

## Short communication

## Phytoplankton and the balance of nature: An opinion

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## ABSTRACT

Recent European Court rulings in the context of eutrophication viewed proliferation of a particular species of algae as a disturbance to the balance of aquatic ecosystems and the proliferation of one or more species as a cause of a reduction in other species. We discuss the scientific basis for this opinion in relation to the growth of marine primary producers and current debates about ecosystem stability. Opposing views in this debate are those of (a) the 'balance of nature' paradigm, in which communities of organisms tend towards a stable climax composition, and (b) communities as dynamic systems that may be governed by 'basins of attraction' in state space. We use data from the Irish Sea and Narragansett Bay, together with a review of the literature, to show that: the dynamics of temperate marine phytoplankton, with seasonal successions, corresponds more to (b) than to (a); the temporary dominance of any one species of micro-alga or cyanobacterium is part of the natural dynamics of phytoplankton communities and does not permanently impact on other species. Understanding the phytoplankton as a dynamic system suggests its status should not be assessed against a 'climax' model and that eutrophication should be diagnosed from fundamental (nutrient-induced) perturbations of ecosystem state and function rather than from changes in fixed assemblages of species and thresholds of abundance.

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## 1. Introduction

There is currently much interest in the stability and resilience of ecosystems, driven, in part, by an appreciation of the threat to natural systems by human pressures on the biosphere. One such pressure is nutrient enrichment of coastal waters. The European Urban Waste Water Treatment Directive (UWWTD; Council Directive 91/271/EEC, 1991) requires nutrient stripping from discharges into waters that are eutrophic or at risk of eutrophication. The Directive defined eutrophication as: "the enrichment of water by nutrients, especially compounds of nitrogen and/or phosphorus, causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned."

In two recent judgements (ECJ, 2004, 2009) the European Court of Justice ruled on several parts of this definition. The ruling of interest here concerns the 'balance of organisms'. In paragraph 21 of ECJ (2004), the Court stated that:

"... the equilibrium of an aquatic ecosystem is the result of complex interactions among the different species present and with the environment. Any proliferation of a particular species of algae or other plant therefore constitutes, as such, a disturbance of the balance of the aquatic ecosystem and, accordingly, of the balance of the organisms present in the water, even when other species remain stable. Moreover, given the competition between plant species for nutrient salts and luminous energy, the proliferation of one or several species, by monopolising the resources necessary to the growth of other algae and aquatic plants, very often if not always entails reductions in other species."

We identify two points for discussion, that proliferation of any primary producer constitutes a disturbance of the balance of organisms and that the proliferation of one or more species necessarily involves reductions in other species. We draw on the scientific literature in support of three main arguments. First, the ruling reflects only one point of view in a continuing debate on the nature of ecosystems. Second, marine ecosystems, especially those involving micro-algal or cyanobacteria primary producers, are naturally highly dynamic. Third, the growth of undisturbed as well as disturbed populations of phytoplankters is typically exponential (which might be called 'proliferation') and although the biomass

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developed as a result of such growth can sequester nutrients and absorb photons, such dominance is typically short-lived and without long-term consequences for other phytoplankters. We support the second and third claims with illustrations of patterns of phytoplankton growth and succession in two temperate coastal waters that we have studied.

## 2. The balance of nature

As reviewed by Cuddington (2001), claims about the balance of nature fell into three categories:

- 1) “natural populations have a more or less constant numbers or individuals”;
- 2) “natural systems have a more or less constant number of species”;
- 3) “communities of species maintain a “delicate balance” of relationships, where the removal of one species could cause the collapse of the whole (an associated claim is that communities form a single biological entity and have a characteristic species composition).”

Point (1) relates to the Court’s concern about proliferation. Point (2) does not seem central to the argument. Point (3) turns on two related matters; how biological communities function, and how they have been conceived to function. Two contrasting views of the natural world have influenced modern ecological thought and environmental management. One view, originating with Heraclitus of Ephesus (c.535–c. 475 BCE: see Graham, 2005) holds that everything is in a state of flux. In contrast, the more widely held view was of the constancy and harmonious working of nature. For example, Herodotus of Halicarnassus (c.484–c.425 BCE) wrote, in book 3 of ‘The Histories’ that the natural world had been made so that predators and prey were in an essentially static balance (Waterfield and Dewald, 1998). According to Egerton (1973), and see also Simberloff (1980), it is this view of natural harmony that has influenced scientific opinion throughout recent history, particularly the 19th century and into the early 20th century. Pickett and Ostfeld (1995) suggested that one consequence of this view is that ecosystems have been considered to be: “*primarily closed, self –regulating, and subject to a single stable equilibrium*”. That is, one which does not change with time unless disturbed and if disturbed returns to the equilibrium state.

A simple view of equilibrium in the biological community is that it is a single state in which each species has a unique abundance. Thus, as developed by Frederic Clements (Clements, 1916), a (climatic) climax community is a biological community of plants and animals which, through the process of ecological succession has reached an equilibrium in response to climate, soil and other environmental factors. In the absence of human interference, this state is self-maintaining. Tansley (1935) argued for a “*relatively stable dynamic equilibrium. Succession and development are instances of the universal processes tending towards the creation of such equilibrated systems.*” In parallel to such views, zoologists developed theories in which inter-species competition led to a state of balance in animal populations (Nicholson, 1933).

This balance of nature paradigm has had much influence on the management of terrestrial ecosystems (Cuddington, 2001; Pickett et al., 2007; Spieles, 2010). In opposition, Gleason (1926) held that terrestrial floras were no more than contingent associations of species, and Davis and Slobodkin (2004) argued that it was a mistake to try to manage ecosystems as if they were organic units. Nevertheless, many ecologists (see Winterhalder et al., 2004) think that ecosystems do behave to some extent as integrated systems. Therefore, the debate is better seen as about what sort of integrated

system: one that tends towards an equilibrium or climax, or one that is best described as oscillating within a ‘basin of attraction’ (Holling, 1973). An ‘attractor’ is the dynamic behaviour that the system tends towards (The Encyclopaedia of Science, 2012). The first type is that of the ‘balance of nature’ view, in which ecosystems are seen as structured functional units in equilibrium in which each species has a unique abundance. The second is a non-equilibrium view with an emphasis on: heterogeneity and instability (Den Boer and Reddingius, 1996); exchanges of energy and matter and shifts in dominance within communities (Pickett and Ostfeld, 1995). Based on evidence, opinion is shifting towards the second view. O’Neill (2001) saw “*ecological systems as meta-stable adaptive systems that may operate far from equilibrium*”. Botkin (1990) took examples from well-documented studies in North America, Africa, Australia and New Guinea, and concluded that there was overwhelming evidence to refute the balance of nature paradigm.

## 3. Growth and proliferation of aquatic primary producers

The adverse effects of coastal eutrophication result from an excessive stimulation of algae and cyanobacteria (Ferreira et al., 2011). These effects can be found in the plankton or benthos and the latter include macro-algae (seaweeds). The excess growth of opportunistic seaweeds, exemplified by *Enteromorpha* spp., often appears as a proliferation of green thalli that can smother other plants and cause sediment deoxygenation (Raffaelli et al., 1998). In the plankton, enrichment can sometimes result in harmful algal blooms that can have a negative impact on ecosystems and the services they provide to humans (Gowen et al., 2012).

In general, the vegetative growth of microalgae (and cyanobacteria) typically involves the binary division of free-living cells (or similar division within chains of cells). This process results in exponential population growth, although the rate of such growth ( $\mu$ ) depends on the interval between cell divisions and hence on the availability of light and nutrients. In addition, populations of phytoplankters are subject to grazing pressure (and to the influence of water movements). First order models of grazing parameterize it as the daily removal of a certain proportion ( $g$ ) of the population, a process that on its own leads to exponential decrease (e.g. Landry and Hassett, 1983). Thus, as a first approximation, the combined rate  $\mu - g$  results in exponential change in the population, at a rate that may be fast or slow, positive or negative. Physical water movements may lead to additional exponential decrease through dilution or dispersal, or to non-exponential increase through concentration of cells at convergences (Pitcher et al., 1998).

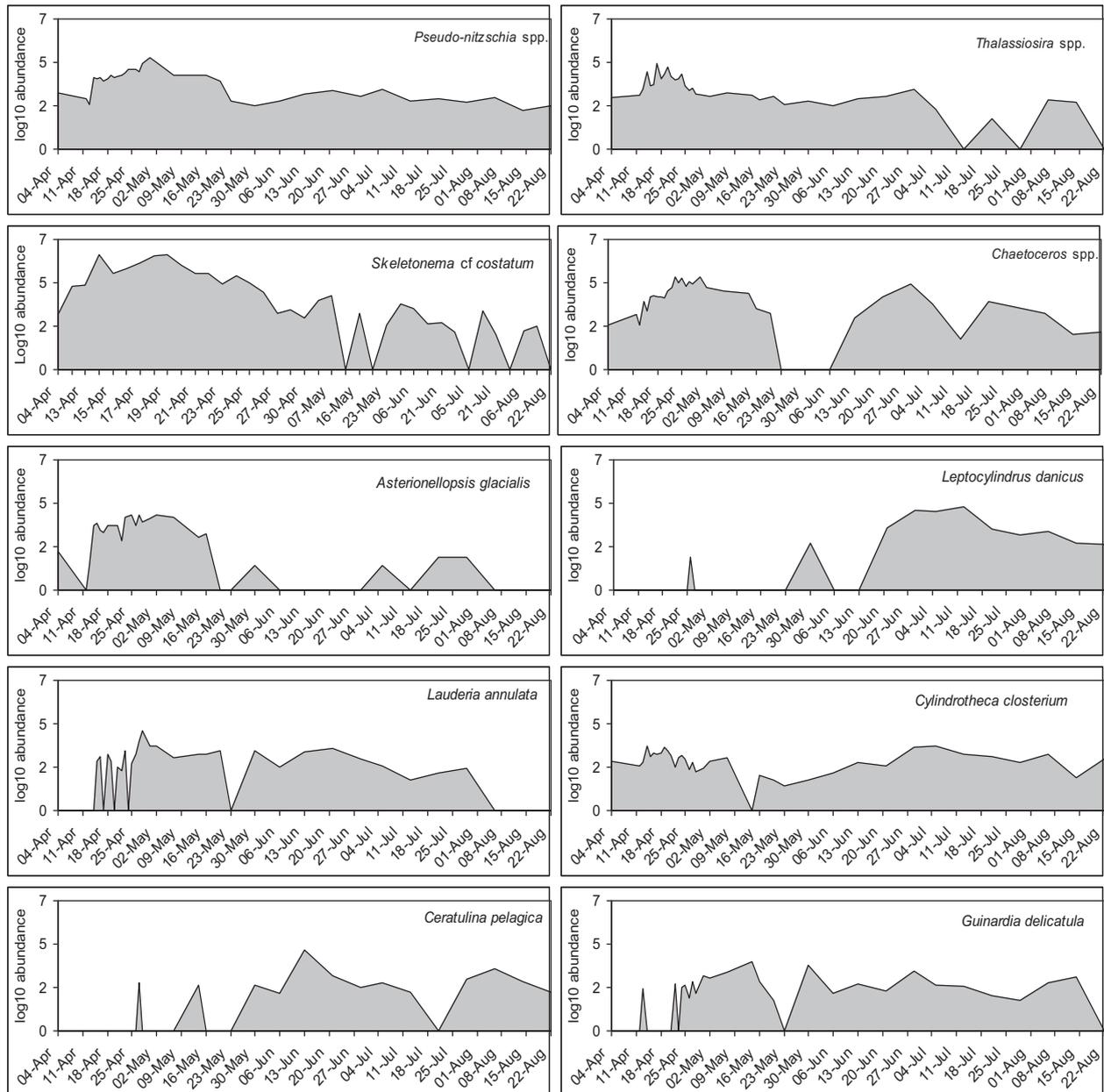
Our argument is that all these processes occur naturally in the sea, although  $\mu$  may remain higher for longer where nutrients have been enriched, or there may be greater population biomass to be concentrated. Competition between species, in terms of nutrient uptake or storage abilities, avoidance of grazing, and ability to exploit water movements or stratification, can be seen as involving differences in exponential rates of population change, with certain species being more successful under certain conditions, only to give way to others as circumstances change. Concern about nutrient enrichment should therefore be focussed on sustained disturbance of the community of phytoplankters rather than on the blooming (proliferation) or enhanced exponential growth of any particular alga. Roelke et al. (2003) make a similar point: “*management approaches should not focus on individual species but rather community behaviour within a desired basin of attraction*”. Many studies of phytoplankton composition and abundance under natural conditions, including those illustrated below, show that successive growth of species populations need entail no permanent reduction in the abundance of species that have been temporarily out-competed for resources.

#### 4. Balance and growth in the phytoplankton

Most studies referenced in Section 2 have dealt with terrestrial ecosystems. Pelagic marine systems may be different. Species of zooplankton have life-spans ranging from weeks to a few years, and species of phytoplankton and pelagic protozoans, like most micro-organisms, are short-lived but are capable of rapid growth. According to Harris (1980) the earliest view of the planktonic environment was of an: “isotropic homogeneous environment at equilibrium over large scales”. However, this has proven not to be the case. Plankton experiences an inherently variable environment as a result of physical variability driven by meteorology and climatology, interacting with tidal and density-driven flows. As a consequence, phytoplankton exhibit variability on a range of spatial and temporal scales (Harris, 1986). Nevertheless, although the mixture

of species, and their abundance, changes even in samples taken in the same water-body in successive weeks, there are higher-order constancies such as the recurrent annual cycle of phytoplankton growth in coastal waters (e.g. Tett and Wallis, 1978; Smayda, 1998; Gowen et al., 2008) and the succession of lifeforms in seasonally stratifying temperate shelf seas (Margalef, 1978). Such recurring but varying cycles could be seen in terms of ‘basins of attraction’ within ecosystem state space (Lewontin, 1969; Holling, 1973).

Much has been written on the underlying causes of variability in the phytoplankton (Margalef, 1978; Kilham and Kilham, 1980; Gaedeker and Sommer, 1986; Harris, 1986; Padišák, 1993; Huisman and Weissing, 1999; Reynolds et al., 2002; Roelke et al., 2003; Smetacek and Cloern, 2008). However, our intention here is not to review this literature but to illustrate the variability in the phytoplankton with observations from two locations, the Irish Sea and



**Fig. 1.** Temporal variation in the 10 most abundant diatoms in near surface offshore waters of the western Irish Sea during spring and summer 1995. Samples were collected using a moored automated water sampler and preserved in Lugol's iodine. Sub-samples (50 mL) were concentrated using a sedimentation technique and an inverted microscopy was used for species identification and enumeration. (Data from McKinney et al. (1997)).

lower Narragansett Bay and from studies in the scientific literature. Fig. 1 shows changes in abundances of the 10 most common diatoms in the near-surface waters of the seasonally stratifying western Irish Sea during the spring and summer of 1995. The abundance scales in the diagram are logarithmic, which tends to conceal, but also illustrate the exponential (i.e. proliferative) nature of phytoplankton growth and decline. The figure illustrates two points: (1) large changes in the abundance of each taxon occur over a few weeks, and; (2) there is replacement of one dominant taxon by another. The site from which the samples were collected was largely beyond the direct effects of human-influenced river discharges into the Irish Sea (Gowen et al., 2008), and so we use these results to support our claim that they exemplify the natural variability in phytoplankton. Such short-term (week to week) variability in coastal phytoplankton is evident in many other data

sets and the commonality of successive growth behaviour in temperate coastal waters is evident from the numerous studies that have described community assemblages (Table 1). For example, in their study of phytoplankton in Delaware Bay (USA), Watling et al. (1979) reported that during spring to autumn, the dominant species changed every one to four weeks. We therefore suggest that the dynamics of the phytoplankton as a whole can be described as the successive growth of populations of different species.

The data sets in Table 2 (western Irish Sea) and Table 3 (lower Narragansett Bay) further illustrate variability in the phytoplankton, in these cases on inter-annual time scales. In temperate waters a spring bloom is often the most important event in the phytoplankton year, as micro-algal growth responds to the astronomically imposed annual cycle of day-length and illumination, and the alternation of vernal and aestival stratification with

**Table 1**

Published studies illustrating variability in the phytoplankton.

Location	Study	Findings	Source
Plymouth Sound (English Channel)	1892	Occurrence of different species during summer and autumn. Inter-annual variation in occurrence of species.	Bles (1892)
Swedish waters	1893	Occurrence of different species at different times of the year.	Cleve (1897)
Gulf of Maine (USA)	1912–1920	Seasonal succession and quasi-synoptic spatial variation in composition.	Bigelow (1924)
Loch Striven (Scotland)	1926 and inter-annual comparison	Changes in abundance of species over time and space (depth) and succession of diatom species. Inter-annual variation in dominant summer diatom species reported.	Marshall and Orr (1927)
Southern California (USA)	1920–1924 (samples from pier)	Marked fluctuations in the abundance of species (week to week) and a succession of dominant species.	Allen (1928)
Waters off Romsdalsfjord (Norway)	1898, 1899, 1900, 1926, 1927	Seasonal succession of species and sequence of abundance peaks sometimes with the same dominant species but often with a different dominant species.	Gran (1929)
Passamaquoddy region (Canada)	1924–1931	Weekly fluctuations in diatom species abundance and a total of 100 diatom species recorded.	Davidson (1934)
English Channel	1933–1934	Sequence of biomass peaks dominated by different species.	Harvey (1934)
Bay of Fundy and Gulf of Maine	1932	Seasonal succession and spatial differences in the sequence of species.	Gran and Braarud (1935)
Lower Narragansett Bay (USA)	1954–1955	Recorded ~75 species. A succession of species (some with single and other with bimodal or more complex patterns of seasonal abundance) resulting in a sequence of maxima.	Smayda (1957)
RiaVigo (Spain)	Review of data from the early 1950s.	Three (possible four), succession stages (1, small diatoms and flagellates; 2, larger diatoms; 3, increased dominance of dinoflagellates) each with three sub-stages.	Margalef (1958)
Sargasso Sea off Bermuda	1957–1958	Short-term week to week fluctuations in the abundance of species. Seasonal succession from diatoms to dinoflagellates and coccolithophorids but not a fixed sequence.	Hulburt et al. (1960)
Dutch coastal waters	1974	Short-term spatial and temporal variation in phytoplankton species.	Gieskes and Kraay (1975)
Southern California	1972–1973	Recorded 90 species and seasonal succession in near-shore phytoplankton species.	Briand (1976)
Delaware Bay (USA)	1974–1975	Recorded 113 species and pronounced shift in dominant species. Species dominant in June were replaced by other species in August. Winter dominants more persistent but at other times of the year the dominant species changed every one to four weeks.	Watling et al. (1979)
English Channel	1964–1974	Seasonal succession from diatoms to dinoflagellates.	Maddock et al. (1981)
Lower Narragansett Bay (USA)	1959–1997	Recorded ~125 species. A succession of species (some with single and other with bimodal or more complex patterns) of seasonal abundance resulting in a sequence of maxima.	Karentz and Smayda (1984, 1998)
NE Atlantic North Sea	1948 to 1984 Review	Seasonal occurrence of different phytoplankton species. Seasonal succession and inter-annual variability in phytoplankton species.	Colebrook (1986) Reid et al. (1990)
Chesapeake Bay (USA)	1984–2004	Recorded 1454 phytoplankton taxa and clear seasonal cycle of species. Diatom dominated spring assemblage replaced by summer/ early autumn assemblage and in turn by an autumn flora with spring species again dominant.	Marshall et al. (2005)
North East Atlantic and North Sea	1948–2003	Long-term inter-annual variability in the abundance of <i>Phaeocystis</i> spp.	Gieskes et al. (2007)
Northern Adriatic Sea	1977–2006	Recorded 372 phytoplankton taxa, seasonal succession and inter-annual variability in taxa.	Aubry et al. (in press)
Coastal northern Adriatic	1986–2010	Recorded 396 micro-algal taxa, seasonal succession of species and inter-annual variability in the species that dominated diatom spring and autumn blooms.	Cabrini et al. (in press)

**Table 2**

The 10 most abundant (cells mL<sup>-1</sup>) diatoms during the spring bloom in near-surface offshore waters of the western Irish Sea. Samples were collected using a moored automated water sampler and preserved in Lugol's iodine. Sub-samples (50 ml) were concentrated using a sedimentation technique and an inverted microscopy was used for species identification and enumeration. (1995 data from McKinney et al. (1997)).

Species	1995	1998	2000	2001	2002	2003
<i>Asterionellopsis glacialis</i>	2.6					
<i>Cerataulina pelagica</i>	0.7		1.2		2.2	1.3
<i>Chaetoceros</i> spp.	17.4	2.2	282.9	0.2	250.2	705.0
<i>Cylindrotheca closterium</i>	0.8	0.7	1.1			0.4
<i>Detonula</i> spp.			0.9			
<i>Ditylum brightwellii</i>		0.4			2.8	
<i>Eucampia zodiacus</i>			0.5			0.4
<i>Guinardia delicatula</i>	0.5	0.2	9.0	0.1	38.5	2.3
<i>Guinardia flaccida</i>			2.1		0.9	
<i>Guinardia striata</i>						0.6
<i>Lauderia annulata</i>	1.3				0.9	
<i>Leptocylindrus danicus</i>	2.0	0.2		0.1	2.4	4.2
<i>Leptocylindrus minimus</i>				0.1	1.2	53.5
<i>Paralia sulcata</i>		0.1				
Pennate diatoms (small)		0.3		0.1		
<i>Pseudo-nitzschia</i> spp.	9.8	1.1	0.7	1.1	11.2	16.5
<i>Rhizosolenia setigera</i>				0.2		
<i>Skeletonema</i> ( <i>costatum</i> )	173			3.0		
<i>Rhizosolenia styliformis</i>			0.4			
<i>Thalassionema nitzschioides</i>		0.2		0.1		
<i>Thalassiosira</i> spp.	4.1	3.0	0.4	4.8	5.9	63.3

autumn and winter mixing and associated nutrient renewal. During winter, growth is minimal but each spring the growing season begins with a spring bloom of phytoplankton stimulated by light and fuelled by nutrients (e.g., Smetacek and Passow, 1990; Tett, 1990; Gowen et al., 1995). The data in Table 2 show inter-annual changes in the diatom species that were most abundant during this bloom in the western Irish Sea. There was little constancy from year to year in the dominant phytoplankton. During the 1995 spring bloom, for example, *Skeletonema* cf. *costatum* was the most

**Table 3**

Annual abundance of the 10 most abundant species of phytoplankton from a station in lower Narragansett Bay. Data are mean annual abundance (cells mL<sup>-1</sup>) at 5-year intervals during 1960–1995 and counted live using a Sedgwick Rafter counting chamber (see Smayda, 1995).

Year	1960	1965	1970	1975	1980	1985	1990	1995
<i>Asterionellopsis glacialis</i>	953	73	172	287	73		187	164
<i>Aureococcus anophagefferens</i>						176		
						281		
<i>Cerataulina pelagica</i>								50
<i>Chaetoceros compressus</i>	150			70				
<i>Chaetoceros debilis</i>			32		35	87		
<i>Chaetoceros socialis</i>				20	41			160
<i>Chaetoceros tortissimus</i>			46					
Cryptomonads				34	57	80	109	416
<i>Cyclotella</i> sp.			54	83				
<i>Cylindrotheca closterium</i>						346		
<i>Dactyliosolen fragilissimus</i>				19		62	225	
<i>Detonula confervacea</i>	208	511	225	276	79		80	121
<i>Ditylum brightwellii</i>		23						
<i>Eucampia zodiacus</i>							75	
<i>Guinardia delicatula</i>	24	66						50
<i>Heterocapsa rotundatum</i>					59	60	75	
<i>Heterosigma akashiwo</i>	13			60	128			
<i>Leptocylindrus danicus</i>		42	32				88	77
<i>Leptocylindrus minimus</i>	17	145	46		39	87		4
<i>Minutocellus polymorphus</i>						608		
<i>Prorocentrum triestinum</i>	14	72						
<i>Rhizosolenia setigera</i>		38						
<i>Skeletonema</i> ( <i>costatum</i> )	1388	954	2584	2505	3168	146	2527	606
<i>Thalassiosira nordenskiöldii</i>	39		31	110	234	211	55	27
<i>Thalassiosira pseudonanna</i>			31					
<i>Thalassiosira rotula</i>	28						108	
<i>Thalassionema nitzschioides</i>		59						

abundant species whereas *Guinardia delicatula* was a minor component. In contrast, the abundance of *G. delicatula* was two orders of magnitude higher during the 2002 spring bloom and *S. cf. costatum* was then not amongst the ten most abundant species. Our conceptual model is that the water in the western Irish Sea contains over-wintering populations of many species, perhaps several hundred (see Tett and Barton, 1995), but at low abundances. As spring approaches, the populations of most of these species begin to grow, at rates that are partly decided by prevailing environmental conditions and partly by the outcomes of chaotic processes (Benincà et al., 2008). There may therefore be a lack of predictability in the species of diatom that initiate and dominate the spring bloom in any particular year. Furthermore, based on results from a modelling study, Dakos et al. (2009) suggested that inter-annual variability in species composition was an intrinsic property of multi-species communities in seasonal environments. Analogously, in the case of dinoflagellates, Smayda and Reynolds (2001) suggested that the species that bloomed, or which dominated a phytoplankton, was often in part simply the result of that “species being in the right place at the right time”.

Our second example (Table 3) is taken from a 39-year plankton time series (1959–1997) based on weekly sampling at a monitoring station near the entrance into Narragansett Bay. Narragansett Bay is a well-mixed, major estuary located southwest of Cape Cod along the eastern U.S. coast (ca. 41°30'N, 71°20'W) and contiguous with Rhode Island and Long Island Sounds. In the 8 years shown, which represent semi-decadal intervals between 1960 and 1995, a total of 27 species contributed to the 10 most abundant species (based on annual mean abundance). The data set shows three facets of variability in the composition of the phytoplankton community as a whole: (1) the abundance of individual species varied from year-to-year. For example, *Skeletonema* cf. *costatum* abundance differed 22 fold (146–3168 cells mL<sup>-1</sup>); (2) no semi-decade had the same 10 most abundant species. *S. cf. costatum* was present each year and some species occurred in most years (e.g. *Asterionellopsis glacialis*, *Detonula confervacea* and *Thalassiosira nordenskiöldii* were amongst the top 10 winter–spring bloom species in 7 of the 8 semi-decadal years compared), but bloom dominance of the 19 other diatom species and 5 taxa representing other phylogenetic groups (e.g., 2 dinoflagellates, 1 raphidophyte, 1 pelagophyte, and “cryptomonads”) was more variable; (3) the dominance ranking of a species varied from year-to-year. For example, *A. glacialis* was ranked 2nd and 3rd in dominance in 2 and 3 winter–spring bloom years, respectively; *D. confervacea* attained each ranking twice.

It is evident from the data sets presented in Tables 2 and 3 that species that are out-competed during a particular year or bloom-event return in subsequent years. The studies summarized in Table 1 provide additional evidence of inter-annual variability. Bles (1892) noted that *Noctiluca* could be present in Plymouth (UK) Sound in “immense profusion” during one year and apparently absent during the next. Working in the Scottish sea loch Striven, Marshall and Orr (1927) reported that *Rhizosolenia fragilissima* [= *Dactyliosolen fragilissimus*] dominated the summer diatom population in 1923, *Chaetoceros socialis* in 1924 and 1925, but that there was a succession of three dominant species (*Nitzschia seriata* [= *Pseudo-nitzschia* spp.], *Leptocylindrus danicus* and *Eucampia zodiacus*) in 1926. Based on a study of the phytoplankton in the English Channel between 1964 and 1974, Maddock et al. (1981) concluded that: “There were some obvious differences between years in that if a certain species was found in a year it often occurred in several consecutive months, while in other years it was totally absent.” Using Continuous Plankton Recorder data, Gieskes et al. (2007) illustrated the long-term inter-annual variability in the abundance of *Phaeocystis* spp. colonies in the North Sea and wider NE Atlantic. Interestingly, in their study of long-term changes in the

phytoplankton of Chesapeake Bay, Marshall et al. (2005) concluded that: "Comparison with collections made ~8 decades ago (1916–1922) within Chesapeake Bay indicated several of the same flora remained dominant today." Furthermore, Marshall et al. (2005) found that contrary to expectation (a decrease in species richness consequent on pollution) the diversity of species had increased over ~80 years.

## 5. Discussion and conclusions

The debate about the 'balance of nature' paradigm, interpreted as a tendency towards a unique equilibrium state and assemblage of species (under given climatic and undisturbed conditions), is moving towards the view that it is an inappropriate model for terrestrial ecosystem management. We consider that this is also the case for pelagic ecosystems dependent on photosynthetic microorganisms. Our first conclusion therefore, is that to assess the status of marine ecosystems and to quantify disturbance to the balance of organisms, it is necessary to take account of the dynamic nature of these marine ecosystems.

The evidence shows that the phytoplankton in temperate coastal waters and shelf seas is made up of a dynamic balance of species resulting from the successive growth of populations of different species with some tendency to return to the same starting point in spring each year. In our view, the phytoplankton should not be seen as an assemblage of species each with its own unique abundance and our second conclusion is that: the state of the phytoplankton should not be assessed by comparing its floristic composition and relative abundances with those of a 'reference' assemblage of species.

The evidence also shows that the growth of (species) populations of phytoplankters does not necessarily lead to long-term disruption of the dynamic balance. Therefore, our third conclusion is that the growth of a single species is not necessarily a disturbance of the equilibrium or optimal state of the phytoplankton. From this it follows that the 'undesirable disturbance' (Tett et al., 2007; Gowen et al., 2008; Ferreira et al., 2011) used to diagnose pelagic eutrophication under the UWWTD, OSPAR's (2003) 'Strategy to Combat Eutrophication', and the European Marine Strategy Framework Directive of 2008 (see Ferreira et al., 2011) must be identified from more fundamental perturbations of ecosystem state and function.

As the data presented here show, it is often difficult to identify a persistently dominant species, in the sense of a phytoplankter that plays the same important role in the seasonal succession in each year as certain species do in plant communities according to climax theory. This makes it difficult to identify indicator species that could be used to assess phytoplankton state. However, we recognise that for some coastal regions the occurrence of a particular species can be used as an indicator of human perturbation. Species of the genus *Phaeocystis* that are regarded as a nuisance in Belgian and Dutch coastal waters provide one example (Lancelot et al., 1987). Interestingly however, Lancelot et al. (2009) concluded that there had been little change in the ecosystem of Belgian coastal waters despite the considerable increase in *Phaeocystis* spp. associated with anthropogenic nutrient enrichment.

The balance of nature paradigm has proved to be an enduring view of the natural world that continues to influence the way ecologists think despite much evidence to the contrary. This evidence suggests that marine pelagic ecosystems should not be conceptualized as naturally tending to simple equilibria. Instead, they are highly dynamic systems but there are observable patterns. The data are often consistent with the idea of a system oscillating within a 'basin of attraction', even if each cycle differs from the previous one. In summary, our opinion is that an 'undesirable

disturbance to the balance of organisms' has to be sought in a disturbance of such patterns, rather than in the 'proliferation' of any single species.

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