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A 60-year ocean colour data set from the continuous plankton recorder

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The phytoplankton colour index (PCI) of the Continuous Plankton Recorder (CPR) survey is an *in situ* measure of ocean colour, which is considered a proxy of the phytoplankton biomass. PCI has been extensively used to describe the major spatiotemporal patterns of phytoplankton in the North Atlantic Ocean and North Sea since 1931. Regardless of its wide application, the lack of an adequate evaluation to test the PCI's quantitative nature is an important limitation. To address this concern, a field trial over the main production season has been undertaken to assess the numerical values assigned by previous investigations for each category of the greenness of the PCI. CPRs were towed across the English Channel from Roscoff to Plymouth consecutively for each of 8 months producing 76 standard CPR samples, each representing 10 nautical miles of tow. The results of this experiment test and update the PCI methodology, and confirm the validity of this long-term *in situ* ocean colour data set. In addition, using a 60-year time series of the PCI of the western English Channel, a comparison is made between the previous and the current revised experimental calculations of PCI.

KEYWORDS: ocean colour; chlorophyll; *in situ*; phytoplankton; CPR; PCI

INTRODUCTION

Phytoplankton are major contributors to global primary production (Falkowski *et al.*, 2004) and, being at the base of the food chain, play a key role in trophic dynamics, biogeochemical cycling and fishery resources (Paerl *et al.*, 2003). As they transfer energy to higher levels of the marine food web (Miralto *et al.*, 1999; Irigoien *et al.*, 2002), they influence the biodiversity of other higher trophic level organisms such as fish and marine mammals (Paerl *et al.*, 2003). Increasing the understanding of phytoplankton ecology is important for several reasons including the assessment of the impacts of climate change and the carrying capacity of fish stocks and its application in marine management and conservation issues.

The Continuous Plankton Recorder survey (CPR) has been sampling plankton in the North Atlantic Ocean and North Sea since 1931. The survey is based on consistent methods of sampling and analysis (Warner and Hays, 1994; Richardson *et al.*, 2006). Since 1948 the preliminary examination of CPR samples, prior to taxonomic analysis, involves the visual estimation of the green colour of the silk mesh that filters surface waters. This ocean colour data set has been used as a proxy of the phytoplankton biomass and is known as the phytoplankton colour index (PCI) (Reid *et al.*, 2003).

PCI has been used as an indicator of phytoplankton biomass (Batten *et al.*, 2003) and also to describe major temporal and spatial patterns of phytoplankton in the North Atlantic (Robinson, 1970; Gieskes and Kraay, 1997; Reid *et al.*, 2003). The decadal changes of phytoplankton biomass have been reported in the North Sea and North Atlantic (Reid *et al.*, 1998; Edwards *et al.*, 2001; Raitosos *et al.*, 2005), and the index has been recently used for comparison with global biogeochemical models (Henson *et al.*, 2009). PCI is one of the largest *in situ* ocean colour data sets in the North Atlantic and the North Sea, and thus is considered valuable for satellite remote sensing ocean colour applications (Batten *et al.*, 2003; Raitosos *et al.*, 2005; McQuatters-Gollop *et al.*, 2007; Raitosos *et al.*, 2008; Henson *et al.*, 2009). Although the PCI is a unique measurement of *in situ* ocean colour, with >200 000 samples taken since 1948, the lack of an adequate evaluation to test its quantitative validity has limited its further application.

The main aim of this study was to test the quantitative validity of the PCI categories. The previous studies of Colebrook and Robinson (Colebrook and Robinson, 1961, 1965) assigned numerical values to the PCI by extracting colour into acetone and diluting the extracts to give samples of equal colour intensity determined by the eye. Here we repeat that work but the pigment

concentration is determined by fluorescence. In addition, a comparative assessment of the decadal trends in the PCI of the western English Channel (WEC) was performed, based on the previous and revised experimental PCI quantifications.

METHODS

Sampling method

The CPR is a high-speed (~35 km/h) plankton sampler towed at 5–10-m depth by ‘ships of opportunity’. Water enters the CPR body through a 1.27-cm² aperture and plankton is filtered onto a constantly moving (powered by an impeller) band of silk mesh (a mesh size of 270 µm). Subsequently, a second band of silk covers the filtering silk mesh to form a ‘sandwich’ enclosing the plankton. This is rolled onto a spool in a storage chamber that normally contains formaldehyde solution for preservation. After the tow, the CPR machine is transferred to the laboratory where the sampling cassette and its enclosed roll of silk is removed. The silk is unrolled and laid out on a bench for the PCI analysis on the filtering silk (Richardson *et al.*, 2006). The CPR filtering silk mesh is assessed for ‘colour’ based on a relative scale of greenness (four categories) and is determined on the silk by reference to a standard colour chart as: no green (NG), very pale green (VPG), pale green (PG) and green (G) (Colebrook, 1960). The pigments that are derived from the chloroplasts of intact and broken cells and small unarmoured flagellates are believed to be responsible for this colouration (Edwards *et al.*, 2002; Batten *et al.*, 2003). To carry out a robust statistical analysis of the PCI, this arbitrary scale needs to be converted into quantitative values so that the colour intensity of the PCI categories can be compared. PCI has been measured by a number of different analysts since 1948. The measurement of colour (greenness) is a task that is typically undertaken by two to three people in a year (Hays and Lindley, 1994; Raitosos *et al.*, 2005). Hays and Lindley (Hays and Lindley, 1994) found a close agreement between the different analysts in their individual assessment of the PCI. Subsequently, the silk mesh is cut into samples corresponding to 10 nautical miles of tow and a standard analysis of zooplankton and phytoplankton taxa is carried out (Warner and Hays, 1994; Richardson *et al.*, 2006).

Colebrook and Robinson (Colebrook and Robinson, 1961, 1965) assigned numerical values for each PCI category (NG, VPG, PG and G) based on the acetone extracts of the quantity of phytoplankton chlorophyll-a

(Chl-a) per sample. Dilutions were carried out to give extracts of similar intensity. Based on these dilutions numerical values were assigned to each colour category for the relative quantity of phytoplankton Chl-a per CPR sample reduced to a value of unity for the colour category VPG. The four PCI categories of Colebrook and Robinson (NG = 0, VPG = 1, PG = 2 and G = 6.5) were derived from a small number of samples, whereas here we run an experiment on a greater number of samples and a more rigorous approach was implemented as the pigment concentration is determined by fluorescence.

For this experimental study, CPRs were towed across the English Channel between Roscoff (France) and Plymouth (UK). The samples from the monthly southbound tows were preserved in formalin under the usual CPR protocols. On the return (usually within 18 h), the northbound samples were not preserved in formalin. Instead, the filtering mesh was stored in a freezer (below -18°C) when the samples were removed from the CPR on return to the laboratory, usually within 12 h of sampling. Prior to storage, a normal visual assessment of greenness for categorization of the PCI was carried out. A comparison of the PCI of the southbound (preserved) and the corresponding northbound (unpreserved) samples indicated that formalin preservation had little effect on the colour of the samples (within the time scale of the experiment). It is possible that there was some degradation of the phytoplankton pigments in the unpreserved samples, but we believe this should be negligible as the samples are protected in the CPR cassette. Thus, the samples have not come in contact with air or sunlight, until they reach the laboratory for assessment.

Samples were collected between August 2004 and April 2005 on a monthly basis, with an additional

tow in April 2006, resulting in 76 samples (Fig. 1). The vessel towing the CPR returned a log sheet detailing the launch, recovery times and positions. From this information the position of each 10 nautical mile (nm) sample was calculated.

Sample analysis

Each of the 76 10-nm samples was cut into three equal (LH, left hand; C, centre and RH, right hand) sections (Fig. 2A). This allowed the experiment to repeat the Chl-a assessment three times per sample and then take the average in order to avoid any potential bias. Thus, the Chl-a concentration was measured on 228 (76×3) sections. The edges of the filtering silk, which represent the part that is not involved in the filtration (Fig. 2A), were removed. Analysis showed they contained negligible amounts of Chl-a (<0.005 mg/sample). From each section, the filtering and covering silk were placed into a test tube along with 10 mL of 90% buffered acetone (diluted with distilled water) and left for the chlorophyll to be extracted at $3-4^{\circ}\text{C}$ for ~ 20 h.

Here we do not distinguish between chlorophyll and other pigments, but make the assumption that the chlorophyll is a fixed proportion of the total pigment and thus we used fluorescence to measure the chlorophyll concentrations.

Assessment of Chl-a by fluorescence

A fluorescence spectrophotometer (Hitachi F-4500) was used to measure the concentration of the Chl-a in the acetone extract for each section. The concentration was determined according to the procedure detailed by Strickland and Parsons (Strickland and Parsons, 1972). A stock solution of 20 mg/L of Chl-a was made from an ampoule containing 1 mg of Chl-a (spinach leaf) and stored in a freezer (below -18°C). Six Chl-a standards were used to calibrate the fluorometer, which covered the whole range of the Chl-a concentrations obtained from the sections: 0.2, 2.0, 5.0, 20, 50, 200 and 1000 mg/m^3 . The instrument was calibrated before each set of analyses and every standard was run five times to gain a mean value. The fluorescence was recorded and plotted against the standard concentration to create a mean calibration curve; the coefficient of regression was around 0.9998.

The acetone extract from each CPR section was examined in the fluorometer and the concentration of the Chl-a was calculated using the calibration curve. The Chl-a (fluorescence) for each of the 228 sections was measured three times and the average was taken to avoid instrument bias.

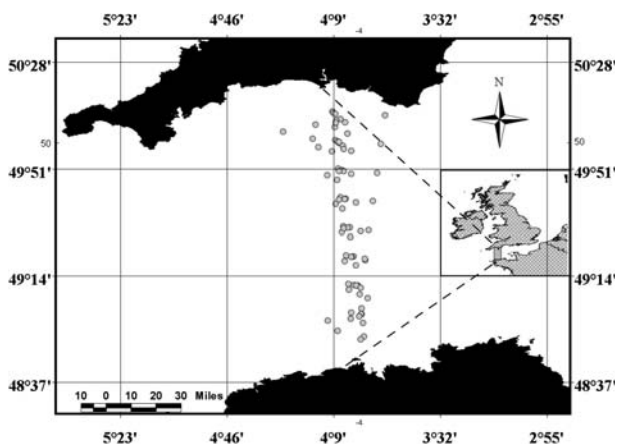


Fig. 1. The positions of the CPR samples ($n = 76$) collected from 2004 to 2006 in the western English Channel.

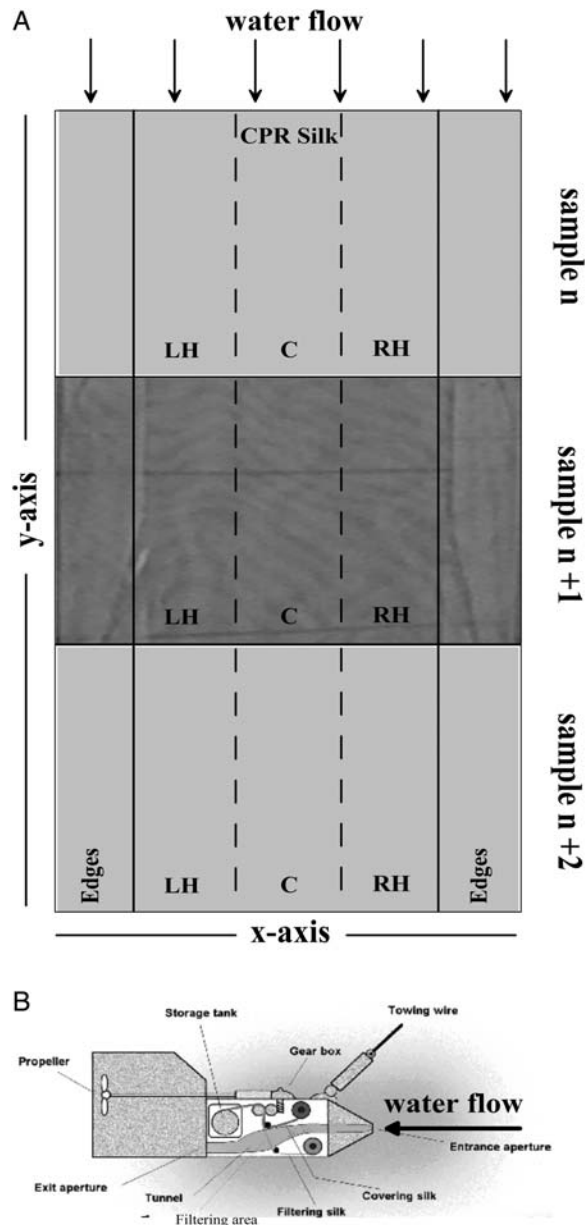


Fig. 2. (A) Three schematic CPR silk samples each divided into three sections used for the analysis; water entering the CPR should distribute plankton uniformly across the CPR silk in the x direction. The edges of the silk were removed prior to acetone extraction as they contained negligible amounts of Chl-*a*. The arrows indicate the direction of the movement of the silk through the CPR (along the y -axis). It is expected that plankton patchiness would be reflected in variation in the PCI in the y direction. (B) The side view of the CPR showing the method of operation.

Following the Chl-*a* fluorescence measurement, an acidification procedure was carried out. Two drops of 2 N (roughly 8% hydrochloric acid) were added and the fluorescence was measured again after 30 s (Strickland and Parsons, 1972). The acidification step enabled the contribution of breakdown pigments (carotenoids) to be

assessed, with the acidified values subtracted from the initial Chl-*a* result to provide the final Chl-*a* measurement. A blank CPR silk was also analysed in order to see if the silk affects the results. No fluorescence response was detected from the blanks, indicating that no fluorescing substance leached from the silk.

The amount of the Chl-*a* per section of the CPR filtering silk was calculated from the concentration of the extracted Chl-*a* and the volume of the acetone. To give a measure of the total Chl-*a*/sample, the amount of the Chl-*a* from the three sections was summed.

Calculation of remotely sensed Chl-*a* for PCI categories

The Level 3, standard 8-day products (9 km² resolution) of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) reprocessed Chl-*a* data (version 9.1) from the NASA Ocean Biology Processing Group were acquired from the Oceancolor website (<http://oceancolor.gsfc.nasa.gov/>).

Within the WEC, the concurrent match-ups between the SeaWiFS Chl-*a* estimates and CPR PCI measurements were extracted for the same spatial and temporal coverage (see Raitosos *et al.*, 2005; Raitosos *et al.*, 2008 for methodological details). In the area of the study, after screening the SeaWiFS data set for CPR match-ups, ~700 samples could be used for comparison. Primarily due to cloud coverage, haze and/or satellite discrepancies >80% of the CPR data did not have a SeaWiFS match-up (Raitosos *et al.*, 2005).

RESULTS

In Fig. 3A the relationship between the amounts of the Chl-*a* retained on all 76 CPR samples (micrograms/sample) is presented for each PCI category. Overall, a clear relationship can be seen; as the quantity of Chl-*a* increases, the PCI categories increase. In addition, a significant positive relationship was found among the four PCI categories determined using Colebrook and Robinson (Colebrook and Robinson 1965) values and the Chl-*a* concentrations ($r^2 = 0.73$, $df = 76$, $P < 0.0001$).

The average of each PCI category and the 95% confidence intervals (CI) are shown in Fig. 3B. There is a relatively small variation in the CI of Chl-*a* for the first three categories with a maximum variation in the fourth category, possibly due to the lower number of cases in that category (see Table I). From Fig. 3 it can also be observed that there is an apparent differentiation for Chl-*a* amongst the PCI categories (95% CI do not overlap); Chl-*a* increases gradually along with PCI categories.

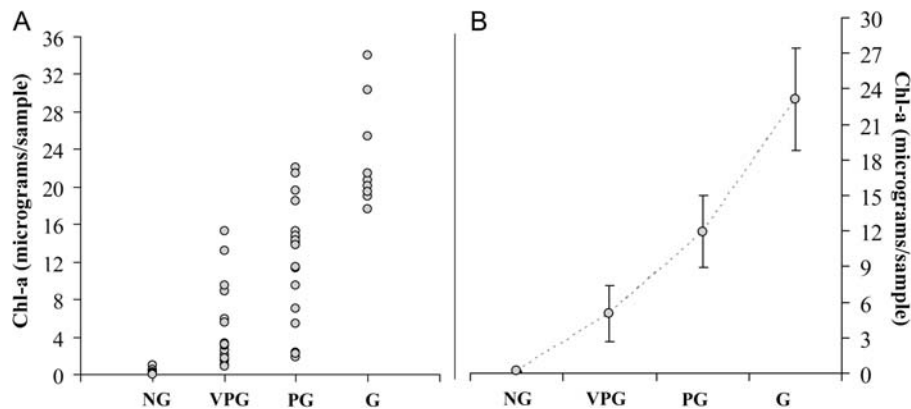


Fig. 3. (A) Distribution of the quantity of Chl-a per CPR sample ($n = 76$) and (B) the mean quantity of Chl-a (micrograms per sample) per PCI category. The PCI is a ratio scale of phytoplankton colour with four ‘greenness’ categories: NG, no green; VPG, very pale green; PG, pale green; G, green. Note: there is no overlap between the CIs for each PCI category.

Table I: Quantity of Chl-a (microgram/sample) for each PCI category

	Mean	Standard deviation	Minimum	Maximum	n	Ratio scale
NG	0.16	0.12	0.03	1	32	0.0
VPG	5.05	4.42	0.88	15.32	16	1.0
PG	11.94	6.33	1.89	22.12	19	2.4
G	23.16	5.62	17.69	34.01	9	4.6

Table I shows the descriptive statistics of the Chl-a (micrograms/sample) for each PCI category; the mean, minimum and maximum values of the Chl-a quantity progressively increase as the PCI categories increase, which supports the differentiation and the significant relationships seen in Fig. 3. The final column shows an arbitrary scale based on the methods of Colebrook and Robinson (Colebrook and Robinson, 1965), standardizing our results to a value of unity for VPG.

DISCUSSION

In this experiment, the values of NG = 0, VPG = 1, PG = 2.4 and G = 4.6 (Table I) are similar to the values reported by Colebrook and Robinson (Colebrook and Robinson, 1965); a relationship that confirms the validity of the PCI. The differentiation, especially in category G, may result from the fact that the samples were taken from different regions, seasons and/or species involved. However, Colebrook and Robinson (Colebrook and Robinson, 1965) reported that category G lies between 4.5 and 9.6 and so our revised values fall within and confirm their primary results.

Although PCI is a visual assessment, and so could be characterized as a crude approach to identify ocean

colour from a silk, its strength lies in a time series that extends over 60 years for much of the western European shelf collected and assessed in a consistent manner. Other studies have attempted to convert PCI values into quantitative estimates of phytoplankton using SeaWiFS measurements of Chl-a (Batten *et al.*, 2003; Raitso *et al.*, 2005), indicating that the phytoplankton colour is a good index of the biomass. The valuable long PCI time series is a unique measure of ocean colour because it includes the small and delicate phytoplankton cells (e.g. naked flagellates, pico and nanoplankton), which break up on contact with the filtering silk, and contribute to the final silk colour (Batten *et al.*, 2003). Due to the mesh size (270 μm) of CPR silks, many phytoplankton species are only semi-quantitatively sampled. There is thus a bias towards recording larger armoured flagellates and chain-forming diatoms, and smaller species abundance estimates would probably be underestimated in relation to other sampling methods (Edwards *et al.*, 2006). However, Robinson (Robinson, 1970) found that the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and composition (i.e. the percentage retention is roughly constant within each species even for very small-celled species). For instance, Raitso *et al.* (Raitso *et al.*, 2006) reported that small coccolithophores such as *Emiliania huxleyi* cells were apparent in CPR samples.

Normally, CPR samples are preserved in formalin as the instrument may take days or weeks to return to the laboratory. However, the phytoplankton Chl-a fluorescence is destroyed by formalin preservative. Thus, for this study unpreserved CPR samples were used instead and the experiment relied on the proximity of the tow route (Roscoff to Plymouth) to the laboratory. Therefore, it is acknowledged that the results obtained

were from a restricted sampling area, and may not be representative of other areas in the globe.

The results are reported in units of quantity of the chlorophyll retained per CPR sample, with PCI being a proxy of the phytoplankton biomass. Batten *et al.* (Batten *et al.*, 2003) and John *et al.* (John *et al.*, 2002) considered that each CPR sample filtered $\sim 3 \text{ m}^3$ of seawater. The range in the quantity of the Chl-a retained on each of the sections (228) was $0.1\text{--}12 \mu\text{g Chl-a/section}$. Thus, the range of the Chl-a concentrations predicted from the CPR results was $0.1\text{--}12 \mu\text{g Chl-a/m}^3$. Whereas, using co-located satellite and CPR samples (as seen in Raitosos *et al.*, 2005), from the English Channel, the typical values for the SeaWiFS Chl-a for each PCI category appeared to be higher (i.e. NG = 1.15, VPG = 1.34, PG = 2.06 and G = 3.92 mg/m^3). This difference may not only result from CPR under-sampling due to the large mesh size of the filtering silk compared with typical phytoplankton size, but also from the optical properties of the English Channel, i.e. these waters are considered as optically complex (CASE II) waters where the SeaWiFS standard Chl-a algorithm is not optimal (see IOCCG, 2000).

Comparison between the original and the revised values of PCI

Here we compare the results obtained in this study (revised PCI values) to the PCI scale derived by Colebrook and Robinson (Colebrook and Robinson, 1965). Data ($n = 5280$) were extracted from the CPR database for the area of the WEC bounded by 50N to 48.3N and 5W to 3W . The annually averaged time series produced from these data cover the period between 1958 and 2010. Fig. 4 shows the PCI averaged for each year using the original values (NG = 0, VPG = 1, PG = 2, G = 6.5) from Colebrook and Robinson (Colebrook and Robinson, 1965), and then repeated using the

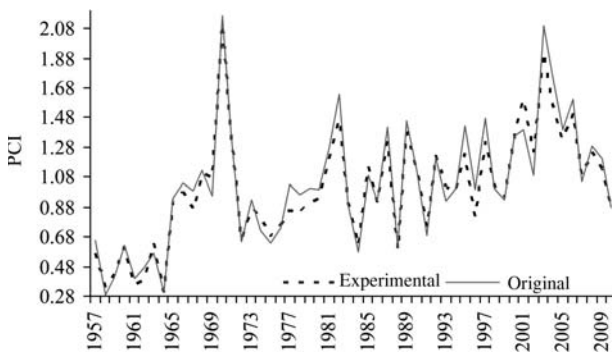


Fig. 4. Annual PCI time series for the western English Channel, from 1957 to 2010. The dashed line shows the PCI values calculated from the fluorometry measurements reported here and the solid line those determined from the original ratio scale (Colebrook and Robinson, 1965).

experimental values reported here (NG = 0, VPG = 1, PG = 2.4, G = 4.6). It is clear that the new experimental results do not have a great impact on the shape of the time series, and the analysis confirms that the two methods (previous and revised) largely agree. However, there are a few cases (such as in 1978) where the averaged PCI using the previous values is higher in comparison with the experimental values reported here, whereas the opposite is apparent in 2001. This is because there was a greater abundance of samples with PCI category G in 1978 and a greater abundance of samples with category PG in 2001.

Although it is beyond the scope of this paper to discuss it further, the PCI time series in the WEC shown in Fig. 4 indicates an increasing trend over the 60-year period. Similar trends are reported by other studies (e.g. Edwards *et al.*, 2001; Raitosos *et al.*, 2005; Southward *et al.*, 2005; McQuatters-Gollop *et al.*, 2011).

The current study used samples from the WEC but we believe similar results will be found elsewhere. However, the phytoplankton community size spectra and the pigment quantity per cell are not always consistent across regions, which may be characterized by very different phytoplankton communities. Thus, although the revised experimental PCI values may be applicable throughout the CPR survey, another broader experiment analysing a higher number of samples deriving from several different areas, could potentially provide more accurate calculations of PCI. We recommend that the revised values should be adopted for all the CPR PCI observations. It should be mentioned that as demonstrated from Fig. 4, the choice of which numerical values (original or revised) are used, has a little impact on the quality of phytoplankton biomass trends.

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REFERENCES

- 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.
- Colebrook, J. M. (1960) Continuous plankton records: methods of analysis, 1950–59. *Bull. Mar. Ecol.*, **5**, 51–64.
- Colebrook, J. M. and Robinson, G. A. (1961) The seasonal cycle of the plankton in the North Sea and the North-eastern Atlantic. *Journal du Conseil international pour l'Exploration de la Mer*, **26**, 156–165.
- Colebrook, J. M. and Robinson, G. A. (1965) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north-eastern Atlantic and North Sea. *Bull. Mar. Ecol.*, **6**, 123–139.
- Edwards, M., Beaugrand, G., Reid, P. C. *et al.* (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar. Ecol. Progr. Ser.*, **239**, 1–10.
- Edwards, M., Johns, D. G., Leterme, S. C. *et al.* (2006) Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnol. Oceanogr.*, **51**, 820–829.
- Edwards, M., Reid, P. C. and Planque, B. (2001) Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES J. Mar. Sci.*, **58**, 39–49.
- Falkowski, P. G., Katz, M. E., Knoll, A. H. *et al.* (2004) The evolution of modern eukaryotic phytoplankton. *Science*, **305**, 354–360.
- Gieskes, W. W. C. and Kraay, G. W. (1997) Continuous plankton records: changes in the plankton of the North Sea and its eutrophic Southern Bight from 1948–1975. *Neth. J. Sea Res.*, **11**, 334–364.
- Hays, G. C. and Lindley, J. A. (1994) Estimating chlorophyll a abundance from phytoplankton colour recorded by the continuous plankton recorder survey: validation with simultaneous fluorometry. *J. Plankton Res.*, **16**, 23–34.
- Henson, S., Raitos, D., Dunne, J. P. *et al.* (2009) Decadal variability in biogeochemical models: comparison with a 50-year ocean colour dataset. *Geophys. Res. Lett.* doi: 10.1029/2009GL040874.
- IOCCG (2000) Remote sensing of ocean colour in coastal, and other optically-complex waters. In Sathyendranath, S. (eds), *Reports of the International Ocean-Colour Coordinating Group, No. 3*. IOCCG, Dartmouth, Canada.
- Irigoiien, X., Harris, R. P., Verheye, H. M. *et al.* (2002) Copepod hatching success in marine ecosystems with high diatom concentrations. *Nature*, **419**, 387–389.
- John, E. H., Batten, S., Stevens, D. *et al.* (2002) Continuous plankton records stand the test of time: evaluation of flow rates, clogging and the continuity of the CPR time-series. *J. Plankton Res.*, **24**, 941–946.
- McQuatters-Gollop, A., Raitos, D. E. and Edwards, M. (2007) A long-term chlorophyll dataset reveals a regime shift in North Sea phytoplankton biomass unconnected to increasing nutrient levels. *Limnol. Oceanogr.*, **52**, 635–648.
- McQuatters-Gollop, A., Reid, P. C., Edwards, M. *et al.* (2011) Is there a decline in marine phytoplankton? *Nature*, **472**, E6–E7.
- Miralto, A., Barone, G., Romano, G. *et al.* (1999) The insidious effect of diatoms on copepod reproduction. *Nature*, **402**, 173–176.
- Paerl, H. W., Valdes, L. M., Pinckney, J. L. *et al.* (2003) Phytoplankton photopigments as indicators of estuarine and coastal eutrophication. *BioScience*, **53**, 953–964.
- Raitos, D. E., Lavender, S. J., Maravelias, C. D. *et al.* (2008) Identifying phytoplankton functional groups from space: an ecological approach. *Limnol. Oceanogr.*, **53**, 605–613.
- Raitos, D. E., Lavender, S. J., Pradhan, Y. *et al.* (2006) Coccolithophore bloom size variation in response to the regional environment of the subarctic North Atlantic. *Limnol. Oceanogr.*, **51**, 2122–2130.
- Raitos, 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. doi:10.1029/2005GL022484.
- Reid, P. C., Edwards, M., Hunt, H. G. *et al.* (1998) Phytoplankton change in the North Atlantic. *Nature*, **391**, 546.
- Reid, P. C., Matthews, J. B. L. and Smith, M. A. (eds). (2003) Achievements of the Continuous Plankton Recorder survey and a vision for its future. *Progr. Oceanogr.*, **58**, 115–358.
- Richardson, A. J., Walne, A. W., John, A. W. G. *et al.* (2006) Using continuous plankton recorder data. *Progr. Oceanogr.*, **68**, 27–74.
- Robinson, G. A. (1970) Continuous plankton records: variation in the seasonal cycle of phytoplankton in the North Atlantic. *Bull. Mar. Ecol.*, **6**, 333–345.
- Southward, A. J., Langmead, O., Hardman-Mountford, N. J. *et al.* (2005) Long-term oceanographic and ecological research in the western English Channel. *Adv. Mar. Biol.*, **47**, 1–105.
- Strickland, J. D. and Parsons, T. R. (1972) *A Practical Handbook of Seawater Analysis Bulletin*, 2nd edn. Fisheries Research Board of Canada, p. 167.
- Warner, A. J. and Hays, G. C. (1994) Sampling by the continuous plankton recorder survey. *Progr. Oceanogr.*, **34**, 237–256.