Use of a Phytoplankton Community Index to assess the health of coastal waters

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Monitoring of marine-ecosystem status and health requires indicators of community structure and function. As a structural indicator, we propose a Phytoplankton Community Index (PCI) based on the abundance of "life-forms" such as "pelagic diatoms" or "medium-sized autotrophic dinoflagellates". To calculate the PCI, data showing seasonal variation in these abundances are plotted in "life-form space" of two or more dimensions. Data from a "type-specific reference condition" are then enclosed within a reference envelope. Comparison data are plotted into the same coordinate system, and the PCI is the proportion (between 0 and 1) of these new data that fall within the reference envelope. Results from initial applications of this method are shown for UK coastal waters in the northern North Sea (near Stonehaven), a Scottish fjord (Loch Creran), and the eastern Irish Sea (including Liverpool Bay). The Stonehaven data (1997–2005) were used to compare values obtained from weekly sampling with those from monthly sampling. A spatial comparison between more- and less-nutrient-enriched waters in the eastern Irish Sea (1991–2003) showed little difference in phytoplankton community structure. Loch Creran has experienced a large change in the "balance of organisms", and hence a reduction in the PCI, between 1979–1981 and 2006/2007, associated with a decrease in chlorophyll but no apparent change in nutrients. These results are discussed in relation to the intended uses of the PCI as an index of biological quality for the Water Framework Directive (WFD) and an index of ecosystem health in the context of eutrophication. Although the method only measures change, it can also be used as an indicator of biological quality if the reference conditions are those defined for a WFD waterbody, and as an indicator of health if appropriately calibrated. Suggestions are made for further development.

Keywords: Irish Sea, life-forms, Loch Creran, nutrients, PCI, phytoplankton, Stonehaven.

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Introduction

We have developed a Phytoplankton Community Index (PCI) that is designed to indicate the state of part of the pelagic ecosystem with respect to some reference condition. There are two contexts for the use of this PCI. The first arises from the Urban Waste Water Treatment Directive (CEC, 1991) and OSPAR's "Strategy to Combat Eutrophication" (OSPAR, 2003). These policies require management action to be taken in the event of an impact defined as "an undesirable disturbance to the balance of organisms" that is consequent on nutrient enrichment and enhanced growth of primary producers. Tett *et al*. (2007) defined "an undesirable disturbance" as a perturbation of a marine ecosystem that appreciably degrades the health, or threatens the sustainable human use, of that ecosystem. Ecosystem health has components that include "structure" and "vigour", and the PCI is proposed as a measure of "structure".

The second context is that of the Water Framework Directive (WFD; CEC, 2000), which defines "ecological status" as "an expression of the quality of the structure and functioning of aquatic ecosystems associated with surface waters ...", to be measured by comparing the state of "biological quality elements", including phytoplankton, with those in a "type-specific reference condition". The PCI is intended as an indicator for the part of the phytoplankton quality element dealing with the extent of change in the "composition and abundance of phytoplanktonic taxa".

Our starting point is the assumption that an ecosystem is a "system" with an instantaneous state defined by values of a set of "system state variables". We further assume that suitable state variables are provided by the abundance of groups of species of similar "life-form", as discussed below. These variables provide the coordinates for points, defining system state, in "life-form state space" of several dimensions. However, the structure of a phytoplanktonic community in a particular waterbody is more than the average pattern of life-form abundances; a large part of phytoplankton biodiversity results from seasonal succession in species and life-forms. This aspect must be taken into account in judging ecosystem state and health, so the normal domain in life-form state space is not a point or small cluster of points, but an envelope resulting from seasonal trajectories through the space (Figure 1). Our method is to establish this envelope for reference conditions relevant to a waterbody, then to measure change by overplotting comparison data and calculating the proportion of new points that remain inside the reference envelope. Theoretical considerations suggest that, if life-forms compete for nutrients while experiencing strong seasonal changes in illumination, the envelope should be a "ring doughnut" in two-dimensional space, and this is how it is shown in Figure 1. Exactly what sort of cake the envelope is like is, however, not crucial to our argument. Figure 1 also presents the idea that a healthy and therefore resilient ecosystem quickly returns to its "natural" state after a small perturbation, whereas a larger perturbation can result in a shift to a new stable state: see Tett *et al*. (2007).

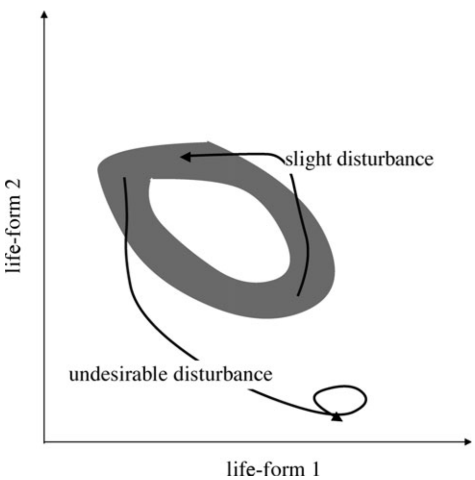

Figure 1. Schematic of the doughnut-shape of the envelope encompassing the state space of two life-forms representing the planktonic community experiencing natural seasonal and interannual variation and the potential excursions of these states upon disturbances caused by external drivers (modified from Tett *et al*., 2007).

The theory supporting the use of life-forms has been developed by Margalef (1978), and by those influenced by his ideas, including Pingree *et al*. (1978), Bowman *et al*. (1981), and Jones and Gowen (1985). More recently, Le Quéré *et al*. (2005) proposed life-forms based on functional biogeochemistry for use in global ocean models, and Escaravage *et al*. (1999) and Escaravage and Prins (2002) developed an empirical categorization based on observations in mesocosms. Arguments in favour of assigning species to life-forms based on taxonomy, biogeochemistry, response to physical environment, and susceptibility to grazing have been set out by Tett *et al*. (2003), and this provides the background to the categorization used here. A somewhat different categorization that takes more account of morphology (especially cell or colony shape) has been developed for fresh-water phytoplankton by Reynolds (1996) and Reynolds *et al*. (2001) and applied to marine dinoflagellates by Smayda and Reynolds (2001).

We applied the PCI method to three datasets, with objectives of: (i) comparing PCI values obtained from weekly sampling in a relatively undisturbed area with those obtained from monthly data; (ii) testing the method in a waterbody where there has been a substantial change, of unknown cause, in phytoplankton; and (iii) investigating spatial differences in a region of nutrient gradient.

Material and methods

The phytoplankton data used came from three sources, all involving Lugol-preserved water samples. The first set (1997–2005) is derived from weekly sampling by the Scottish Government's Fisheries Research Service (FRS) of a single station 3 km from the Scottish east coast near Stonehaven in a well-mixed water column of 50-m depth (bottle samples were taken from the upper 10 m). Although nutrients are moderately high as a result of inflow of Atlantic water into the North Sea, there is no reason to think that conditions at this station are disturbed, and for reference conditions, we have simply used the first few years of the time-series.

Table 1. Overview of life-forms used in the different studies.

Major taxon	Life-form name and abbreviation	Definition and examples	Life-forms used		
			Stonehaven	Creran	Eastern Irish Sea
Bacillariophyceae	Diatoms	All diatoms	LF1	–	–
	Pelagic diatoms (PD, p4)	Lightly silicified, fully pelagic diatoms, mainly centrics, e.g. *Skeletonema*, *Thalassiosira*, *Chaetoceros*, *Leptocylindrus*	–	LF1 = PD	LF2 = p4
	Weed diatoms (p6)	Members of the former genus *Nitzschia*, including *Pseudo-nitzschia* and *Cylindrotheca*, called weeds because they came to dominate microcosm experiments by Jones *et al*. (1978)	–	–	LF6 = p6
	Tychopelagic diatoms (p5)	Proposed by Smetacek (1986) for heavily silicified forms kept in suspension by turbulence	–	–	LF5 = p5
Dinophyceae	Dinoflagellates	All dinoflagellates	LF2	–	–
	Medium autotrophic dinoflagellates (MAD, p1)	Medium sized (20–50 μm) autotrophs (and myxotrophs) e.g. *Gonyaulax*, *Scrippsiella*, *Dinophysis*	–	LF2 = MAD	LF1 = p1
	Big dinoflagellates (p2)	Large (>50 μm) autotrophs and myxotrophs, mainly *Ceratium*	–	–	LF3 = p2
	Heterotrophic dinoflagellates (p3)	All heterotrophs, e.g. *Protoperidinium*, *Gyrodinium*	–	–	LF4 = p3

Table 2. Environmental data and PCI values for the three regions investigated.

Parameter	Stonehaven	Creran	Eastern Irish Sea (1999–2005)
Ref(erence)	1997–1999	1975–1981	NE Irish Sea
Comp(arison)	2000–2005	2006/2007	Liverpool Bay
DAIN (μM)—Ref	10 (−NH)	7.5	26
DAIN (μM)—Comp	9.5 (−NH)	7.5	55
DSi (μM)—Ref	5.5	8.6	>8
DSI (μM)—Comp	6.0	9.5	>16
Chl (μg l^{-1})—Ref	4.4	12	10.0
Chl (μg l^{-1})—Comp	2.6	2.5	16.0
PCI estimates			
Phytoplankton sample frequency	Weekly	Weekly/sporadic	Mainly seasonal
Number of samples for reference envelope	139	154	117
LF2 on LF1—all data	0.93* (283/21)	0.50*** (14/7)	0.92 n.s. (159/12)
LF2 on LF1—month-averaged	0.86** (72/10)	–	–
LF2 on LF1—one sample in four	0.68*** (59/19) to 0.95 n.s.	–	–
LF4 on LF3	–	–	0.92 n.s. (159/13)
LF6 on LF5	–	–	0.97 n.s. (159/5)

The environmental data are the 90th percentile (the value exceeded by 10% of samples) for dissolved available inorganic nitrogen (DAIN: nitrate, nitrite, ammonium; −NH: ammonium not included) and dissolved silica or silicate (DSi) during winter (December–March), and of chlorophyll during the growth season (March–October). See Table 1 for the life-forms used in the calculation of the PCI. In relation to the PCI: n.s., not significant; $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; figures in parentheses indicate total number of samples in reference set/number of samples outside reference envelope.

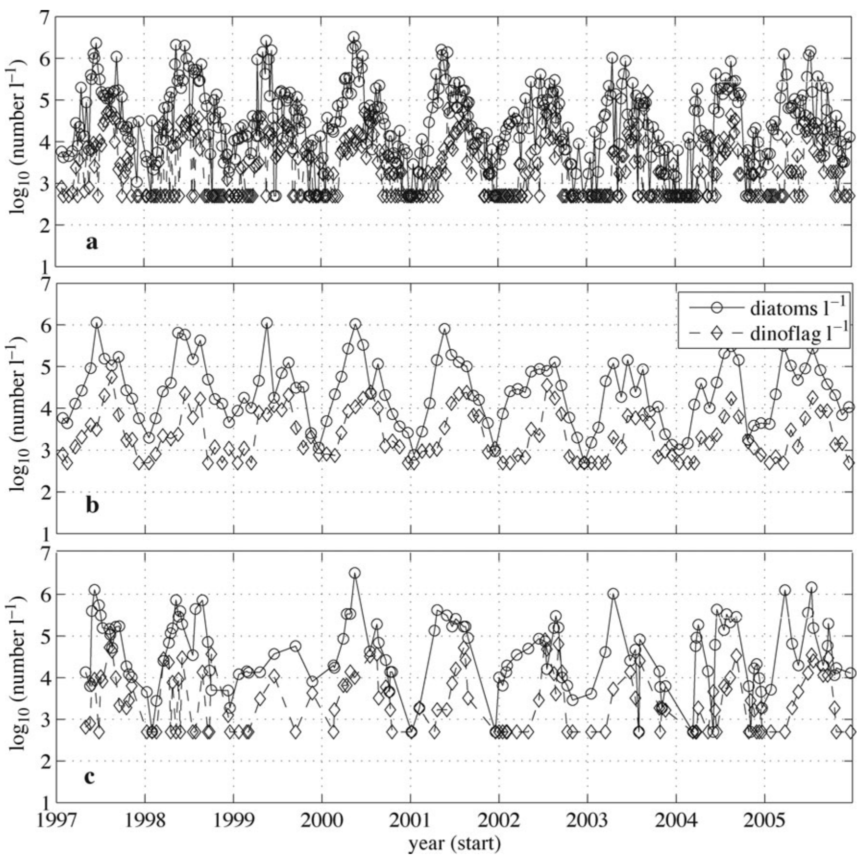

Figure 2. Three views of the Stonehaven time-series of diatoms and dinoflagellates based on: (a) weekly samples; (b) monthly averages; and (c) one realization of randomly selecting one weekly sample in four.

The second set (1979–1981; 2006/2007) was derived from sampling carried out at several positions in Loch Creran, on the west coast of Scotland. Samples were taken either with a water bottle at a depth of 1 m from a pier, or using ship-lowered water bottles at depths between 0 and 10 m, or with an integrating 10-m tube lowered from a small boat. Descriptions of the loch,

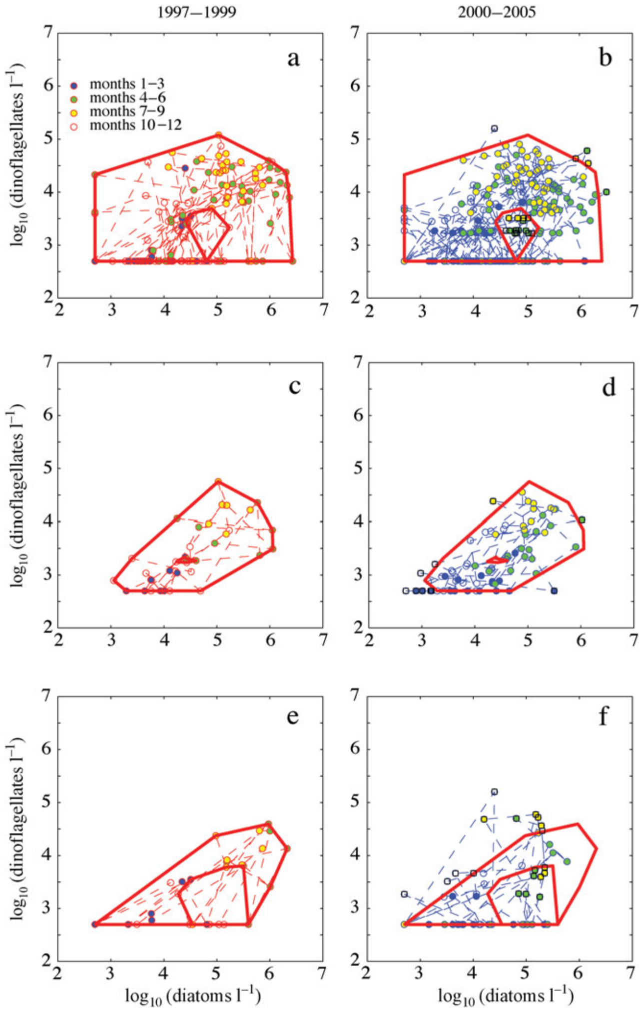

Figure 3. Plots of individual pairs of diatom and dinoflagellate abundances in state space and the calculated envelopes for the reference period 1997–1999 (panels a, c, and e), and plots of the corresponding values for 2000–2005 relative to these envelopes (b, d, and f) based on (a and b) weekly samples, (c and d) monthly averages, and (e and f) one realization of randomly selecting one weekly sample in four.

its pelagic state at various times, and sampling methods, have been published elsewhere (Tett and Wallis, 1978; Tett *et al*., 1981, 1985; Tett, 1986, 1987; Laurent *et al*., 2006). Creran is a shallow fjord in which haline stratification persists throughout most of the year, and exchange with the sea results from tidal exchange and an estuarine circulation. The fjord has been sampled intensively through the 1970s, and we consider it to have been in a near-pristine condition at this time. Phytoplankton data from the period 1979–1981, and nutrient and chlorophyll data from 1975, have been used as reference conditions. During recent years, the loch has held a salmon farm of 1500 t consented annual production and it is now a recognized "shellfish water" with increasing production of cultivated mussels and oysters. Although a relatively small increase in dissolved nitrogen and phosphorus might be expected as a result of farm input in recent years, observations (Laurent *et al*., 2006) have not revealed a significant difference between these nutrients in 1975 and in 2003, but have shown a marked decrease in chlorophyll concentration over the same period.

The third set is derived from samples taken at many stations in the eastern Irish Sea by various organizations on behalf of the UK's Department for Environment, Food and Rural Affairs (Defra) and the Environment Agency (EA) of England and Wales. For purposes of reporting to OSPAR, the near-coastal waterbody of Liverpool Bay is distinguished from mostly offshore waters of the northeastern (NE) Irish Sea, and we used these OSPAR areas for grouping the phytoplankton data. Both areas are nutrient-enriched by rivers and by direct discharges from coastal development. We used the less-enriched offshore waters of the NE Irish Sea as a (spatial) reference condition for the more-enriched Liverpool Bay (in particular adjacent to the Mersey). Phytoplankton data (1991–2005) were extracted from the EA database, excluding samples from transitional waters, i.e. estuaries.

Except for the Stonehaven data, which were already aggregated in diatoms and dinoflagellates, the raw data (by species or low-level taxa) were processed by Matlab scripts to give cells per litre by life-form categories (Table 1). Further Matlab scripts were written to plot abundances into life-form space after $\log_{10}(x + z)$ transformation, where x is abundance and z is half the least abundance recorded for that life-form. Logarithmic transformation was needed to make variance independent of mean, and the addition of z avoids errors when x is zero.

In principle, "life-form space" consists of as many orthogonal dimensions (axes) as there are life-forms to consider. In practice, we used sets of Cartesian plots in two-dimension, and dealt with life-forms pairwise when there were more than two. First, a reference set of data was plotted onto these surfaces. An envelope was drawn around each two-dimensional reference plot using a "convex hull" method (Weisstein, 2006), and another one was drawn inside the plots by the same method after inverting the cloud of points about their centre. The centre was uniquely defined by the coordinates of the median of each life-form, and the internal envelope surrounds the empty space that in theory exists at the centre of each set of seasonal trajectories. Mapping thus the "hole in the doughnut" increases the potential sensitivity of the PCI method to change, but it is not crucial. If no true empty space exists in a given cloud of points, the inner envelope shrinks to a tiny region around the cloud centre.

The PCI resulted from a comparison between new data and this reference envelope. New data were plotted into the same space, and the value of the index was calculated as

$$\mathrm{PCI} = \frac{\text{new points between inner and outer envelopes}}{\text{total new points}}.$$

Thus, a PCI of 1 shows no change from the reference condition, and a PCI of 0 shows a complete change. The significance of a value was calculated by an exact binomial test, which evaluated the probability of finding 0.95 or more of new data between the envelopes. When there were many data, a Chi-squared approximation was used. Further details of life-forms and plotting methods are given by Tett (2006). We are still exploring the best way to combine PCI values obtained from more than one pair of life-forms, or to estimate the significance of a combined value. In this paper, therefore, all values for PCIs derive from pairs of life-forms, and several values are reported when we used data for more than two life-forms.

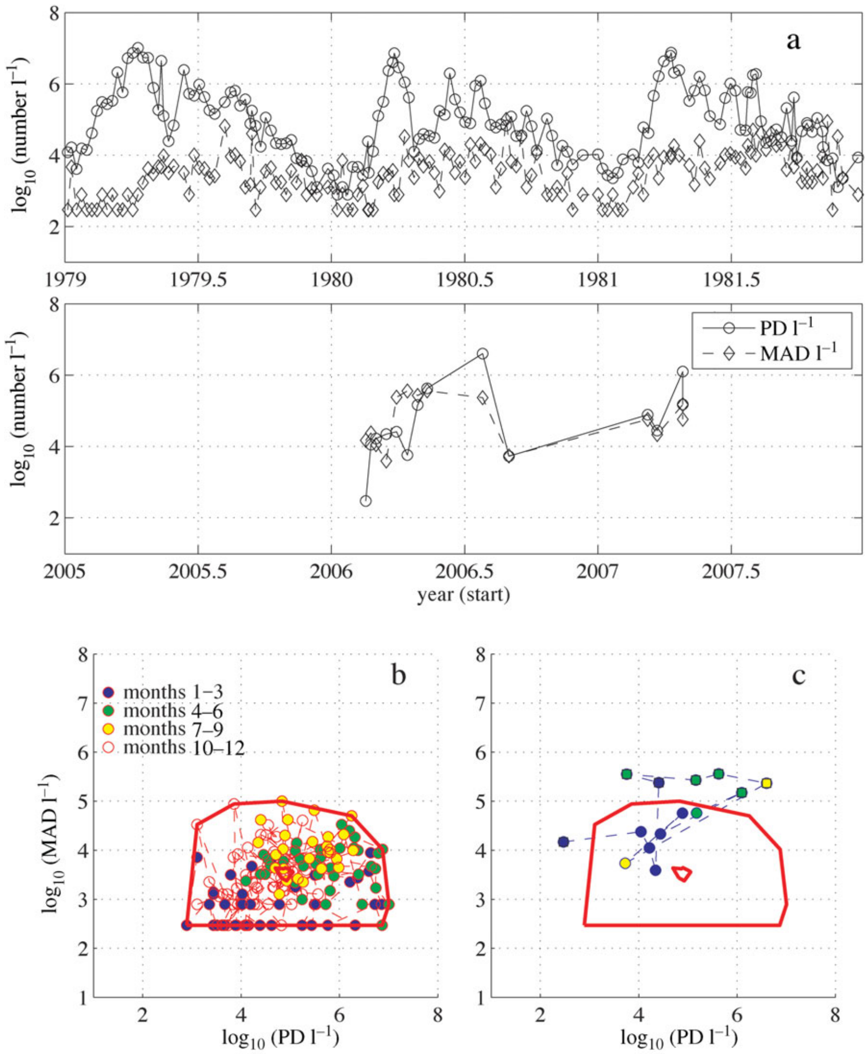

Figure 4. Data on plankton community structure (PD, pelagic diatoms; MAD medium-sized dinoflagellates; see also Table 1) in Loch Creran: (a) time-series data on the two life-form abundances, 1979–2007; and plots in space scale with calculated envelopes for (b) reference years (1979–1981) and (c) for later years (2006/2007).

Nutrient and total chlorophyll (Chl *a* and *b* + Chlorophyllide *c*; excluding Phaeopigments) data were collected by routine UK monitoring programmes in the eastern Irish Sea and as part of the Stonehaven time-series by FRS. Comparable data from Creran were, mostly, obtained during PhD research projects (Jones, 1979; Laurent *et al.*, 2006). Values of these indicators are given in Table 2 as upper 90 percentiles to allow comparisons of typical maximum values.

Results

The Stonehaven data have been used to explore the effect of sampling frequency on the value of the PCI. We used three sets of data: the actual time-series with weekly resolution, a time-series obtained by averaging weeks within months, and a monthly sampling series simulated by picking one sample in four at random (Figure 2).

Figure 3 shows the results. The greater variability evident in the weekly data (Figure 3a, b) resulted in more extensive reference envelopes. Consequently, more new points fell within these envelopes, leading to a higher value of the PCI (0.93) than was the case for the two monthly series (0.86 for the averaged data in Figure 3c and 3d, and 0.68 for the subsampled data in Figure 3e and 3f). However, the result shown in Figure 3e and f is just one of many possible realizations, differing in both the reference condition envelopes and the new data. Repeated random selection gave a PCI range from 0.95 to 0.68, with just over two in three realizations proving significant.

The "flat bottom" (and vertical left sides), apparent in Figures 3a, 3b, 3e, and 3f, suggests insufficient dynamic range in the data, implying that it would be desirable to examine a larger volume of water during winter, to get a better estimate of abundance during periods of low phytoplankton biomass. Averaging the data over a month improved this, as shown in Figures 3c and 3d. Because the resulting reference envelope was smaller, the analysis was more sensitive to deviations in the new data, giving a lower and more significant value of the PCI (Table 2).

Observations in Loch Creran show marked changes between phytoplankton in the 1970s and the 2000s. Results are presented here only for pelagic diatoms and medium-sized autotrophic dinoflagellates (Table 1). Figure 4 shows a large and highly

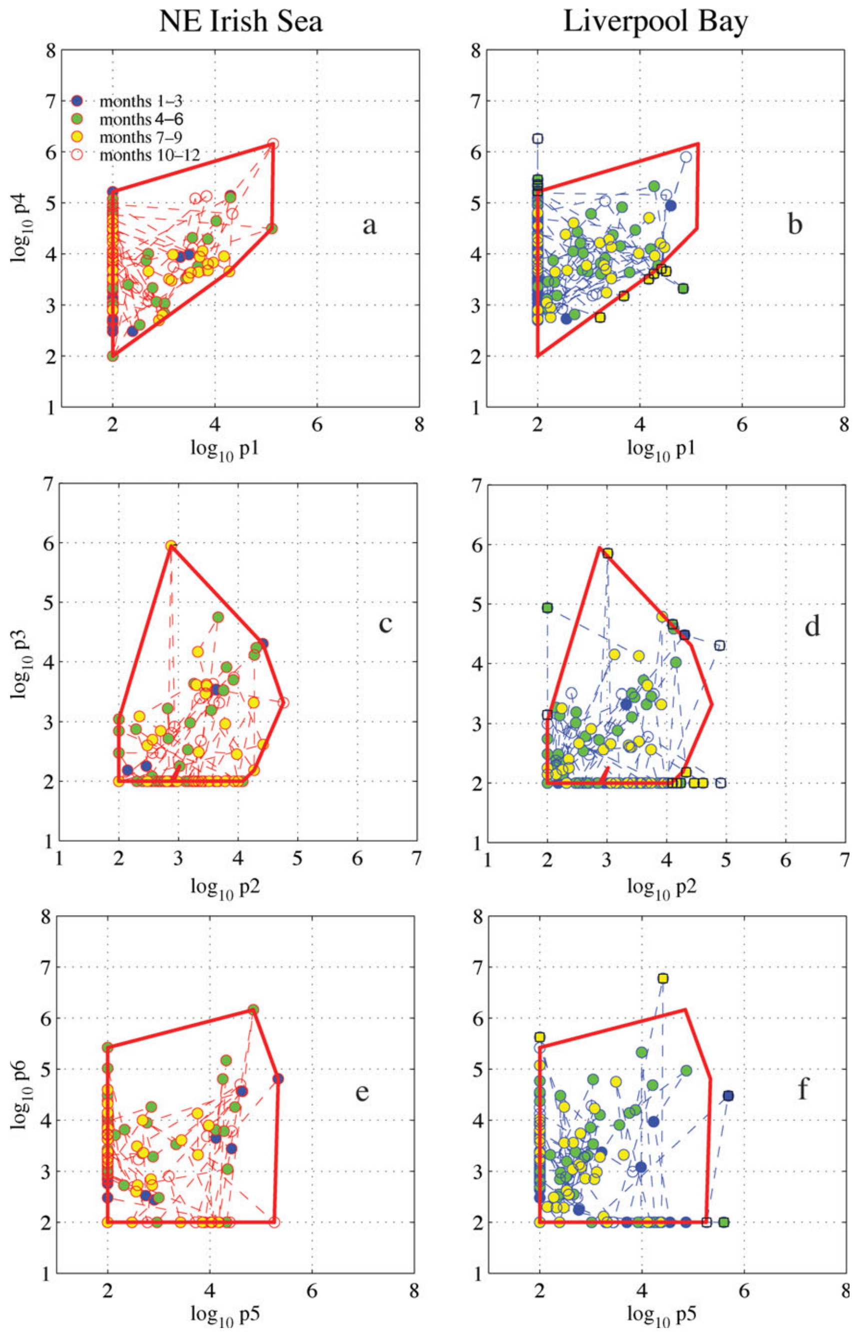

Figure 5. Reference envelopes calculated for the eastern Irish Sea (panels a, c, and e) and pairs of life-form abundances (for definition see Table 1) as observed in the more enriched waters of Liverpool Bay plotted relative to these envelopes, using all available data (1991–2005): (a and b) "pelagic diatoms" (p4) vs. "autotrophic dinoflagellates" (p1), (c and d) "heterotrophic dinoflagellates" (p3) vs. "big dinoflagellates" (p2), and (e and f) "weed diatoms" (p6) vs. "tychopelagic diatoms" (p5) vs.

significant change in the balance between these life-forms when modern times are compared with the reference condition in the period 1979–1981. Despite apparent lack of change in nutrients, and no evidence of shifts in the N:Si ratio, the dinoflagellates have become relatively more abundant. Diatoms have become less abundant, especially in spring. The diatom *Skeletonema costatum*, which dominated the spring bloom in all years between 1972 and 1982, decreased in numbers by more than an order or magnitude during March and April. Along with the diatom decrease has gone a substantial reduction in chlorophyll concentration (Table 2 and Laurent *et al*., 2006).

The results in Figure 5 for the eastern Irish Sea use a spatial rather than a temporal reference. Although both waterbodies are nutrient-enriched, that of Liverpool Bay is more enriched, and has higher chlorophyll (Table 2). In this case, we have been able to use data for three pairs of life-forms, but none of the three resulting values of the PCI showed any significant difference between the NE Irish Sea and Liverpool Bay.

Discussion

Stonehaven coastal waters (Table 2) have winter nutrient concentrations towards the top end of the natural range in UK coastal waters, owing to their proximity to the Atlantic inflow to the northern North Sea. Maximum chlorophyll is low, however, which may be due to the low mean light available for phytoplankton growth in tidally stirred coastal waters. The life-form PCI has indicated little change between the periods 1997–1999 and 2000–2005 in these comparatively pristine coastal waters, although this may be due to the relatively short time-series available for analysis. As studies with the Continuous Plankton Recorder have shown (Brander *et al*., 2003), climate change effects would be better revealed by multi-decadal data.

Loch Creran is considered to have been in a near-pristine state during the 1970s, with low maximum nutrient concentrations but high chlorophyll because of nutrient re-supply by the estuarine circulation (Tett and Wallis, 1978). Despite the presence of a salmon farm, winter nutrients have not shown a significant change between 1975 and 2003, whereas chlorophyll has decreased significantly, for unknown reasons (Laurent *et al*., 2006). The PCI indicates a highly significant change in the "balance of organisms" in this loch between 1979–1981 and 2006/2007. Although this change is in the direction expected from eutrophication (a shift towards dinoflagellates), it is associated with a decrease in chlorophyll concentration, whereas there has been no significant change in nutrients. Therefore, it may be better explained as a loss of diatoms and a consequent shift towards dinoflagellates. Whatever the ultimate cause of the changes in Creran—and it does not appear to be nutrient increase—the PCI clearly shows a marked change in the "balance of organisms" of the type associated with eutrophication. A further point is that, although a high-frequency time-series was used to generate the reference envelope, the change was evident despite the sparse sampling during 2006/2007.

In the comparison between the NE Irish Sea and Liverpool Bay, the latter has higher winter nutrients and greater maximum chlorophyll and has demonstrably suffered the first two stages (nutrient enrichment and enhanced biomass) of eutrophication, but appears not to have suffered "undesirable disturbance" (Gowen *et al*., 2008). The PCI results support this conclusion, showing no significant difference in plankton community structure between the less-enriched outer and more-enriched inner waters of the eastern Irish Sea. Much of the eastern Irish Sea is a "region of freshwater influence" (as defined by Simpson, 1997), with alternating periods of intermittent haline stratification and mixing, and variable physical transports. Perhaps we failed to detect a difference because the PCI reference envelope was large as a result of high physical variability in this region. Alternatively, perhaps phytoplankton community structure has not been perturbed by nutrient enrichment because it was already adapted to the high natural variability in this region.

These findings result from the first application of the PCI method to phytoplankton in coastal waters. We have shown that the index responds appropriately to small changes (Stonehaven) and large changes (Loch Creran) in phytoplankton composition, and we have gained some insights into the data needs of the method. For example, the Creran results suggest that the extent of change can be established with few new data so long as the reference envelope is well defined. However, comparing results from weekly data and month-averaged data from Stonehaven shows that more frequent sampling is not an entirely good thing for defining a reference envelope, because it increases the chance of including especially high or low abundances for a life-form, so broadening the envelope. It might therefore be better to define an envelope for 90 or 95%, rather than 100%, of the reference data.

The PCI is intended as an index of biological quality for the WFD and an index of ecosystem health in the context of eutrophication. Because it is in itself only an index of change away from a reference condition, it will need calibration for use in the management of environmental quality. We need to be able to relate the PCI, as an indicator of change in ecosystem state, to changes in environmental pressures such as increased nutrient loading. Such a relationship might be developed empirically by analysing further time-series from other sites covering a larger range of values for various pressure indicators. However, further development would be facilitated by having a theory that predicts reference envelopes for particular eco-hydrodynamic water types, i.e. in relation to the physical environment and undisturbed levels of nutrients and grazing. Tett and Lee (2005) used a one-dimensional physical-biological model to suggest how this might be done for the seasonally stratified waters of the northern North Sea.

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References

Bowman, M. J., Esias, W. E., and Schnitzer, M. B. 1981. Tidal stirring and the distribution of phytoplankton in Long Island and Block Island Sounds. Journal of Marine Research, 39: 587–603.

Brander, K. M., Dickson, R. R., and Edwards, M. 2003. Use of Continuous Plankton Recorder information in support of marine management: applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. Progress in Oceanography, 58: 175–191.

CEC. 1991. Council Directive of 21 May 1991 concerning urban waste water treatment (91/271/EEC). Official Journal of the European Communities, L135: 40–52.

CEC. 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities, L327: 1–73.

Escaravage, V., and Prins, T. C. 2002. Silicate availability, vertical mixing and grazing control of phytoplankton blooms in mesocosms. Hydrobiologia, 484: 33–48.

Escaravage, V., Prins, T. C., Nijdam, C., Smaal, A. C., and Peeters, J. C. H. 1999. Response of phytoplankton communities to nitrogen input reduction in mesocosm experiments. Marine Ecology Progress Series, 179: 187–199.

Gowen, R. J., Tett, P., Kennington, K., Mills, D. K., Shammon, T. M., Stewart, B. M., Greenwood, N., *et al.* 2008. The Irish Sea: is it eutrophic? Estuarine, Coastal and Shelf Science, 76: 239–254.

Jones, K. J. 1979. Studies on nutrient levels and phytoplankton growth in a Scottish Sea Loch. PhD thesis, University of Strathclyde.

Jones, K. J., and Gowen, R. J. 1985. The influence of advective exchange on phytoplankton in Scottish fjordic sea lochs. *In* Toxic Dinoflagellates, pp. 207–212. Ed. by D. M. Anderson, A. W. White, and D. G. Baden. Elsevier, New York.

Jones, K. J., Tett, P., Wallis, A. C., and Wood, B. J. B. 1978. The use of small, continuous and multispecies cultures to investigate the ecology of phytoplankton in a Scottish sea-loch. Mitteilungen–

Internationale Vereinigung für theoretische und angewandte Limnologie, 21: 398–412.

Laurent, C., Tett, P., Fernandes, T., Gilpin, L., and Jones, K. J. 2006. A dynamic CSTT model for the effects of added nutrients in Loch Creran, a shallow fjord. Journal of Marine Systems, 61: 149–164.

LeQuéré, C., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., *et al.* 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. Global Change Biology, 11: 2016–2040.

Margalef, R. 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, 1: 493–509.

OSPAR. 2003. Strategies of the OSPAR Commission for the Protection of the Marine Environment of the North-East Atlantic (Reference number: 2003-21). OSPAR Convention for the Protection of the Marine Environment of the Northeast Atlantic, Meeting of the OSPAR Commission, Bremen, 23–27 June 2003. OSPAR 03/17/1-E; Annex 31 (Ref. B-4.2).

Pingree, R. D., Holligan, P. M., and Mardell, G. T. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the Northwest European shelf. Deep Sea Research, 25: 1011–1028.

Reynolds, C. S. 1996. Plant life of the pelagic. Proceedings of the International Association for Theoretical and Applied Limnology, 26: 97–113.

Reynolds, C. S., Irish, A. E., and Elliott, J. A. 2001. The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). Ecological Modelling, 140: 271–291.

Simpson, J. H. 1997. Physical processes in the ROFI regime. Journal of Marine Systems, 12: 3–15.

Smayda, T. J., and Reynolds, C. S. 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. Journal of Plankton Research, 23: 447–461.

Smetacek, V. S. 1986. Impact of freshwater discharges on production and transfer of materials in the marine environment. *In* The Role of Freshwater Outflow in Coastal Marine Ecosystems, pp. 85–106. Ed. by S. Skreslet. Springer, Berlin.

Tett, P. 1986. Physical exchange and the dynamics of phytoplankton in Scottish sea-lochs. *In* The Role of Freshwater Outflow in Coastal Marine Ecosystems, pp. 205–218. Ed. by S. Skreslet. Springer, Berlin.

Tett, P. 1987. Plankton. *In* Biological Survey of Estuaries and Coasts, pp. 280–341. Ed. by J. Baker and W. J. Wolff. Cambridge University Press, Cambridge, UK.

Tett, P. 2006. Using the PCI-LF—a Draft User Guide. Napier University, Edinburgh. http://www.lifesciences.napier.ac.uk/research/Envbiofiles/PCI.htm.

Tett, P., Drysdale, M., Shaw, J. 1981. Phytoplankton in Loch Creran in 1979 and its effect on the rearing of oyster larvae. Scottish Marine Biological Association, Oban, Report 52. 77 pp.

Tett, P., Gowen, R., Mills, D., Fernandes, T., Gilpin, L., Huxham, M., Kennington, K., *et al.* 2007. Defining and detecting undesirable disturbance in the context of eutrophication. Marine Pollution Bulletin, 53: 282–297.

Tett, P., Heaney, S. I., and Droop, M. R. 1985. The Redfield ratio and phytoplankton growth rate. Journal of the Marine Biological Association of the UK, 65: 487–504.

Tett, P., Hydes, D., and Sanders, R. 2003. Influence of nutrient biogeochemistry on the ecology of north-west European shelf seas. *In* Biogeochemistry of Marine Systems, pp. 293–363. Ed. by G. Schimmield, and K. Black. Sheffield Academic Press Ltd, Sheffield.

Tett, P., and Lee, Y. 2005. N:Si ratios and the 'balance of organisms': PROWQM simulations of the northern North Sea. Journal of Sea Research, 54: 70–91.

Tett, P., and Wallis, A. 1978. The general annual cycle of chlorophyll standing crop in Loch Creran. Journal of Ecology, 66: 227–239.

Weisstein, E. W. 2006. "Convex Hull". From MathWorld–A Wolfram Web Resource. http://mathworld.wolfram.com/ConvexHull.html (last accessed February 2006).

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