adopted. Such measures will depend on many factors within the planning process, such as whether a zoning approach is being used, or not. However, measures may include, for example, not recommending development within regions of particular importance with regards to primary production, or requiring developers to take certain measures within such areas (e.g. particular placement of turbines within a wind farm to avoid localized regions of increased primary productivity).

Shucksmith et al. [78] presented a 7 step process for the spatial data collection and mapping process of marine planning. Within this, data on phytoplankton parameters should be incorporated explicitly into Steps 2, 3 and 4: identifying important marine features and ES within

the plan area (which should include phytoplankton parameters if accounting for the issues identified here); collection of relevant data and mapping; and consultation with stakeholders on mapped data accuracy and precision. These data can then be used to identify areas of high value and/or high interactions with human activities [79].

Marine Protected Areas (MPAs) are a valuable spatial management tool for marine conservation and environmental protection. When contemplating the consideration of phytoplankton parameters in marine protected area (MPA) establishment, there are several routes which can be taken. A co-location between [Chl] and top predators has been noted (e.g. [17,18]), although it is not fully understood why, and has led to the use of remotely sensed [Chl] fronts being used as indicators of areas of importance to mobile species in previous Scottish MPA considerations [80]. This method ultimately provides protection only for co-located animals, not the supporting phytoplankton. In Scotland, certain bathymetric features which drive locally increased productivity and biodiversity are protected (e.g. the Firth of Forth Banks Complex MPA). Although protection of phytoplankton parameters is not explicitly stated, the protection of features which support increased primary productivity, and an objective to maintain in favourable condition processes supporting the biological communities, should mean phytoplankton parameters are indeed considered. Here, however, another route is proposed, where areas of high primary productivity would be identified and phytoplankton parameters explicitly considered within conservation objectives, due to their importance in supporting ecosystem functions and ES. The protection afforded to phytoplankton parameters, and management measures applied, within such an MPA would be down to stakeholders and policy makers, but increased value placed upon phytoplankton parameters in sectoral licensing decisions on developments (e.g. windfarms, [63]) within the MPA is suggested, at minimum. Implementing management measures which protect the drivers of identified important areas of high productivity would be similar to the route above, where features such as bathymetry are afforded a measure of protection. However, with protection of high primary productivity explicit, any proposals to change, e.g., the bathymetry would have to explicitly consider impacts on primary production. One difficulty of this route to MPA establishment will be recognition in stakeholders of the importance of primary producers, as compared to the “charismatic megafauna” which are better known by the public. The use of knowledge exchange tools, such as developed by Scott et al. [77], can assist in educating on the importance of primary producers and, importantly, setting primary producers in the context of stakeholders’ values.

Another major issue for consideration of phytoplankton parameters in MSP is data availability. Global coverage is available of surface water [Chl] via remote sensing, however data processing and analysis skills may not be easily available or affordable to planners. Furthermore, satellite data does not provide information on subsurface phytoplankton populations, which in seasonally stratifying regions can account for over 50% of annual primary production [13].

Our increasing ability to map, monitor and/or predict areas of high phytoplankton parameters throughout the water column will be of great benefit, with gliders and other autonomous underwater vehicles and increasingly complex monitoring platforms providing spatially synoptic subsurface information to complement satellite data. However, information on phytoplankton parameters does not necessarily provide information on ES supported by the phytoplankton parameters within a plan area, and further research needs to be carried out into the precise linkages and into how impacts to phytoplankton parameters may then impact on ES provision.

5.3. Maritime licensing

Sectoral licensing decisions are reliant on local, national and international policies and legislation. Within this framework, consideration of the impact of a marine development on phytoplankton

parameters should be of importance in development siting decisions (Table 1). Scope should be available to consider the impact of a development on phytoplankton parameters, consider any impact on supported ES (e.g. the carbon footprint of the development), consider mitigation strategies for potential impacts, and for inclusion of impacts within cumulative impact assessments. For example, in the case of an off-shore wind farm, any changes to phytoplankton parameters at the scale of the development should be compared to changes in phytoplankton parameters induced by climate change scenarios unmitigated by renewable energy use, and the net change should be included in calculating net carbon footprint. Additionally, the placement of individual turbines within the development could take account of natural areas of high primary productivity, in order to minimize impact.

In the EU, the Strategic Environmental Assessment (SEA) Directive (SEA Directive 2001/42/EC) requires an SEA to be carried out for any plan or program of activity for which significant environmental impacts are expected. The Environmental Impact Assessment (EIA) Directive (EIA Directive 85/337/EEC) requires an EIA to be carried out on any project which is expected to have significant environmental impacts. A development in USA Federal waters is required to be analysed for environmental impacts by federal agencies under the National Environmental Policy Act of 1969, a requirement often met through an Environmental Impact Statement (EIS), or Environmental Assessment (EA) if impacts are found to be low. Consideration of impacts by a proposed development on phytoplankton parameters could be adopted within these frameworks for waters under these or similar processes.

In the terrestrial environment, tools have been developed to allow developers to calculate the carbon footprint of a development or activity, and explore mitigation options (e.g. the Cool Farm Tool, <http://www.coolfarmtool.org>). The development of understanding of impacts on phytoplankton parameters due to changes in spatial management, and of such tools for the marine environment, is to be encouraged, and any tool to be built recommended to include primary productivity by marine phytoplankton, to include estimated development carbon footprints. To enable this more research needs to be carried out into the impacts of maritime developments and activities on phytoplankton parameters, such as impacts by offshore wind farms [62,63], and consequential effects on linkages up through the food webs.

6. Challenges set for the scientific community

In order for marine managers to fully incorporate consideration of phytoplankton into marine management processes, there are several interesting challenges to be resolved (Table 1). Further development of tools for use in data collection on phytoplankton parameters are valuable, such as improved algorithms for deriving primary production from satellite and survey data, or non-computationally expensive models for predicting finer scale patches of increased surface or subsurface phytoplankton parameters. New techniques such as using gliders and AUVs [81] or airborne LIDAR [82], are providing more information than ever before on subsurface communities, and the use of isotopic signatures to determine food web structure [83,84] is assisting us in understanding complex trophic interactions. Advances such as these, combined with further understanding of biogeochemical cycles, ecological processes, ES provision, and human values, will all add to the ability of marine managers to incorporate phytoplankton into marine management processes. In a time of projected climate change and increased anthropogenic activity, the impacts on phytoplankton parameters and linked ES, at spatial and temporal scales useful to marine planning and development licensing, need to be established, in order to allow decisions to be made within the context of an increasing background rate of change.

7. Final thoughts

“Protecting” naturally high and spatially distinct phytoplankton

concentrations and rates of primary productivity in reality means also protecting the physical processes driving them. Connecting the loop between the ecological consequences and physical drivers of plankton production will provide a robust framework within marine planning. In adopting this framework, due consideration must then be made of how changes to hydrography, for example by the placement of proposed developments such as offshore marine renewables, oil & gas platforms or the placement of MPAs, may impact on phytoplankton parameters. The EU MSFD, which assesses over large scales, does require consideration that permanent alteration of hydrographical conditions (Descriptor 7) does not adversely affect marine ecosystems, but indicators and targets are not yet well developed, and impacts on important (submesoscale) phytoplankton patches are not being considered.

Ideally, species composition of phytoplankton populations will be included in any considerations, as species are of importance both when considering HAB species and in considering functional traits; different groups and species have different functions in biogeochemical cycling [85] and ES provision. Assessing species composition will also merge with efforts concerning non-native species, with non-native phytoplankton having been reported in waters around the world, and in tracking species range-changes [86].

We suggest that accounting for the effects of physical changes up through plankton to ES, will allow marine management processes to make the connection between impacts to phytoplankton parameters at the sub-mesoscale to large global scale issues, such as climate change. For example, consideration of phytoplankton parameters in sectoral licensing decisions for off-shore wind farms, will place expected changes in phytoplankton parameters due to the development alongside projected changes due to unmitigated climate change, and the net change incorporated into decision making. As people move into the oceans to deal with humanity's growing needs for both food and energy security, our understanding of the ecosystem, including around phytoplankton parameters, needs to be applied within marine management processes.

Acknowledgements

J F Tweddle was supported by MarCRF, the Marine Collaboration Research Forum jointly sponsored by the University of Aberdeen and Marine Scotland Science, and by the Natural Environment Research Council (NERC grant reference number NE/P005756/1). We thank the anonymous reviewer for their comments, which have resulted in a much improved manuscript.

Conflict of interest

The authors declare no conflict of interest.

References

- [1] Millennium Ecosystem Assessment, Ecosystems and Human Well-being: Synthesis, 2005. <<http://dx.doi.org/10.1196/annals.1439.003>>.
- [2] C.B. Field, Primary production of the biosphere: integrating terrestrial and oceanic components, *Science* 281 (80-) (1998) 237–240, <https://doi.org/10.1126/science.281.5374.237>.
- [3] S.M. Vallina, R. Simó, Strong relationship between DMS and the solar radiation dose over the global surface ocean, *Science* 315 (2007) 506–508, <https://doi.org/10.1126/science.1133680>.
- [4] M. Burrows, N. Kamenos, D. Hughes, Assessment of Carbon Budgets and Potential Blue Carbon Stores in Scotland's Coastal and Marine Environment, (2014) <<http://eprints.gla.ac.uk/96572/>>.
- [5] P. Martin, R.S. Lampitt, M. Jane Perry, R. Sanders, C. Lee, E. D'Asaro, Export and mesopelagic particle flux during a North Atlantic spring diatom bloom, *Deep. Res. Part I Oceanogr. Res. Pap.* 58 (2011) 338–349, <https://doi.org/10.1016/j.dsr.2011.01.006>.
- [6] S. Khatiwala, F. Primeau, T. Hall, Reconstruction of the history of anthropogenic CO₂ concentrations in the ocean, *Nature* 462 (2009) 346–349, <https://doi.org/10.1038/nature08526>.
- [7] T.R. Anderson, P.J.L. Williams, Modelling the seasonal cycle of dissolved organic carbon at station E-1 in the English Channel, *Estuar. Coast. Shelf Sci.* 46 (1998) 93–109, <https://doi.org/10.1006/ecs.1997.0257>.
- [8] J. Huisman, B. Sommeijer, Population dynamics of sinking phytoplankton in light-limited environments: simulation techniques and critical parameters, *J. Sea Res.* 48 (2002) 83–96, [https://doi.org/10.1016/S1385-1101\(02\)00137-5](https://doi.org/10.1016/S1385-1101(02)00137-5).
- [9] M.J. Behrenfeld, R.T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman, A.J. Milligan, P.G. Falkowski, R.M. Letelier, E.S. Boss, Climate-driven trends in contemporary ocean productivity, *Nature* 444 (2006) 752–755, <https://doi.org/10.1038/nature05317>.
- [10] A.R. Longhurst, W. Glen Harrison, The biological pump: profiles of plankton production and consumption in the upper ocean, *Prog. Oceanogr.* 22 (1989) 47–123, [https://doi.org/10.1016/0079-6611\(89\)90010-4](https://doi.org/10.1016/0079-6611(89)90010-4).
- [11] I. Joint, S.B. Groom, Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing, *J. Exp. Mar. Biol. Ecol.* 250 (2000) 233–255, [https://doi.org/10.1016/S0022-0981\(00\)00199-4](https://doi.org/10.1016/S0022-0981(00)00199-4).
- [12] T.G. Nielsen, B. Lokkegaard, K. Richardson, F.B. Pedersen, L. Hansen, B. Lokkegaard, K. Richardson, F.B. Pedersen, L. Hansen, Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation, *Mar. Ecol. Prog. Ser.* 95 (1993) 115–131, <https://doi.org/10.3354/meps095115>.
- [13] K. Richardson, A. Visser, F. Pedersen, Subsurface phytoplankton blooms fuel pelagic production in the North Sea, *J. Plankton Res.* 22 (2000) 1663–1671, <https://doi.org/10.1093/plankt/22.9.1663>.
- [14] J.M. Napp, L.S. Incze, P.B. Ortner, D.L.W. Siefert, L. Britt, The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival, *Fish. Oceanogr.* 5 (1996) 19–38, <https://doi.org/10.1111/j.1365-2419.1996.tb00080.x>.
- [15] J.L. Blanchard, S. Jennings, R. Holmes, J. Harle, G. Merino, J.I. Allen, J. Holt, N.K. Dulvy, M. Barange, Potential consequences of climate change for primary production and fish production in large marine ecosystems, *Philos. Trans. R. Soc. B Biol. Sci.* 367 (2012) 2979–2989, <https://doi.org/10.1098/rstb.2012.0231>.
- [16] J.W. Young, R. Bradford, T.D. Lamb, L.A. Clementson, R. Kloser, H. Galea, Yellowfin tuna (*Thunnus albacares*) aggregations along the shelf break off south-eastern Australia: links between inshore and offshore processes, *Mar. Freshw. Res.* 52 (2001) 463–474.
- [17] B. Scott, J. Sharples, O. Ross, J. Wang, G. Pierce, C. Camphuysen, Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll, *Mar. Ecol. Prog. Ser.* 408 (2010) 207–226, <https://doi.org/10.3354/meps08552>.
- [18] K.L. Scales, P.I. Miller, L.A. Hawkes, S.N. Ingram, D.W. Sims, S.C. Votier, REVIEW: on the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates, *J. Appl. Ecol.* 51 (2014) 1575–1583, <https://doi.org/10.1111/1365-2664.12330>.
- [19] P.G. Falkowski, J.A. Raven, *Aquatic Photosynthesis*, Blackwell Science, Oxford, 1997.
- [20] T.P. Boyer, J.I. Antonov, O.K. Baranova, C. Coleman, H.E. Garcia, A. Grodsky, D.R. Johnson, R. a Locarnini, A.V. Mishonov, T.D.O. Brien, C.R. Paver, J.R. Reagan, D. Seidov, I.V. Smolyar, M.M. Zweng, K.D. Sullivan, *World Ocean Database 2013*, NOAA Atlas (2013) 209, <https://doi.org/10.7289/V5NZ85MT>.
- [21] J.H. Simpson, J. Sharples, *Introduction to the Physical and Biological Oceanography of Shelf Seas*, Cambridge University Press, Cambridge, 2012.
- [22] D.J. Hydes, A.C. Le Gall, A.E.J. Miller, U. Brockmann, T. Raabe, S. Holley, X. Alvarez-Salgado, A. Antia, W. Balzer, L. Chou, M. Elskens, W. Helder, I. Joint, M. Orren, Supply and demand of nutrients and dissolved organic matter at and across the nw european shelf break in relation to hydrography and biogeochemical activity, *Deep. Res. Part II Top. Stud. Oceanogr.* 48 (2001) 3023–3047, [https://doi.org/10.1016/S0967-0645\(01\)00031-5](https://doi.org/10.1016/S0967-0645(01)00031-5).
- [23] J.F. Tweddle, J. Sharples, M.R. Palmer, K. Davidson, S. McNeill, Enhanced nutrient fluxes at the shelf sea seasonal thermocline caused by stratified flow over a bank, *Prog. Oceanogr.* 117 (2013) 37–47, <https://doi.org/10.1016/j.pocan.2013.06.018>.
- [24] A.M. Kaltenberg, K.J. Benoit-Bird, Marine science, *ICES J. Mar. Sci.* 70 (2013) 883–891, <https://doi.org/10.1093/icesjms/fst034>.
- [25] C. Chen, H. Liu, R.C. Beardsley, An unstructured grid, finite-volume, three-dimensional, primitive equations Ocean Model: application to Coastal Ocean and Estuaries, *J. Atmos. Ocean. Technol.* 20 (2003) 159–186.
- [26] J.H. Steele, E.W. Henderson, M. Mangel, C. Clark, Coupling between physical and biological scales, *Philos. Trans. R. Soc. B Biol. Sci.* 343 (1994) 5–9, <https://doi.org/10.1098/rstb.1994.0001>.
- [27] R.D. Pingree, P.M. Holligan, G.T. Mardell, R.N. Head, The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea, *J. Mar. Biol. Assoc. U.K.* 56 (1976) 845–873, <https://doi.org/10.1017/S0025315400020919>.
- [28] M.J.R. Fasham, P.M. Holligan, P.R. Pugh, The spatial and temporal development of the spring phytoplankton bloom in the Celtic Sea, April 1979, *Prog. Oceanogr.* 12 (1983) 87–145, [https://doi.org/10.1016/0079-6611\(83\)90007-1](https://doi.org/10.1016/0079-6611(83)90007-1).
- [29] H. van Haren, D.K. Mills, L.P.M.J. Weststeyn, Detailed observations of the phytoplankton spring bloom in the stratifying central North Sea, *J. Mar. Res.* 56 (1998) 655–680, <https://doi.org/10.1357/002224098765213621>.
- [30] S.A. Henson, J.P. Dunne, J.L. Sarmiento, Decadal variability in North Atlantic phytoplankton blooms, *J. Geophys. Res.* 114 (2009) C04013, <https://doi.org/10.1029/2008JC005139>.
- [31] J. Sharples, J.F. Tweddle, J.A.M. Green, M.R. Palmer, Y.-N. Kim, A.E. Hickman, P.M. Holligan, C.M. Moore, T.P. Rippeth, J.H. Simpson, V. Krivtsov, Spring-neap modulation of internal tide mixing and vertical nitrate fluxes at a shelf edge in summer, *Limnol. Oceanogr.* 52 (2007) 1735–1747.
- [32] J.F. Tweddle, *Nutrient Fluxes Into the Seasonal Thermocline of the Celtic Sea*,

- University of Southampton, Southampton, UK, 2007.
- [33] J.J. MacIsaac, R.C. Dugdale, R.T. Barber, D. Blasco, T.T. Packard, Primary production cycle in an upwelling center, *Deep Sea Res. Part A. Oceanogr. Res. Pap.* 32 (1985) 503–529, [https://doi.org/10.1016/0198-0149\(85\)90042-1](https://doi.org/10.1016/0198-0149(85)90042-1).
- [34] I. Joint, R. Wollast, L. Chou, S. Batten, M. Elskens, E. Edwards, A. Hirst, P. Burkill, S. Groom, S. Gibb, A. Miller, D. Hydes, F. Dehairs, A. Antia, R. Barlow, A. Rees, A. Pomroy, U. Brockmann, D. Cummings, R. Lampitt, M. Loijens, F. Mantoura, P. Miller, T. Raabe, X. Alvarez-Salgado, C. Stelfox, J. Woolfenden, Pelagic production at the Celtic Sea shelf break, *Deep. Res. Part II Top. Stud. Oceanogr.* 48 (2001) 3049–3081, [https://doi.org/10.1016/S0967-0645\(01\)00032-7](https://doi.org/10.1016/S0967-0645(01)00032-7).
- [35] V.M.T.T. Garcia, C.A.E.E. Garcia, M.M. Mata, R.C. Pollery, A.R. Piola, S.R. Signorini, C.R. McClain, M.D. Iglesias-Rodriguez, Environmental factors controlling the phytoplankton blooms at the Patagonia shelf-break in spring, *Deep Sea Res. Part I Oceanogr. Res. Pap.* 55 (2008) 1150–1166, <https://doi.org/10.1016/j.dsr.2008.04.011>.
- [36] C. Videau, Primary production and physiological state of phytoplankton at the Ushant tidal front west coast of Brittany, France, *Mar. Ecol. Prog. Ser.* 35 (1987) 141–151, <https://doi.org/10.3354/meps035141>.
- [37] E.P.W. Horne, J.W. Loder, C.E. Naimief, N.S. Oakey, Turbulence dissipation rates and nitrate supply in the upper water column on Georges Bank, *Deep. Res. Part II Top. Stud. Oceanogr.* 43 (1996) 1683–1712, [https://doi.org/10.1016/S0967-0645\(96\)00037-9](https://doi.org/10.1016/S0967-0645(96)00037-9).
- [38] J. Sharples, B.E. Scott, M.E. Inall, From physics to fishing over a shelf sea bank, *Prog. Oceanogr.* 117 (2013) 1–8, <https://doi.org/10.1016/j.pocan.2013.06.015>.
- [39] J. Sharples, M.C. Moore, T.P. Rippeth, P.M. Holligan, D.J. Hydes, N.R. Fisher, J.H. Simpson, Phytoplankton distribution and survival in the thermocline, *Limnol. Oceanogr.* 46 (2001) 486–496, <https://doi.org/10.4319/lo.2001.46.3.0486>.
- [40] R. Wollast, Evaluation and comparison of the global carbon cycle in the coastal zone and in the open ocean, in: K.H. Brink, A.R. Robinson (Eds.), *Sea, Glob. Coast. Ocean - Process. Methods*, Wiley, New York, USA, 1998, pp. 213–252.
- [41] F.E. Muller-Karger, R. Varela, R. Thunell, R. Luerssen, C. Hu, J.J. Walsh, The importance of continental margins in the global carbon cycle, *Geophys. Res. Lett.* 32 (2005) 1–4, <https://doi.org/10.1029/2004GL021346>.
- [42] D. Pauly, V. Christensen, S. Guénette, T.J. Pitcher, U.R. Sumaila, C.J. Walters, R. Watson, D. Zeller, Towards sustainability in world fisheries, *Nature* 418 (2002) 689–695.
- [43] M. Frankignoulle, A.V. Borges, for Atmospheric Carbon Dioxide Jan 98, 15, 2001, pp. 569–576.
- [44] A. Yool, M.J.R. Fasham, An examination of the “continental shelf pump” in an open ocean general circulation model, *Glob. Biogeochem. Cycle* 15 (2001) 831–844 <http://eprints.soton.ac.uk/6008/>.
- [45] C.D. Thomas, A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. Van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, S.E. Williams, Extinction risk from climate change, *Nature* 427 (2004) 145–148, <https://doi.org/10.1038/nature02121>.
- [46] A.V. Borges, B. Delille, M. Frankignoulle, Budgeting sinks and sources of CO₂ in the coastal ocean: diversity of ecosystems counts, *Geophys. Res. Lett.* 32 (2005), <https://doi.org/10.1029/2005GL023053>.
- [47] W.-J. Cai, M. Dai, Y. Wang, Air-sea exchange of carbon dioxide in ocean margins: a province-based synthesis, *Geophys. Res. Lett.* 33 (2006) L12603, <https://doi.org/10.1029/2006GL026219>.
- [48] S. Tsunogai, S. Watanabe, T. Sata, Is there a “continental shelf pump” for the absorption of atmospheric CO₂? *Tellus* 51B (1999) 701–712.
- [49] B.S. Halpern, S. Walbridge, K. Selkoe, C. Kappel, A Global Map of Human Impact on Marine Ecosystems, *Science* 319 (80-) (2008) 948–952, <https://doi.org/10.1126/science.1149345>.
- [50] T.K. Westberry, M.J. Behrenfeld, P. Schultz, J.P. Dunne, M.R. Hiscock, S. Maritorena, J.L. Sarmiento, D.A. Siegel, Annual cycles of phytoplankton biomass in the subarctic Atlantic and Pacific Ocean, *Glob. Biogeochem. Cycles* 22 (2008) 1–16, <https://doi.org/10.1002/2015GB005276>. Received.
- [51] P.M. Holligan, D.S. Harbour, The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976, *J. Mar. Biol. Assoc. U.K.* 57 (1977) 1075, <https://doi.org/10.1017/S002531540002614X>.
- [52] K. Davidson, L.C. Gilpin, R. Pete, D. Brennan, S. McNeill, G. Moschonas, J. Sharples, Phytoplankton and bacterial distribution and productivity on and around Jones Bank in the Celtic Sea, *Prog. Oceanogr.* 117 (2013) 48–63, <https://doi.org/10.1016/j.pocan.2013.04.001>.
- [53] M.T. Kavanaugh, B. Hales, M. Saraceno, Y.H. Spitz, A.E. White, R.M. Letelier, Hierarchical and dynamic seascapes: a quantitative framework for scaling pelagic biogeochemistry and ecology, *Prog. Oceanogr.* 120 (2014) 291–304, <https://doi.org/10.1016/j.pocan.2013.10.013>.
- [54] M. Morales-Pineda, A. Cózar, I. Laiz, B. Úbeda, J.Á. Gálvez, Daily, biweekly and seasonal temporal scales of pCO₂ variability in two stratified Mediterranean reservoirs, *J. Geophys. Res. Biogeosciences* 119 (2014) 509–520, <https://doi.org/10.1002/2013JG002317>.
- [55] P. Marrec, T. Cariou, M. Latimier, E. Macé, P. Morin, M. Vernet, Y. Bozec, Spatio-temporal dynamics of biogeochemical processes and air-sea CO₂ fluxes in the Western English Channel based on two years of FerryBox deployment, *J. Mar. Syst.* 140 (2014) 26–38, <https://doi.org/10.1016/j.jmarsys.2014.05.010>.
- [56] S.E. Hartman, Z.-P. Jiang, D. Turk, R.S. Lampitt, H. Frigstad, C. Ostle, U. Schuster, Biogeochemical variations at the Porcupine Abyssal Plain sustained Observatory in the northeast Atlantic Ocean, from weekly to inter-annual timescales, *Biogeosciences* 12 (2015) 845–853, <https://doi.org/10.5194/bg-12-845-2015>.
- [57] J.H. Steeler, E.W. Henderson, Spatial patterns in North Sea plankton, *Deep Sea Res. Part II* 26 (1979) 955–963.
- [58] T. Pripp, T. Gammelsrød, J.O. Krakstad, T. Gammelsrød, J.O. Krakstad, Physical influence on biological production along the western shelf of Madagascar, *Deep Sea Res. Part II Top. Stud. Oceanogr.* 100 (2014) 174–183, <https://doi.org/10.1016/j.dsr2.2013.10.025>.
- [59] K.J. Benoit-Bird, B.C. Battaile, S.A. Heppell, B. Hoover, D. Irons, N. Jones, K.J. Kuletz, C.A. Nordstrom, R. Paredes, R.M. Suryan, C.M. Waluk, A.W. Trites, Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies, *PLoS One* 8 (2013) e53348, <https://doi.org/10.1371/journal.pone.0053348>.
- [60] K. Benoit-Bird, B. Battaile, C. Nordstrom, A. Trites, Foraging behavior of northern fur seals closely matches the hierarchical patch scales of prey, *Mar. Ecol. Prog. Ser.* 479 (2013) 283–302, <https://doi.org/10.3354/meps10209>.
- [61] K.J. Benoit-Bird, M.A. McManus, Bottom-up regulation of a pelagic community through spatial aggregations, *Biol. Lett.* 8 (2012) 813–816, <https://doi.org/10.1098/rsbl.2012.0232>.
- [62] J. van der Molen, H.C.M. Smith, P. Lepper, S. Limpenny, J. Rees, Predicting the large-scale consequences of offshore wind turbine array development on a North Sea ecosystem, *Cont. Shelf Res.* 85 (2014) 60–72, <https://doi.org/10.1016/j.csr.2014.05.018>.
- [63] J.F. Tweddle, R.O.H. Murray, B. Scott, M. Gubbins, Evaluating ecosystem services: Starting at the bottom of the food-chain? Results and Discussion: References, in: *ICES C. 2014/3548*, 2014, p. N:01.
- [64] A. Farmer, L. Mee, O. Langmead, P. Cooper, A. Kannen, P. Kershaw, V. Cherrier, The Ecosystem Approach in Marine Management, EU FP7 KNOWSEAS Project, 2012. <http://www.knowseas.com/>.
- [65] E. Bresnan, K. Cook, J. Hindson, S. Hughes, J.-P. Lacaze, P. Walsham, L. Webster, W.R. Turrell, The Scottish Coastal Observatory 1997 - 2013 Part 1 – executive summary, Aberdeen (2016), <https://doi.org/10.7489/1881-1>.
- [66] M. Dickey-collas, A. McQuatters-gollop, E. Bresnan, A.C. Kraberg, J.P. Manderson, R.D.M. Nash, S.A. Otto, A.F. Sell, J.F. Tweddle, V.M. Trenkel, Food for Thought. Pelagic habitat: exploring the concept of good environmental status, *ICES J. Mar. Sci.* (2017), <https://doi.org/10.1093/icesjms/lsx158>.
- [67] A. McQuatters-Gollop, M. Edwards, P. Helaouët, D.E. Raitsos, D. Schroeder, J. Skinner, R.F. Stern, The continuous plankton recorder survey: how can long-term phytoplankton datasets contribute to the assessment of Good Environmental Status? *Estuar. Coast. Shelf Sci.* 162 (2015) 88–97, <https://doi.org/10.1016/j.ecss.2015.05.010>.
- [68] P. Tett, C. Carreira, D.K. Mills, S. Van Leeuwen, J. Foden, E. Bresnan, R.J. Gowen, Use of a Phytoplankton Community Index to assess the health of coastal waters, *ICES J. Mar. Sci.* 65 (2008) 1475–1482, <https://doi.org/10.1093/icesjms/fsn161>.
- [69] R. Howarth, F. Chan, D.J. Conley, J. Garnier, S.C. Doney, R. Marino, G. Billen, Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems, *Front. Ecol. Environ.* 9 (2011) 18–26, <https://doi.org/10.1890/100008>.
- [70] E. Berdalet, L.E. Fleming, R. Gowen, K. Davidson, P. Hess, L.C. Backer, S.K. Moore, P. Hoagland, H. Enevoldsen, Marine harmful algal blooms, human health and wellbeing: challenges and opportunities in the 21st century, *J. Mar. Biol. Assoc. U.K.* (2015) 1–31, <https://doi.org/10.1017/S0025315415001733>.
- [71] CEFAS, MSFD UK priority monitoring species list, 2015. <http://www.nonnativepecies.org/index.cfm?Pageid=597>.
- [72] C. Scherer, R.J. Gowen, P. Tett, Assessing the state of the pelagic habitat: a case study of plankton and its environment in the Western Irish Sea, *Front. Mar. Sci.* 3 (2016), <https://doi.org/10.3389/fmars.2016.00236>.
- [73] A. McQuatters-Gollop, Challenges for implementing the Marine Strategy Framework Directive in a climate of macroecological change, *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 370 (2012) 5636–5655, <https://doi.org/10.1098/rsta.2012.0401>.
- [74] C.N. Ehler, F. Douvère, Marine spatial planning: a step-by-step approach toward ecosystem-based management, *IOC Man. Guid.* 53 (2009) 99 <http://www.vliz.be/imisdocs/publications/153333.pdf>.
- [75] I.J. Bateman, A.R. Harwood, G.M. Mace, R.T. Watson, D.J. Abson, B. Andrews, A. Binner, A. Crowe, B.H. Day, S. Dugdale, C. Fezzi, J. Foden, D. Hadley, R. Haines-Young, M. Hulme, A. Kontoleon, A. Lovett, P. Munday, U. Pascual, J. Paterson, G. Perino, A. Sen, G. Siriwardena, D. van Soest, M. Termansen, Bringing ecosystem services into economic decision-making: land use in the United Kingdom, *Science* 341 (2013) 45–50, <https://doi.org/10.1126/science.1234379>.
- [76] R. Pomeroy, F. Douvère, The engagement of stakeholders in the marine spatial planning process, *Mar. Policy* 32 (2008) 816–822, <https://doi.org/10.1016/j.marpol.2008.03.017>.
- [77] B.E. Scott, K.N. Irvine, A. Byg, M. Gubbins, A. Kafas, J. Kenter, A. MacDonald, R. O'Hara Murray, T. Potts, A.M. Slater, J.F. Tweddle, K. Wright, I.M. Davies, The cooperative participatory evaluation of renewable technologies on ecosystem services (CORPORATES), *Scott. Mar. Freshw. Sci.* 7 (2016) 88, <https://doi.org/10.7489/1681-1>.
- [78] R. Shucksmith, L. Gray, C. Kelly, J.F. Tweddle, Regional marine spatial planning – the data collection and mapping process, *Mar. Policy* 50 (2014) 1–9, <https://doi.org/10.1016/j.marpol.2014.05.012>.
- [79] R.J. Shucksmith, C. Kelly, Data collection and mapping – Principles, processes and application in marine spatial planning, *Mar. Policy* 50 (2014) 27–33, <https://doi.org/10.1016/j.marpol.2014.05.006>.
- [80] P.I. Miller, W. Xu, P. Lonsdale, Seasonal shelf-sea front mapping using satellite ocean colour to support development of the Scottish MPA network, *Deep Sea Res. Part II Top. Stud. Oceanogr.* (2014).
- [81] L. Suberg, R.B. Wynn, J. van der Kooij, L. Fernand, S. Fielding, D. Guihen, D. Gillespie, M. Johnson, K.C. Glikopoulou, I.J. Allan, B. Vrana, P.I. Miller, D. Smeed, A.R. Jones, Assessing the potential of autonomous submarine gliders for

- ecosystem monitoring across multiple trophic levels (plankton to cetaceans) and pollutants in shallow shelf seas, *Methods Oceanogr.* 10 (2014) 70–89, <https://doi.org/10.1016/j.mio.2014.06.002>.
- [82] J.H. Churnside, R.D. Marchbanks, Subsurface plankton layers in the Arctic Ocean, *Geophys. Res. Lett.* (2015), <https://doi.org/10.1002/2015GL064503>.
- [83] P. Quillfeldt, K. Ekschmitt, P. Brickle, R.A.R. McGill, V. Wolters, N. Dehnhard, J.F. Masello, Variability of higher trophic level stable isotope data in space and time - a case study in a marine ecosystem, *Rapid Commun. Mass Spectrom.* 29 (2015) 667–674, <https://doi.org/10.1002/rcm.7145>.
- [84] N.E. Hussey, M.A. Macneil, B.C. Mcmeans, J.A. Olin, S.F.J. Dudley, G. Cliff, S.P. Wintner, S.T. Fennessy, A.T. Fisk, Rescaling the trophic structure of marine food webs, *Ecol. Lett.* 17 (2014) 239–250, <https://doi.org/10.1111/ele.12226>.
- [85] E. Litchman, P. de Tezanos Pinto, K.F. Edwards, C.A. Klausmeier, C.T. Kremer, M.K. Thomas, Global biogeochemical impacts of phytoplankton: a trait-based perspective, *J. Ecol.* 103 (2015) 1384–1396, <https://doi.org/10.1111/1365-2745.12438>.
- [86] M. Edwards, P. Helaouet, D.G. Johns, S. Batten, G. Beaugrand, S. Chiba, J. Hall, E. Head, G. Hosie, J. Kitchener, P. Koubbi, A. Kreiner, C. Melrose, M. Pinkerton, A.J. Richardson, K. Robinson, K. Takahashi, H.M. Verheye, P. Ward, M. Wootton, *Global Marine Ecological Status Report: Results from the Global CPR Survey 2013/2013*, Plymouth, UK, 2014.