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HORIZONS

Plankton indicators and ocean observing systems: support to the marine ecosystem state assessment

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Ecological indicators are used extensively as tools to manage environmental resources. In the oceans, indicators of plankton can be measured using a variety of observing systems including: mooring stations, ships, autonomous floats and ocean colour remote sensing. Given the broad range of temporal and spatial sampling resolutions of these different observing systems, as well as discrepancies in measurements obtained from different sensors, the estimation and interpretation of plankton indicators can present significant challenges. To provide support to the assessment of the state of the marine ecosystem, we propose a suite of plankton indicators and subsequently classify them in an ecological framework that characterizes key attributes of the ecosystem. We present two case studies dealing with plankton indicators of biomass, size structure and phenology, estimated using the most spatially extensive and longest *in situ* and remote-sensing observations. Discussion of these studies illustrates how some of the challenges in estimating and interpreting plankton indicators may be addressed by using for example relative measurement thresholds,

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interpolation procedures and delineation of biogeochemical provinces. We demonstrate that one of the benefits attained, when analyzing a suite of plankton indicators classified in an ecological framework, is the elucidation of non-trivial changes in composition, structure and functioning of the marine ecosystem.

KEYWORDS: phytoplankton; marine ecosystem assessment; indicators; ocean observing systems; ecological framework

INTRODUCTION

At the beginning of the twentieth century, bulk biological properties of the ocean were often sampled at a fixed marine laboratory stations, allowing for the development of time series. Half a century later, rapid advances in sampling techniques, development of autonomous instrumentation and use of ships of opportunity, have permitted us to explore vast areas of the world oceans and to investigate the variability of a broad range of biological properties both in time and space dimensions. In the late 1970s, remote-sensing technology revolutionized ocean observations by providing the first high-resolution synoptic fields of phytoplankton biomass at a global scale. Analyses of these historical observations have revealed a marked sensitivity of marine plankton to changes in climate, with significant impact on marine food web interactions and commercial fisheries (Beaugrand *et al*., 2002; Edwards and Richardson, 2004; Hays *et al*., 2005; Koeller *et al*., 2009; Martinez *et al*., 2009; Thackeray *et al*., 2010).

Although decision makers and management authorities require a clear and unequivocal assessment of ecosystem state, scientists are still striving to understand the underlying mechanisms controlling variability in primary producers. Not unexpectedly, conflicting findings are difficult to resolve. In a recent comparison involving four types of *in situ* measurements of phytoplankton biomass, independent estimates of multi-decadal trends were incongruent in several oceanic basins (Boyce *et al*., 2010; Mackas, 2011; McQuatters-Gollop *et al*., 2011; Rykaczewski and Dunne, 2011; Wernand *et al*., 2013). Such discrepancies underline the need to foster evidence-based research (Sutherland and Pullin, 2004) and to promote integrated long-term monitoring strategies (Edwards *et al*., 2010).

Here, we argue that only data from a combination of ocean observing systems can allow us to construct, and subsequently implement, a suite of plankton indicators that would characterize key ecological attributes (such as composition, structure and functioning), permitting a comprehensive assessment of the marine ecosystem. First, we discuss the definition and usage of ecological indicators and propose an ecological framework to classify a number of plankton indicators according to their different ecosystem attributes. Second, we review the different observing systems (available to measure the indicators) and their sampling scales. Third, we highlight the technical and conceptual impediments that can be encountered when analyzing a suite of indicators estimated from different observing systems. Finally, using two case studies dealing with indicators of phytoplankton biomass, size structure and phenology, we provide examples of solutions to reduce the challenges of analyzing data from a range of *in situ* and remote-sensing observing systems, discussing some of the benefits that can be attained in the assessment of the state of the marine ecosystem.

ECOLOGICAL FRAMEWORK OF PLANKTON INDICATORS

Indicators have been widely developed as instruments to provide specific information about the state of a system. Assessment of the system may be discipline specific with economic, societal and environmental indicators, may link two disciplines with socio-economic indicators (Bowen and Riley, 2003) or may take a holistic approach with sustainability indicators (Rapport *et al*., 1998; Pajak, 2000). The term indicator is used collectively by scientists, policymakers and the general public. However, there is considerable diversity in the ways indicators are perceived and applied by various user communities. For instance, indicators can be used to judge the effectiveness of policies on nature (Herzi and Dovers, 2006), objectify the quality of nature (Turnhout *et al*., 2007), monetize the functions of nature (Costanza *et al*., 1997) or assess the health and benefits of nature (Halpern *et al*., 2012). In plankton ecology, indicators are used essentially to capture the condition of the environment, as early-warning signals and as barometers of long-term trends (Niemi and McDonald, 2004). Selecting and interpreting plankton indicators to assess ecosystem health (referred by recent EU directives as 'good ecological or environmental status'; Tett *et al*., 2013) can be challenging.

An ecological framework can be used as an aid to enable comprehensive ecosystem state assessment. This type of conceptual framework incorporates key attributes of composition, structure and function of the ecosystem (Dale and Beyeler, 2001). These attributes are used to identify a suite of plankton indicators to assess the state of the marine ecosystem and capture some of the impacts of climate change on the base of the food chain (Table I). We then organize an ecological framework into three classes of indicators: (i) a synthetic indicator representing the overarching objective of assessing the state of the ecosystem, (ii) three composite indicators providing information about key attributes of the ecosystem, and (iii) a suite of measurable plankton indicators adducing evidence from field observations at the individual, community and regional levels. The plankton indicators listed in the framework (Table I) are not exhaustive but emanate from the extensive literature collated in academic publications and expert management group reports aiming at reviewing and establishing marine ecosystem indicators which can be used in policies (Rice and Rochet, 2005; Platt and Sathyendranath, 2008; Cardoso *et al.*, 2010; Ferreira *et al.*, 2011; Edwards *et al.*, 2013). The realization of the ecosystem state assessment then requires implementation and interpretation of these plankton indicators, which are two challenging steps, especially given the diversity of characteristics of ocean observing systems.

OCEAN OBSERVING SYSTEMS TO IMPLEMENT PLANKTON INDICATORS

Pelagic ecosystem properties are typically measured either directly by *in situ* sampling or remotely by collecting water-leaving radiance. The latter method, using satellite-borne instruments, can provide the highest area coverage (global oceans), spatial resolution (∼1 km) and sampling frequency (∼1 day) of phytoplankton biomass (Fig. 1). Ocean-colour remote sensor began to be operational in 1978 and, to date, it is the most cost-efficient method to retrieve large-scale observations of phytoplankton. The second largest-scale measurements of plankton data come from the Continuous Plankton Recorder (CPR) program. The program relies on a network of volunteer ships, which collect plankton data along the shipping routes. The network led by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in the UK, has enabled *in situ* basin-scale monitoring of plankton in the North Sea since 1931 and across the North Atlantic since 1958 (Richardson *et al.*, 2006). CPR programs have also been more recently implemented by institutes in Australia, Canada, Japan, New Zealand, South Africa and USA. In 2011, the Global Alliance of CPR Surveys (GACS) was created to coordinate CPR monitoring programs throughout the world oceans. However, observations of phytoplankton from CPR, as well as those from visible spectral radiometry, are limited to the surface layer of the oceans (i.e. well-mixed ∼20 m surface layer and first optical depth, respectively). These methods do not account for biological processes occurring at depth such as, for instance, deep chlorophyll maxima.

Vertical profiles of the water column can be sampled from oceanographic research vessels, moorings and autonomous underwater instruments (Fig. 1). Although these *in situ* deployments provide relatively scarce discrete observations over the vast oceans, their number is increasing, allowing for higher coverage and three-dimensional exploration from surface to deep-water

Table I: Plankton indicators organized in an ecological framework

Plankton indicators	Mooring	Ship	Glider	CPR	Satellite	Ecosystem attributes	Ecosystem state assessment
Taxonomic diversity	×	×		×		Composition	Impacts of climate on ocean primary producers
Dominant phytoplankton groups	×	×		×	×		
Biogeochemical provinces					×		
Chlorophyll concentration	×	×	×	×	×	Structure	
Size fraction spectrum	×	×			×		
C:Chl ratio	×	×			×		
Spatial variance in biomass			×		×		
Phenology			×	×	×		
Euphotic depth	×		×		×		
Photosynthesis–irradiance parameters	×	×				Functioning	
Primary production	×	×			×		
Net community production	×	×			×		
Net community losses	×	×			×		

The indicators are presented together with the sampling capability of current relevant observing systems. Indicators classified in the composition attribute provide information about the identity and variety of plankton cells and populations. This attribute also includes information about ocean provinces based on their physical, chemical and biological characteristics. Indicators presented in the structural attribute are related to the organization, arrangement and patterns of the occurrence of plankton in the system, which can be provided, for example, as measures of concentration, abundance, size fractions and timing of events. This attribute also includes the delineation of water depth boundaries where ecological processes can occur. Indicators classified in the functioning attribute represent measures of rates of physiological activity or ecological processes.

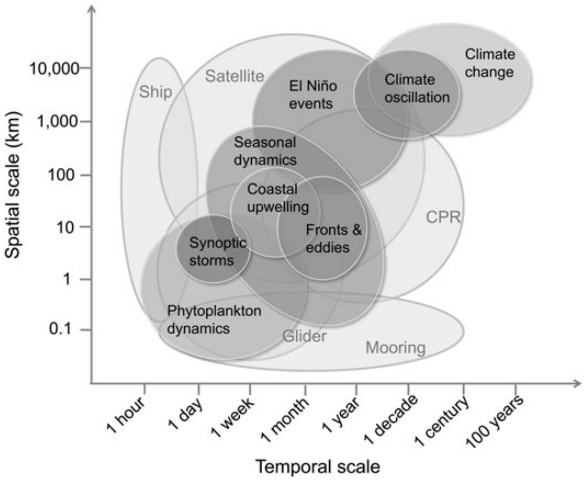

Fig. 1. Spatial and temporal scale characteristics of ocean observing systems and of environmental and climate forcing.

layers, in time and space dimensions. Such *in situ* phytoplankton observations have been collected at weekly to monthly frequency for several decades at various stations around the world (e.g. the BATS and HOTS time-series stations; Karl *et al*., 2001). More recently, fixed sampling platforms have been deployed, such as IORS (IEODO Ocean Research Station) in the Korean Sea, permitting continuous and autonomous measurements of bio-optical properties and monitoring of phytoplankton communities (Noh *et al*., 2005). The ARGO program, first initiated in 1999 specifically for observations of physical variables, is now deploying drifting buoys equipped with fluorescence, absorption and backscattering sensors, and thus provides bio-optical observations from surface to ~1000 m depth (IOCCG, 2011). Further efforts to collect *in situ* three-dimensional observations of bio-optical properties are provided by autonomous underwater vehicles such as gliders. These instruments sample vertical profiles of water between surface and ~1000 m depth autonomously for periods of up to 6 months (Rudnick *et al*., 2004). The numbers deployed are increasing steadily, reaching nearly 100 in 2013 (http://www.ego-network.org/dokuwiki/doku.php) and the data collected are revolutionizing our approach to monitoring ocean phytoplankton, allowing us to bridge spatial and temporal gaps between moorings and research vessels (Swart *et al*., 2012).

TOWARDS A COMPREHENSIVE INTERPRETATION OF PLANKTON INDICATORS

The capabilities of the different ocean-observing systems to estimate plankton indicators are presented in Table I. Some indicators such as phytoplankton biomass can be estimated from a wide range of observing systems, whereas other indicators may only be measured following specific experimental protocols (e.g. primary production) or may require microscopic identification (e.g. taxonomic diversity) and therefore are currently estimated from a limited set of observing systems. The large discrepancies in coverage between the diverse *in situ* and remote-sensing observations, as well as the large spatial, temporal and intrinsic variability of some indicators (e.g. observations from chlorophyll concentrations commonly span at least four orders of magnitude), can impede blending of data from multiple observing systems and interpreting indicators in the context of an ecological framework. Technical impediments to be overcome commonly include: (i) application of systematic quality-control procedures (Aiken *et al*., 2009; Glover *et al*., 2011); (ii) validation and calibration methods for *in situ* or remote-sensing measurements (Batten *et al*., 2003; Bailey and Werdell, 2006); (iii) merging procedures for ocean-colour products collected from different radiometric sensors (Gregg and Conkright, 2002; Antoine *et al*., 2005; Mélin and Zibordi, 2007); (iv) extension of the chlorophyll record using empirical relationships between *in situ* (e.g. CPR Phytoplankton Colour Index) and ocean-colour observations (Raitsos et al., 2005; Raitsos *et al*., 2012); (v) interpolation, re-gridding and averaging procedures to compare or blend data sets with different spatial and temporal sampling resolutions (Mackas, 2011; Lavigne *et al*., 2013).

Analysis of a combination of indicators from the functional, compositional and structural attributes may also bear significant benefits: it can help ensuring that the different scales of variability within the ecological system are represented (Fig. 1). For instance, indicators of dominant phytoplankton groups (composition attribute, Table I) and chlorophyll concentration (structure attribute) can both vary on seasonal, inter-annual and longer time scales in response to the same environmental and climate forcing. However, whereas large-scale shifts in the relative dominance of diatoms in response to climate indices can be observed within less than a decade of observations (Alvain *et al*., 2013), detection of global warming trends on bulk properties of the ecosystem (such as chlorophyll concentration) can require multi-decade-long observations (Henson *et al*., 2010). Additional benefits may be envisaged when measures of one or several indicators provide relevant information to estimate another indicator. This transfer of information can be achieved using empirical or analytical models. A good example is the objective assignment of parameters required to implement a primary production model, which includes photosynthesis–irradiance curve parameters (functioning attribute, Table I), chlorophyll concentration (structure attribute) and sea-surface temperature (Platt *et al.*, 2008).

In the two case studies presented below, we demonstrate some of the benefits and provide insights to help surmount some of the technical impediments that can be encountered when analysing plankton indicators estimated from different observing systems.

CASE-STUDY I: TRENDS IN PHYTOPLANKTON BIOMASS AND SIZE FRACTIONS

The AMT program is a unique observing system, sampling biogeochemical and plankton data along a ~13 500 km north−south transect in the Atlantic Ocean. Since 1995, ~50−80 stations along the transect have been sampled at bi-annual to annual frequencies, allowing us to improve our understanding of the variability of plankton ecosystems (Aiken *et al.*, 2000; Robinson *et al.*, 2006). In the present case study, chlorophyll and accessory pigments were sampled within the first optical depth during the boreal autumn cruises of eight AMT expeditions, and are used here to analyse trends during the period 2003−2010 (Fig. 2a). Remote-sensed chlorophyll data collected by the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) were obtained at resolutions of 8-day and 9 km from NASA ocean-colour project (McClain *et al.*, 1998). Resolution and coverage discrepancies between *in situ* and remote-sensing chlorophyll observations are addressed here by averaging each type of measurements within three biogeochemical provinces of the Atlantic Ocean (Longhurst, 1998). The trends are estimated using linear regression analysis on the log-transformed data. The general linear model is applied to the data for comparisons. Analysis of the trends in chlorophyll concentration reveals that measurements are consistent between *in situ* and remote-sensing observations in the North and South Atlantic gyre provinces. In the tropical Atlantic province, although the trends in chlorophyll concentration estimated from *in situ* and remote-sensing observations do not differ statistically (i.e. the error bars are overlapping), the trend in chlorophyll estimated from *in situ* observations is close to zero, whereas based on the remote-sensing observations, the chlorophyll trend shows a significant decrease during the 2003−2010 period (Fig. 2b). This discrepancy may arise from limited availability of remote-sensing observations due to persistent cloud cover in the tropical Atlantic region (Antoine *et al.*, 2005). In addition to the analysis of chlorophyll-*a* concentration, the fractional structure of the phytoplankton community can be characterized by applying empirical models to *in situ* sampled pigment data (Uitz *et al.*, 2006; Brewin *et al.*, 2010). Here, we use the model of Uitz *et al.* (Uitz *et al.*, 2006). This involved selecting from the pigment data seven diagnostic pigments, which, together with multiple linear regression coefficients, are used to reconstruct the chlorophyll concentration and estimate the fractional contribution of pico-, nano- and microplankton to the total chlorophyll concentration (further details of this approach can be found in Uitz *et al.*, 2006). In the analysis of the trends over the period 2003−2010, it is noteworthy that even though inter-annual trends in chlorophyll concentration

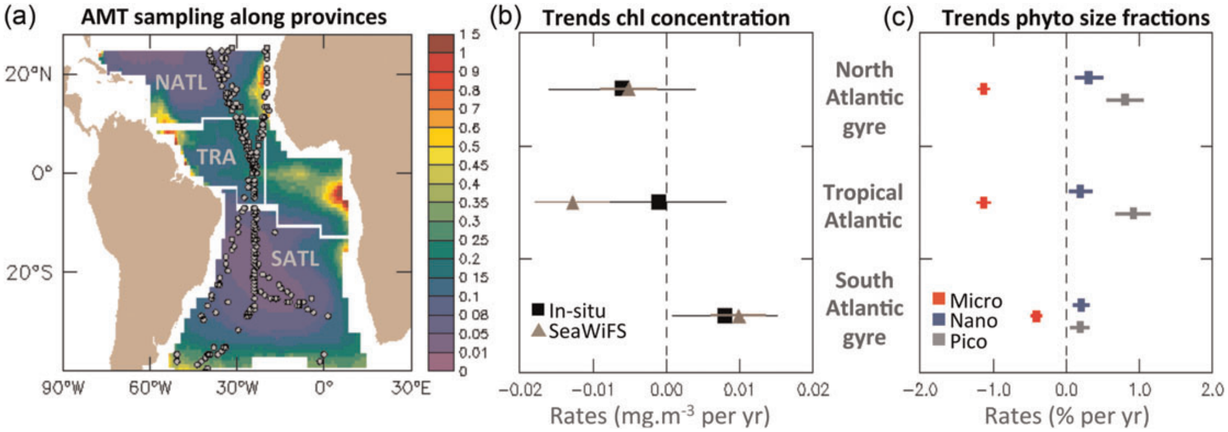

Fig. 2. Case study I: Trends in chlorophyll concentration and phytoplankton size fractions. (**a**) Positions of phytoplankton chlorophyll and accessory pigment samples collected during Atlantic Meridional Transects (AMT) expeditions in boreal autumns over the period 2003−2010. Chlorophyll data were checked following the quality control procedure of Aiken *et al.* (Aiken *et al.*, 2009). The ecological province partitioning of Longhurst (Longhurst, 1998) is overlaid on remote-sensing chlorophyll concentration (mg.m^{-3}, SeaWiFS, mean 2003−2010). (**b**) Trends in chlorophyll concentration from *in situ* (black) and remote sensing (blue). (**c**) Trends in phytoplankton size fractions (micro-in red, nano-in blue, and picophytoplankton-in gray) estimated from *in situ* pigment data using the model of Uitz *et al.* (Uitz *et al.*, 2006). The error bars represent ±1 standard deviation.

are not significant within two of the three biogeochemical provinces, the relative contribution of the different phytoplankton size fractions shows a significant and coherent decline in microphytoplankton in all three provinces (Fig. 2c). On average in the Tropical Atlantic ocean, microphytoplankton declined by 0.88% year^{-1}, while nano- and picophytoplankton increased by 0.24 and 0.64% year^{-1}, respectively. Integration of observations from multiple observing systems and the synergistic analysis of different indicators (i.e. chlorophyll concentration and phytoplankton size fraction) permit us to demonstrate that an apparent inter-annual stability in chlorophyll concentration can conceal significant variation in the community size fraction on the same time scale. Such changes can alter significantly the structure and functioning of food web, which can engender higher variability in fish recruitment and trigger shifts in species dominance, such as for example, the alternation of sardine or anchovy regimes in upwelling ecosystems (Cury *et al.*, 2008).

CASE-STUDY II: DECADAL VARIABILITY IN PHYTOPLANKTON PHENOLOGY

Synoptic fields of phytoplankton biomass were first recorded in 1978. The Coastal Zone Color Scanner (CZCS) was the first sensor specifically developed to study ocean colour properties from space. It remained operational for seven-and-a-half years until 1986. Power restrictions, darkness, clouds, low solar angles and light saturation over ice or snow masses have restricted its sampling coverage. The next major ocean colour satellite instrument, named SeaWiFS, acquired data for nearly 14 years from 1997 until 2010. These chlorophyll time series provided by these two sensors are separated by a gap of more than 10 years and, due to technical differences in the sensors, effective comparison of their absolute values of chlorophyll concentrations is not straightforward (Gregg and Conkright, 2002; Antoine *et al.*, 2005). The CPR survey provides five decades of continuous basin-scale records of phytoplankton biomass. Semi-quantitative measurements of chlorophyll are estimated using a phytoplankton colour index (PCI), which is assigned by visual comparison with a standard semi-logarithmic scale of increasing colour intensity, calibrated with numerical values of phytoplankton pigment concentrations. Monthly PCI measurements from ship tracks are gridded into 41 standard areas across the North Atlantic (Richardson *et al.*, 2006). To compare CPR and remote-sensing observations, spatial averages of remote-sensing chlorophyll concentrations were computed over the CPR standard areas (Fig. 3a). Combined analysis of the different data sets is achieved by analyzing phenology indicators, which characterize relative patterns in the annual signal of phytoplankton biomass, and thus are not sensitive to sensors' differences in absolute values of chlorophyll or PCI. To support the detection of phenological changes in CPR time series, monthly PCI data are re-gridded to weekly resolution using linear interpolation. The phenology indicator of duration of phytoplankton growing period is estimated as the number of weeks between the timings of initiation and termination of the phytoplankton growth. The timings are detected using a threshold criterion (we use here the median plus 5% chlorophyll concentration threshold; Siegel *et al.*, 2002; Racault *et al.*, 2012). The presence of gaps in the CPR sampling (which were reduced by filling through interpolation of temporally adjacent PCI values, when these were available) limits the estimation of

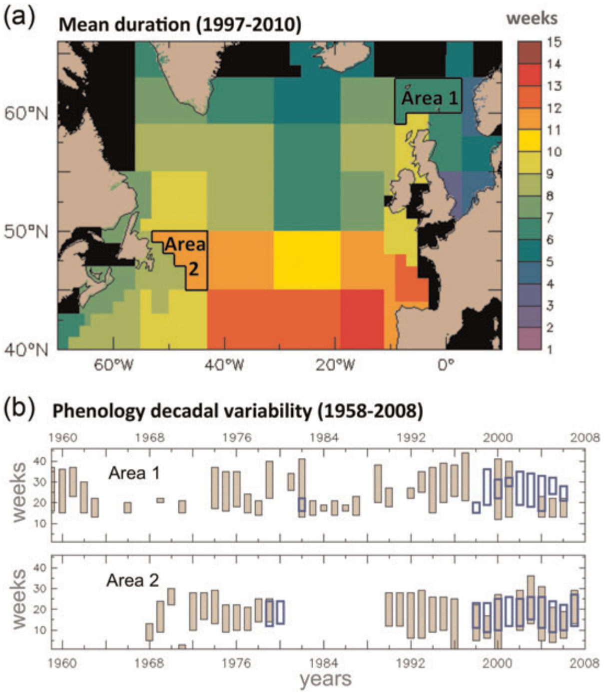

Fig. 3. Case study II: decadal variability in phytoplankton phenology. (**a**) Mean duration of phytoplankton growing period estimated from remote-sensing chlorophyll (SeaWiFS) over the period 1998–2010. The chlorophyll data were averaged for each continuous plankton recorder (CPR) standard area prior to estimating the duration indicator; (**b**) time series from 1958 to 2010 of phytoplankton phenology estimated from phytoplankton colour index (CPR survey, brown-filled rectangles) and from chlorophyll concentrations (SeaWiFS and CZCS, empty blue rectangles). The vertical length of the rectangles shows the duration of the growing period and the lower and upper edges of the rectangles indicate for each year the timings of initiation and termination, respectively. The location of the selected areas is shown in (a): Northern Northeast Atlantic (area 1) and Southern Northwest Atlantic (area 2). The two areas have been selected for illustration purposes. Missing phenology estimates are due to insufficient temporal coverage in CPR colour index or remote-sensing chlorophyll data.

phytoplankton phenology to 30 years (out of the 50 years long record) on average across the basin. Results are presented for two areas (Fig. 3b) where coherent duration of phytoplankton growing period could be estimated between the different types of observations. Estimates of duration appear to agree closely at lower latitudes (area 2) but show larger offsets at higher latitudes (area 1). The discrepancy observed in the comparison of discrete-time properties might expose the limitations of: (i) the different sampling resolutions and coverage between the CPR and remote-sensing observations, (ii) the calibration of satellite sensors and the chlorophyll-retrieval algorithm (Moore *et al.*, 2009), and (iii) the numerical methods used by the CPR to analyse the semi-quantitative silk colour data (Batten *et al.*, 2003). The relationship between PCI and chlorophyll can change markedly from season to season, leading to possible under- or overestimation of chlorophyll concentrations. Furthermore, regional and seasonal variations in phytoplankton cell sizes and species dominance (e.g. dinoflagellates or diatoms) can impact the extent to which the CPR silk accurately sample phytoplankton populations, leading to possible inconsistencies between estimates of chlorophyll form PCI and remote sensing (Raitsos *et al.*, 2005). These results highlight the considerations that need to be taken when drawing strong conclusions about long-term trends from combining different types of observations. Despite these limitations, analysis of the different data sets reveals an apparent large variation in phytoplankton phenology in the North Atlantic over five decades 1960–2010. Such variations can have a profound impact altering: (i) the efficiency of the biological pump, with knock-on effects to the global carbon cycle; and (ii) the interactions across different trophic levels, which can have broad impacts on the survival of commercially important fish and crustacean larvae (Platt *et al.*, 2003; Koeller *et al.*, 2009).

CONCLUDING REMARKS

Discrepancies in resolution (time and space) encountered when estimating a suite of plankton indicators from different observing systems (e.g. mooring stations, ships, autonomous floats and remote-sensing) can be reduced by using relative measurement thresholds, interpolation procedures and delineation of biogeochemical provinces. Once observational challenges are surmounted, the interpretation of a suite of indicators classified in an ecological framework may help support a more holistic (ecologically comprehensive) assessment of the state of the marine ecosystem. It allows us to consider changes in key attributes of the ecosystem and to account for the different sensitivities of plankton indicators to climate variability and change. The next step towards a more systematic and transparent selection of indicators would be for instance, to consider and investigate the use of weighting systems to aggregate and analyse plankton indicators (Rice and Rochet, 2005; Niemeijer and de Groot, 2008). Such weighting systems have been incorporated in terrestrial ecology and have been shown to reduce the risk of reaching non-evidenced-based conclusions and arbitrary decision-making (Sutherland and Pullin, 2004; Lin *et al.*, 2009). Further information to consider in the assessment of ecosystem status is the propagation of uncertainty from *in situ* or remotely sensed measurements of a bulk property, to the indicator estimates and then to the analysis of indicators. There are increasing efforts to provide uncertainty estimates for *in situ* and remotely sensing products (e.g. Moore *et al.*, 2009), and together with statistical procedures (e.g. Monte Carlo methods), the propagation of uncertainty to ecological indicators is feasible and likely to increase our level of confidence on the assessment of the state of the marine ecosystem. In addition to development and analysis of plankton indicators using ocean observations, progress towards their numerical representation in ecosystem models should provide a valuable tool to explore and predict future trends in the state of the marine ecosystem. This will be essential to underpin strategic and long-term stewardship of the oceans.

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REFERENCES

Aiken, J., Pradhan, Y., Barlow, R. *et al.* (2009) Phytoplankton pigments and functional types in the Atlantic Ocean: a decadal assessment, 1995–2005. *Deep-Sea Res. II*, **56**, 899–917.

Aiken, J., Rees, N., Hooker, S. *et al.* (2000) The Atlantic Meridional Transect: overview and synthesis of data. *Prog. Oceanogr.*, **45**, 257–312.

Alvain, S., Le Quéré, C., Bopp, L. *et al.* (2013) Rapid climatic driven shifts of diatoms at high latitudes. *Remote Sens. Environ.*, **132**, 195–201.

Antoine, D., Morel, A., Gordon, H. R. *et al.* (2005) Bridging ocean color observations of the 1980s and 2000s in search of long-term trends. *J. Geophys. Res.*, **110**, C06009.

Bailey, S. W. and Werdell, P. J. (2006) A multi-sensor approach for the on-orbit validation of ocean color satellite data products. *Remote Sens. Environ.*, **102**, 12–23.

Batten, S. D., Walne, A. W., Edwards, M. *et al.* (2003) Phytoplankton biomass from continuous plankton recorder data: an assessment of the phytoplankton colour index. *J. Plankton Res.*, **25**, 697–702.

Beaugrand, G., Reid, P. C., Ibañez, F. *et al.* (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.

Bowen, R. E. and Riley, C. (2003) Socio-economic indicators and integrated coastal management. *Ocean Coast. Manage.*, **46**, 299–312.

Boyce, D., Lewis, M. and Worm, B. (2010) Global phytoplankton decline over the past century. *Nature*, **466**, 591–596.

Brewin, R. J. W., Sathyendranath, S., Hirata, T. *et al.* (2010) A three-component model of phytoplankton size class for the Atlantic Ocean. *Ecol. Model.*, **221**, 1472–1483.

Cardoso, A. C., Cochrane, S., Doerner, H. *et al.* (2010) *Scientific support to the European Commission on the Marine Strategy Framework Directive*. Management Group Report, Office for Official Publications of the European Communities, Luxembourg, pp. 65.

Costanza, R., Arge, R., Groot, R. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.

Cury, P. M., Shin, Y.-J., Planque, B. *et al.* (2008) Ecosystem oceanography for global change in fisheries. *Trends Ecol. Evol.*, **23**, 338–346.

Dale, V. H. and Beyeler, S. C. (2001) Challenges in the development and use of ecological indicators. *Ecol. Indic.*, **1**, 3–10.

Edwards, M., Beaugrand, G. and Hays, G. (2010) Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends Ecol. Evol.*, **25**, 602–610.

Edwards, M., Beaugrand, G., Helaouët, P. *et al.* (2013) Marine ecosystem response to the Atlantic Multidecadal Oscillation. *PLoS ONE*, **8**, e57212.

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

Ferreira, J. G., Andersen, J. H., Borja, A. *et al.* (2011) Overview of eutrophication indicators to assess environmental status within the European Marine Strategy Framework Directive. *Estuarine Coastal Shelf Sci.*, **93**, 117–131.

Glover, D. M., Jenkins, W. J. and Doney, S. C. (2011) *Modeling Methods for Marine Science*. Cambridge University Press, Cambridge.

Gregg, W. W. and Conkright, M. E. (2002) Decadal changes in global ocean chlorophyll. *Geophys. Res. Lett.*, doi:10.1029/2002GL014689.

Halpern, B. S., Longo, C., Hardy, D. *et al.* (2012) An index to assess the health and benefits of the global ocean. *Nature*, **488**, 615–620.

Hays, G., Richardson, A. and Robinson, C. (2005) Climate change and marine plankton. *Trends Ecol. Evol.*, doi:10.1016/j.tree.2005.03.004.

Henson, S., Sarmiento, J. L., Dunne, J. P. *et al.* (2010) Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. *Biogeosciences*, **7**, 621–640.

Hezri, A. and Dovers, S. R. (2006) Sustainability indicators, policy and governance: issues for ecological economics. *Ecol. Econ.*, **60**, 86–99.

IOCCG. (2011) Bio-Optical Sensors on Argo Floats. In Claustre, H. (ed.), *Reports and Monographs of the International Ocean-Colour Coordinating Group*. Report No. 11, IOCCG, Dartmouth, Canada, pp. 89.

Karl, D., Dore, J., Lukas, R. *et al.* (2001) Building the long-term picture: the U.S. JGOFS Time-series Programs. *Oceanography*, **14**, 6–17.

Koeller, P., Fuentes-Yaco, C., Platt, T. *et al.* (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science*, **324**, 791–793.

Lavigne, H., D'Ortenzio, F., Migon, C. *et al.* (2013) Enhancing the comprehension of mixed layer depth control on the Mediterranean phytoplankton phenology. *J. Geophys. Res.*, **118**, 3416–3430.

Lin, T., Lin, J., Cui, S. *et al.* (2009) Using a network framework to quantitatively select ecological indicators. *Ecol. Indic.*, **9**, 1114–1120.

Longhurst, A. (1998) *Ecological Geography of the Sea*. Academic Press, California.

Mackas, D. L. (2011) Does blending of chlorophyll data bias temporal trend? *Nature*, doi:10.1038/nature09951.

Martinez, E., Antoine, D., D'Ortenzio, F. *et al.* (2009) Climate-driven basin-scale decadal oscillations of oceanic phytoplankton. *Science*, **326**, 1253–1256.

McClain, C. R., Cleave, M. L., Feldman, G. C. *et al.* (1998) Science quality SeaWiFS data for global biosphere research. *Sea Tech.*, **39**, 10–16.

McQuatters-Gollop, A., Reid, P. C. and Edwards, M. (2011) Is there a decline in marine phytoplankton? *Nature*, doi:10.1038/nature09950.

Mélin, F. and Zibordi, G. (2007) Optically based technique for producing merged spectra of water-leaving radiances from ocean color remote sensing. *Appl. Opt.*, **46**, 3856–3869.

Moore, T. S., Campbell, J. W. and Dowell, M. D. (2009) A class-based approach to characterizing and mapping uncertainty of the MODIS ocean chlorophyll product. *Remote Sens. Environ.*, **113**, 2424–2430.

Niemeijer, D. and De Groot, R. S. (2008) A conceptual framework for selecting environmental indicator sets. *Ecol. Indic.*, **8**, 14–25.

Niemi, G. J. and McDonald, M. E. (2004) Application of Ecological Indicators. *Annu. Rev. Ecol. Evol. Syst.*, **35**, 89–111.

Noh, J. H., Yoo, S., Lee, J. A. *et al.* (2005) Phytoplankton in the waters of the Ieodo Ocean Research Station determined by microscopy, flow cytometry, HPLC pigment data and remote sensing. *Ocean Polar Res.*, **27**, 397–417.

Pajak, P. (2000) Sustainability, ecosystem management, and indicators: thinking globally and acting locally in the 21st century. *Fisheries*, **25**, 16–30.

Platt, T., Fuentes-Yaco, C. and Frank, K. (2003) Spring algal bloom and larval fish survival. *Nature*, **423**, 398–399.

Platt, T. and Sathyendranath, S. (2008) Ecological indicators for the pelagic zone of the ocean from remote sensing. *Remote Sens. Environ.*, **112**, 3426–3436.

Platt, T., Sathyendranath, S., Forget, M.-H. *et al.* (2008) Operational estimation of primary production at large geographical scales. *Remote Sens. Environ.*, **112**, 3437–3448.

Racault, M.-F., Le Quéré, C., Buitenhuis, E. *et al.* (2012) Phytoplankton phenology in the global ocean. *Ecol. Indic.*, **14**, 152–163.

Raitsos, D. E., Walne, A. W., Lavender, S. J. *et al.* (2012) A 60-year ocean colour data set from the continuous plankton recorder. *J. Plankton Res.*, **35**, 158–164.

Raitsos, D. E., Reid, P. C., Lavender, S. J. *et al.* (2005) Extending the SeaWiFS chlorophyll data set back 50 years in the northeast Atlantic. *Geophys. Res. Lett.*, **32**, L06603.

Rapport, D. J., Costanza, R. and McMichael, A. J. (1998) Assessing ecosystem health. *Trends Ecol. Evol.*, **13**, 397–402.

Rice, J. C. and Rochet, M.-J. (2005) A framework for selecting a suite of indicators for fisheries management. *ICES J. Mar. Sci.*, **62**, 516–527.

Richardson, A. J., Walne, A. W., John, A. W. G. *et al.* (2006) Using continuous plankton recorder data. *Prog. Oceanogr.*, **68**, 27–74.

Robinson, C., Poulton, A. J., Holligan, P. M. *et al.* (2006) The Atlantic Meridional Transect (AMT) Programme: a contextual view 1995–2005. *Deep-Sea Res. II*, **53**, 1485–1515.

Rudnick, D. L., Davis, R. E., Eriksen, C. C. *et al.* (2004) Underwater gliders for ocean research. *Mar. Technol. Soc. J.*, **38**, 48–59.

Rykaczewski, R. R. and Dunne, J. P. (2011) A measured look at ocean chlorophyll trends. *Nature*, **472**, E5–E6.

Siegel, D. A., Doney, S. C. and Yoder, J. A. (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science*, **296**, 730–733.

Sutherland, W. and Pullin, A. (2004) The need for evidence-based conservation. *Trends Ecol. Evol.*, **19**, 4–7.

Swart, S., Chang, N., Fauchereau, N. *et al.* (2012) Southern Ocean Seasonal Cycle Experiment 2012: Seasonal scale climate and carbon cycle links. *S. Afr. J. Mar. Sci.*, **108**, 1–3.

Tett, P., Gowen, R., Painting, S. *et al.* (2013) A framework for understanding marine ecosystem health. *Mar. Ecol. Prog. Ser.*, doi:10.3354/meps10539.

Thackeray, S. J., Sparks, T. H., Frederiksen, M. *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biol.*, **16**, 3304–3313.

Turnhout, E., Hisschemöller, M. and Eijsackers, H. (2007) Ecological indicators: between the two fires of science and policy. *Ecol. Indic.*, **7**, 215–228.

Uitz, J., Claustre, H., Morel, A. *et al.* (2006) Vertical distribution of phytoplankton communities in open ocean: an assessment based on surface chlorophyll. *J. Geophys. Res.*, **111**, C08005.

Wernand, M. R., Van der Woerd, H. J. and Gieskes, W. W. C. (2013) Trends in ocean colour and chlorophyll concentration from 1889 to 2000, worldwide. *PLoS ONE*, **8**, e63766.