

Patterns of variability characterizing marine phytoplankton, with examples from Narragansett Bay

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Some features of the patterns of variability which characterize phytoplankton species occurrences, community organization, biomass levels, blooms, and associated physico-chemical growth regulators are considered. Phytoplankton variability occurs in various patterns: as cycles, trends, fluctuations, unusual events, irregular pulses; at various scales: hourly or less, daily, seasonally, annually, decadal, etc.; even chaotically, and at various frequencies. Variability in winter–spring bloom inception, duration and magnitude is discussed, and 11 types of species-specific patterns of variability are described, with some examples from Narragansett Bay highlighted. It is suggested that the variable response capabilities of planktonic communities act as restructuring mechanisms which allow the community and its foodweb linkages to modify their dynamics to accommodate the changed(-ing) environmental conditions. The distinction between point and threshold events embedded within patterns of plankton variability is discussed. The inadequacy of traditional monitoring approaches and the need to replace such sampling strategies with a combination of observational and process-oriented, *in situ* rate measurements to quantify the causes and effects of plankton variability are pointed out.

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Key words: blooms, cycles, monitoring, Narragansett Bay, phytoplankton variability, time-series, trends.

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Introduction

All trophic components of the marine ecosystem exhibit annual variations and long-term changes (Cushing, 1978; 1982). Some of this variability results from trophodynamic linkages, as in the “Russell Cycle” reported for the North Sea. In this cycle, long-term cooling and warming trends and oscillations in westerly wind frequency induce inter-linked and recurrent cyclical patterns in nutrients (see, however, Joint *et al.*, 1997), plankton, benthos, fish stocks, and trophodynamic shifts (Russell *et al.*, 1971; Cushing, 1982). Similar long-term trends and linkages in trophodynamic, chemical, and physical habitat features occur in the Wadden Sea (Lindeboom *et al.*, 1995). Paradoxically, with the possible exception of fish stocks, trophodynamic variability appears to be better understood than the variability characterizing individual trophic components.

For plankton, long-term variability was first documented by Johnstone *et al.* (1928) based on a 14-year time series (1906–1920) of weekly net tows. In the 90

years since that study began, qualitative surveys have provided the primary insights into phytoplankton variability. Of these, the ongoing Continuous Plankton Recorder (CPR) surveys begun in 1948 over selected North Sea and oceanic transects have been of exceptional importance in molding current views on plankton variability (see Colebrook, 1979, 1986; Gieskes and Kraay, 1977; Reid *et al.*, 1987). The CPR surveys have clearly revealed that selected species of zooplankton and large-sized phytoplankton (the sampling mesh-size is 270 μm) exhibit variable and statistically definable inter-annual and regional trends in response to hydrographic and climatological perturbations and patterns. Although the CPR surveys sample only the largest phytoplankton size class, variability is undoubtedly a property of all phytoplankton size classes, and influenced by *in situ* chemical and biological perturbations and processes. Unfortunately, neither qualitative nor quantitative surveys generally sample the phytoplankton adequately, nor make the type of concurrent measurements of biological processes and physical and chemical habitat

variables needed to quantify this variability. As a result, many first principles of phytoplankton variability have yet to be elucidated, and quantification of the causes and trophic consequences of variability are rarely achieved. The usual duration of a time series is one year. However, even when longer time series are available, the observations usually are significantly compromised, either because the time series is still too short and/or relevant variables were not measured. For example, phytoplankton community structure is often analysed without concurrent measurements of nutrients, or zooplankton, etc.

Phytoplankton variability is commonplace and easily detectable, but the limited data on its properties of scale, multiple varieties, different periods, amplitudes and response times, and biological interactions make quantification of cause and effect and predictions problematic. In fact, natural variability, fluctuations, and change are probably the least understood major characteristics of marine ecosystems, despite numerous descriptive and process-oriented studies, and mechanistic modelling efforts. This poses a related problem. Natural variation is the essential “baseline” against which the effects of human-induced changes in the ocean are to be detected, measured, and predicted. Our relative inability to distinguish anthropogenic effects from responses induced by natural climatic, hydrographic, and habitat changes and their variability increasingly compromises this growing need.

The present contribution seeks to put into perspective some features of phytoplankton variability relevant to these various issues. It is not a literature review, and not all known varieties of phytoplankton variability are considered. In selecting examples to illustrate specific types, I have focused upon a long-term, quantitative data set available for Narragansett Bay, Rhode Island. Sampling details and some relevant results of this 37-year time series are given in Smayda (1976, 1984), Karentz and Smayda (1984, 1998), Li and Smayda (1998), Borkman and Smayda (1998).

Phytoplankton habitat variability: some characteristics

Pelagic environments inherently are continuously variable; all physical, chemical, and biological features of the planktonic niche are affected. Of these, physical variability, driven primarily by external forcing events (meteorology, climatology), is fundamental. Wind- and weather-driven events cause physical changes and disruptions. These lead to variability in temperature, irradiance, precipitation, run-off, nutrient loading (in coastal regions), mixed-layer depth, etc. This variability is not only random; trends and cycles also occur, the wavelength of which varies with the parameter. For

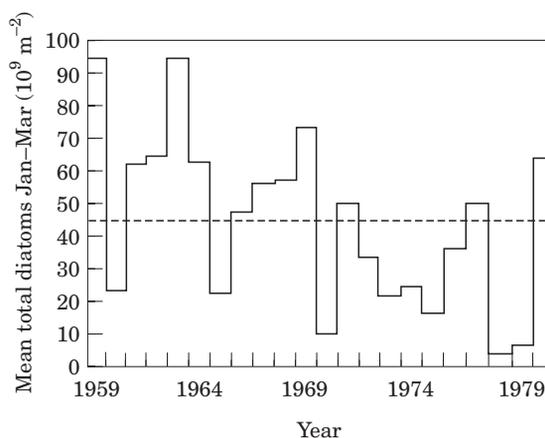


Figure 1. Mean total diatom population during January–March at a long-term monitoring station in lower Narragansett Bay based on weekly measurements (1959–1980). Hatched line indicates mean for period. Note the 5-year cycles embedded within the long-term downward trend.

example, there are different hydrographic cycles, with periods of 3–4, 6–7, 10–11, 18–20, and 100 years (Gray and Christie, 1983). Cycles may be superimposed upon long-term trends (Reynolds, 1990), such as the cyclical occurrences of wet and dry years (Currie, 1984) and inter-annual shifts in wind stress patterns (Horne and Platt, 1984). Variance in the physical habitat leads to variance in plankton cycles, ecosystem structure, and productivity. A 30-year decline in phytoplankton and zooplankton could be related to changes in mixed-layer depth associated with a long-term increase in northerly winds (Dickson *et al.*, 1988). Two crisp peaks of warm-water phytoplankton abundance characterized a 24-year time series, with each pulse lasting 2 years (Maddock *et al.*, 1989). A series of 5-year cycles in mean total winter diatom abundance in Narragansett Bay is embedded within the progressive, ca. 20-fold downward trend in abundance which occurred between 1959 and 1978 (Fig. 1). The inverse correlation of these patterns with temperature suggests a climatologically induced response.

Chemical (=nutrient) variability, driven by external and *in situ* processes, is a prominent habitat characteristic at scales ranging from diel-to-seasonal-to-annual-to-decadal. Within this variability, cycles and trends in nutrients occur, with cultural eutrophication increasingly important. Well-known sources of new nutrient inputs leading to variable concentrations include seasonal mixing, run-off, discharge of domestic and agro-industrial wastes, and watershed management practices. Inputs are balanced against phytoplankton uptake, itself a cause of nutrient variability. Chemical variability occurs in various forms: (1) as increased nutrient concentrations (Hickel *et al.*, 1993); (2) as a trend of

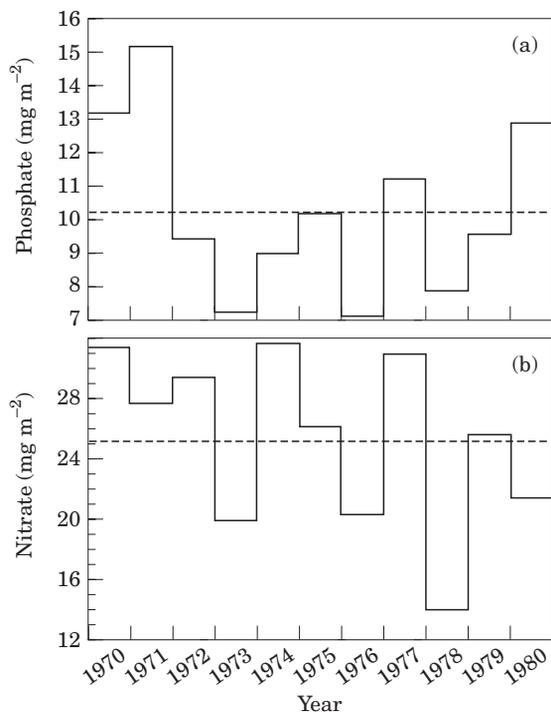


Figure 2. Mean annual water column concentrations of (a) nitrate and (b) phosphate at a long-term monitoring station in lower Narragansett Bay based on weekly measurements (1970–1980). Hatched lines represent the mean annual level.

decreasing nutrients following a period of increase (Honjo, 1992); (3) as altered nutrient ratios, and possibly a factor in the selection and blooms of harmful algal species (Smayda, 1990); and (4) a nutrient-“rich” year in terms of phosphorus or nitrogen levels can be followed by a nutrient-poor year. In Narragansett Bay, mean annual NO_3^- and PO_4^{3-} concentrations vary twofold, from year-to-year (Fig. 2).

Changes and variability within the chemical habitat, at least for macro-nutrients, are easily measured, but their multiple effects on phytoplankton variability and response are difficult to quantify. Among these, and least controversial, are yield-dose effects, e.g. the trend in which phytoplankton biomass increases with nutrient availability. The effect of nutrient variability and that of “water quality” on species’ selection is more complicated. At some point, or threshold, during a period of progressive increase, a differential and variable selection of bloom species will occur in response to the elevated nutrient levels and/or altered nutrient ratios (Riegman and Kuipers, 1994). Since this nutrient-based threshold of species’ switchovers is itself variable, and is also dependent upon grazing structure, the relationships between variable nutrient supply rates and phytoplankton variability are obscure. *In situ* nutrient concentrations are routinely used to assess statistically the

probability that they (or eutrophication) are regulating phytoplankton dynamics. However, the extent to which the statistically derived inferences of ecological consequences actually contribute to the observed variability in phytoplankton behaviour is often unresolved (Lindeboom *et al.*, 1995). This reflects a dual feature of the nutrient-phytoplankton relationship: variability of both is under multifactorial control. While nutrient availability influences nutrient uptake rates and sets the biomass carrying capacity, actual uptake follows Droop’s (1973) model of cell quota kinetics, i.e. as a response to internal cellular concentrations. Since cell quotas of natural populations are rarely measured, this further compromises analyses of the effects of variable nutrient levels and change on phytoplankton variability (see Smayda, 1997).

Unlike physical habitat parameters, the effects of chemical variability on phytoplankton dynamics and linked trophodynamic responses are poorly quantified. Suggested relationships between variability of the chemical habitat and phytoplankton responses, such as the much discussed effects of eutrophication, are primarily anecdotal. Available observations reveal that physical and chemical variability has random and non-random components, predictable and unpredictable features, and are driven both by external (i.e., meteorological, climatological) and internal (*in situ* processes) forcing events.

What is known about phytoplankton variability?

Persistent variation, change, and disruption in phytoplankton niche structure and biomass-carrying capacity result from the continuous variability of the physical and chemical habitat. Phytoplankton variability is thus commonplace and easily measured; but this has an enigmatic aspect. Despite the high degree of variability in the planktonic habitat, there is impressive, quasi-regular, predictable annual occurrences of major blooms, in seasonal cycles, of species’ succession, in nutrient cycles, in zooplankton pulses, etc. Auto-regulation (internal control) of phytoplankton community organization and blooms is thought to be relatively weak *vis-à-vis* that induced by external forcing (meteorology), unlike terrestrial plant communities (Margalef, 1978; Smayda, 1997). Phytoplankton communities appear to have little internal (biological) buffering capacity against physically or chemically induced changes in their dynamics. Yet, chaotic behaviour is less than expected (Ascoti *et al.*, 1993). This, taken together with the quasi-regular, annual cycles, suggests that the reiterative seasonal and annual chemical and planktonic patterns are under tight environmental regulation. A generally held view which appears to have developed

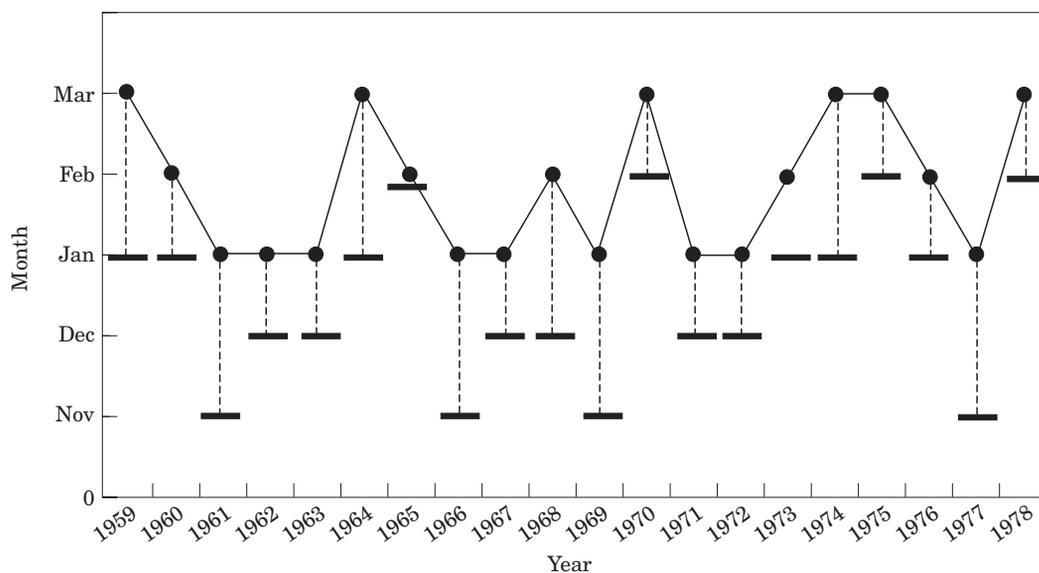


Figure 3. Annual variations in month of inception of the winter-spring bloom in Narragansett Bay (—) and subsequent month of bloom maximum (●).

from this enigma contends that the variances within time series are relatively insignificant variations around more or less constant seasonal and regional plankton responses and trophodynamic inputs. This may have deflected investigation away from time-series studies of plankton variability, and inquiry into how these cycles and patterns persist and are maintained within the variable planktonic habitat. There has been even less interest in carrying out studies of variability as a property of planktonic behaviour worthy of investigation in, and of, itself. Consequently, insights into plankton variability are basically synthetic, derived mostly from short-term investigations focusing on specific plankton processes, and supplemented by a limited number of qualitative and quantitative regional studies of variable duration.

Harris (1980) has suggested that phytoplankton rectify long-term climatic trends, such as during Russell Cycles, by “flip-flop” responses. I suggest that the variable response capabilities of planktonic communities act as restructuring mechanisms which allow the community and its foodweb linkages to modify dynamics to accommodate the changed(-ing) environmental conditions. Collectively, the limited number of time series, based primarily on qualitative net tows and statistical procedures using proxy variables, suggest phytoplankton variability: (1) is commonplace and easily detectable; (2) occurs in various patterns: as cycles, trends, fluctuations, unusual events, irregular pulses; (3) occurs at various scales: hourly or less, daily, seasonally, annually, decadal; even chaotically; (4) occurs at various frequencies; and (5) the entire community may respond (fluctuate) as a unit (Colebrook, 1977), as individual

species (Boalch, 1987), or in response to site-specific and regionally variable factors.

Variability in winter-spring bloom dynamics

The classical paradigm of the winter-spring bloom is that the population, initially light-limited, awaits partial stratification (critical depth achieved) to bloom, with its subsequent collapse a result of the progressive depletion of nutrients under increasing zooplankton grazing. The timing, trigger, and subsequent pattern of this bloom are commonly considered to be relatively stable from year-to-year. The Narragansett Bay observations refute this (Fig. 3). The time of inception, the duration, and the magnitude of this bloom show remarkably high inter-annual variability. Bloom inception has a 4-month window (November–February). Monthly inception (x) frequencies during 1959–1978 were: 4x November; 6x December; 6x January; 4x February. In contiguous Long Island Sound, the time of inception, magnitude, and duration of the spring bloom also varied significantly over six consecutive annual cycles (Riley, 1967). Nor is the time and magnitude of maximal bloom abundance fixed: it occurs as early as January (most frequently), but as late as April, and ranges (1959–1974) at least 10-fold, from 4500 cells ml^{-1} in 1970 to 42 000 cells ml^{-1} in 1963 (Smayda, 1976). Most extraordinarily, the annual maximum shifted seasonally from a winter-spring to a mid-August event in 7 of the 16 years between 1970 and 1985.

The factors controlling bloom inception also vary from year-to-year; this also contributes to inter-annual variability. Temperature and irradiance acting either

alone, or interactively, have been implicated as the primary bloom trigger in different years in Narragansett Bay (Smayda, 1973; Hitchcock and Smayda, 1977), as has removal of nutrient limitation (Pratt, 1965), and reduced zooplankton grazing pressure (Pratt, 1965; Martin, 1965, 1970). Temperature has a strong effect on development of *Acartia hudsonica* Pinhey, the dominant winter–spring copepod (Durbin *et al.*, 1992). This contributes to a subtle, but important and variable, inter-annual role of grazing in bloom regulation. A +1°C departure from mean winter temperatures would cause up to a 2-month difference in its maturation time. *Acartia hudsonica* hatchlings spawned in mid-November in a slightly warmer year would mature in late December, for example, but not until late February or early March in a slightly colder year.

Temperature not only influences bloom inception, but likewise contributes to inter-annual variability during the bloom period. Temperatures below 1°C were not recorded in 1975 in Narragansett Bay, persisted for 51 days in 1971 (14% of the year), and in 1967 during 10% of the year. During 1972–1975, temperatures exceeded 3°C during much of the period from December to March; the annual bloom maximum then shifted from a winter–spring to an August event. Temperature did not regulate the 1959–1963 winter–spring bloom dynamics, although blooms which began earlier reached a greater maximum and lasted longer (Pratt, 1965). Such plankton cycle attributes are sensitive to inter-annual variations in temperature (Riley, 1967). In contiguous Long Island Sound, during “cold” years the winter–spring bloom begins later and lasts longer than during “warm” years. Blooms then tend to occur earlier, are shorter, and reach greater magnitude (Riley, 1955). Blooms which started later and lasted longer provided “maximum benefit for the zooplankton population”. A different effect and expanded role of temperature, based on events in the Gulf of Maine, were proposed by Townsend and Cammen (1988): in “cold” winters, blooms occur earlier, are more productive, and deposit greater amounts of biomass to sediments than “warm”-winter blooms. These stimulate greater zooplankton grazing, reduced benthic fluxes and productivity. “Cold” winter blooms were hypothesized to favour pelagic-benthic coupling; “warm” winter blooms to favour phytoplankton–zooplankton coupling, with temperature-induced, inter-annual variations occurring in the strength of coupling.

The variable control of winter–spring bloom dynamics in Narragansett Bay, in which temperature, irradiance, or zooplankton grazing become the primary bloom regulator during different years, contradicts the classically held view of fixed, single-factor regulation. Plankton biologists relentlessly have sought to identify limiting factors in the sea, fixating on presumed single-factor regulation, such as Liebig’s Law of Minimal

Table 1. Typical patterns of phytoplankton variability, with example species.

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- Episodic bloom occurrences (*Asterionellopsis glacialis*)
 - Cyclical bloom abundance (*Thalassiosira nordenskiöldii*)
 - Seasonal shift in predominance (*Skeletonema costatum*)
 - Trend: decreasing abundance (*Detonula confervacea*)
 - Trend: disappearance (*Skeletonema costatum*)
 - Trend: increasing abundance (*Prorocentrum minimum*)
 - Stochastic bloom occurrences (many taxa)
 - Novel appearances, followed by:
 - a. persistence (*Coscinodiscus wailesii*)
 - b. perennial predominance (*Aureococcus anophagefferens*)
 - c. establishment as keystone species (*Phaeocystis pouchetii*)
 - d. regional spreading and persistence (*Gyrodinium aureolum*)
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Nutrients (de Baar, 1994). The scientific literature is filled with efforts to reconcile divergent regional findings on environmental control mechanisms, and within a given location, as though only one explanation applies, and particularly so when there are contradictions for the same system. This often leads to futile nullification arguments. However, the identification of different, primary bloom regulators from year-to-year, or regionally, may not only be correct. This is an expected consequence of temporal and habitat variability. Variability in bloom dynamics reflects variable, not fixed, single-factor regulation, and reflects inter-annual variations in the mechanisms controlling blooms and other responses.

Species-specific patterns

There is considerable variation in the bloom and occurrence patterns of individual species. At least 11 distinct patterns of variability are recognizable (Table 1). Episodic bloom occurrences of indigenous species that normally do not bloom, or show only modest seasonal increases, are common. Within Narragansett Bay, the diatom *Asterionellopsis glacialis* Castracane periodically exhibits such blooms. These periods, accompanied by other changes in the annual bloom cycle, have been termed “*Asterionellopsis*” years. Many of the species responsible for the apparent global increase in harmful algal blooms are of this type (Smayda, 1989, 1990). Other species exhibit cycles in bloom abundance, as found for the boreal diatom *Thalassiosira nordenskiöldii* Cleve, which exhibited peak abundances at 5-year intervals (Fig. 4). Seasonal shifts in predominance and trends of decreasing abundance also occur, as found for *Skeletonema costatum* and the Arctic–Boreal diatom, *Detonula confervacea* (Cleve) Gran, respectively (Figs 5, 6). Since *S. costatum* accounts for about 75% of the total annual mean numerical abundance in Narragansett Bay, this long-term trend is a major event. The 10-fold decrease in *D. confervacea* between 1959 and 1980 was

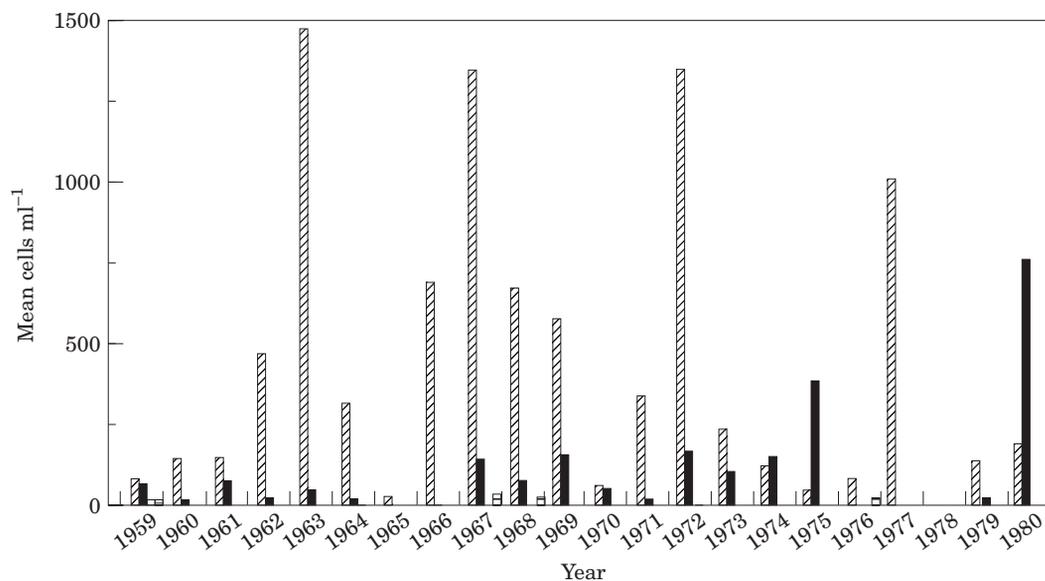


Figure 4. Annual variations in maximal winter-spring bloom abundance of *Thalassiosira nordenskiöldii* in Narragansett Bay based on weekly measurements. Histograms indicate the 4 quarters of the year: January-March (▨); April-June (■); July-September (□); October-December (▤).

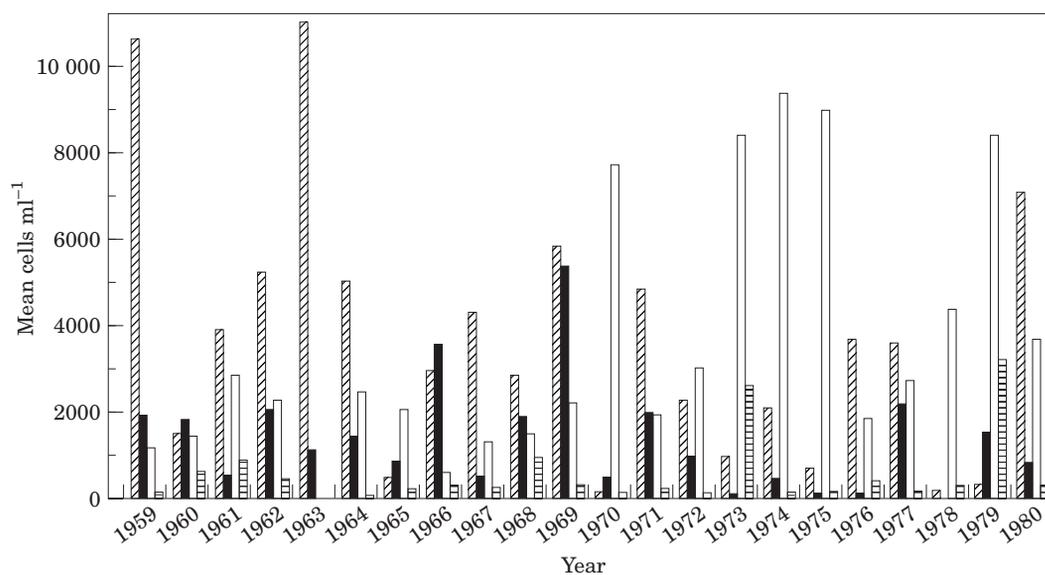


Figure 5. Maximal quarterly abundance of *Skeletonema costatum* in Narragansett Bay based on weekly measurements. Histograms indicate the 4 quarters of the year: January-March (▨); April-June (■); July-September (□); October-December (▤).

accompanied by a temperature increase, which suggests an *in situ* warming effect.

Trends of disappearance are also known, such as documented for *S. costatum* in the English Channel (Boalch, 1987). There are also trends of increasing abundance. In the Black Sea, maximal bloom abundance of the dinoflagellate *Prorocentrum minimum* (Pavillard) Schiller increased 1000-fold over a 30-year

period (Smayda, 1990). Stochastic bloom occurrences are particularly well documented, such as the exceptional frequency of such blooms recorded in recent decades in the North Sea and contiguous Scandinavian waters (Fig. 7). In the 27-year period since 1964, 28 taxa, many newly recorded, have exhibited novel, extraordinary occurrences or blooms (Smayda, 1989). These include (1) indigenous species (*Emiliania huxleyi*

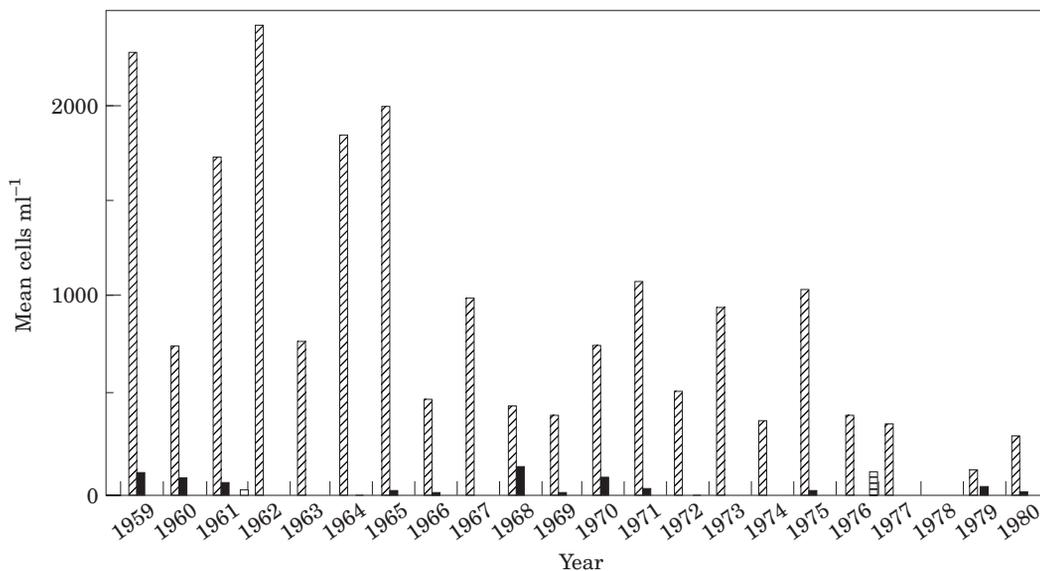


Figure 6. Long-term decline in mean winter-spring bloom abundance of *Detonula confervacea* in Narragansett Bay based on weekly measurements. Histograms indicate the 4 quarters of the year: January-March (▨); April-June (■); July-September (□); October-December (▩).

(Lohmann) Hay et Mohler; *Nodularia spumigena* Mertens ex Bornet et Flahaut) known to have bloomed prior to 1964; (2) species which have probably been introduced (*Coscinodiscus wailesii* Gran, *Thalassiosira punctigera* (Castracane) Hasle, *Gyrodinium aureolum* Hulburt); (3) species responding to eutrophication (*Phaeocystis pouchetii* (Hariot) Lagerheim); and (4) those identified because of improved taxonomy (*Corymbellus aureus* Green). Some novel diatom behaviour is possibly related to long-term climatic changes (Lange *et al.*, 1992). The unprecedented 1988 bloom of *Chrysochromulina polylepis* Manton et Parke in southern Scandinavian waters (Granéli *et al.*, 1993) has been followed by moderate blooms of four toxic prymnesiophytes at fish-farm sites in Norwegian coastal waters (Eikrem and Throndsen, 1993).

Novel appearances (? invasions) of immigrant species leading to their successful assembly within local communities and subsequent persistence, perennial predominance, establishment as keystone species, or regional spreading, with subsequent persistence, have been increasingly documented. *C. wailesii* has become a persistent member of the phytoplankton community in the English Channel, since its novel bloom in 1977 when its copious production of mucilage impaired fisheries (Boalch and Harbour 1977; Boalch, 1987). The previously unknown, harmful chrysophyte, *Aureococcus anophagefferens* Hargraves et Sieburth, is a spectacular example of a novel species achieving perennial predominance. Its blooms have become a perennial nuisance in Long Island embayments following its unprecedented and synchronous bloom along a ca. 500 km coastline

extending from Narragansett Bay to Barnegat Bay (Smayda and Villareal 1989; Bricelj and Lonsdale, 1997). A related species has exhibited similar behaviour in Laguna Madre, Texas (Stockwell *et al.*, 1993). A small (~10 µm) *Thalassiosira* spp. complex has become a major summer bloom cohort in Narragansett Bay where it has continuously increased in mean annual abundance since 1974 after being first detected in 1967 (Karentz and Smayda, 1984). *P. pouchetii*, with its increasingly prolonged and abundant blooms, has established itself as a keystone species in the Dutch Wadden Sea since the 1970s in apparent response to nutrification (Cadée, 1986; Cadée and Hegeman, 1986; Riegman *et al.*, 1992). [Note: although reference is to *P. pouchetii*, it has become evident that *P. globosa*, previously considered to be conspecific, is a separate species (Janhke and Baumann, 1987; Medlin *et al.*, 1994). It is uncertain which species is responsible for the blooms recorded.] The harmful dinoflagellate, *Gyrodinium aureolum*, has spread, persisted, and bloomed throughout the North Sea, since its first registered bloom off the southern Norwegian coast in 1966 (Braarud and Heimdal, 1970; Partensky and Sournia, 1986).

Whatever factors influence these different patterns, including recruitment from the "hidden flora" and ballast-water introductions of immigrant species, phytoplankton niche structure is clearly variable. The increase and global expansion in harmful algal blooms (Anderson, 1989; Hallegraeff, 1993; Smayda, 1989, 1990) suggests that phytoplankton niches are easily modified and increasingly being opened, expanded, and even being newly created. This significant niche

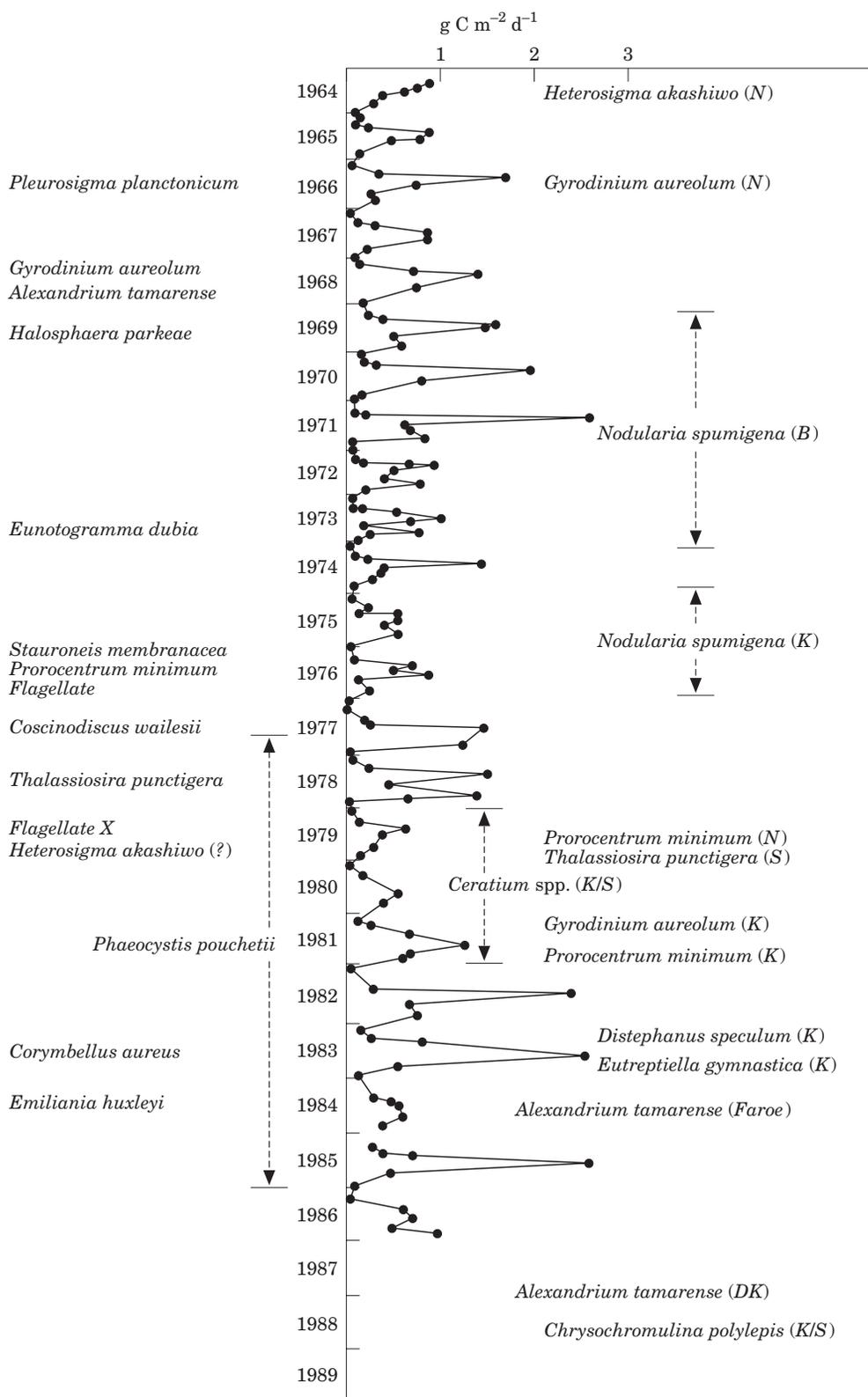


Figure 7. First occurrences and/or persistence of some novel, exceptional phytoplankton species' blooms during 1964–1988 in waters around the North Sea. (N: Norwegian coastal waters; D: Danish fjords; K: Kattegat; S: Skagerrak; B: Baltic Sea; F: Faroe (F); modified from Smayda, 1989).

disturbance may result from increasing cultural discharge of nutrients and chemical toxicants, i.e. “bottom-up” effects, modification of the food web through fisheries, i.e. “top-down” effects, or be due to natural, physical variance accompanying climatological change.

Variability as “events”

Variable responses are more than stochastic departures, or anomalous behaviour around a baseline. They also result from the variable interplay among the physical, chemical, and biological parameters which control phytoplankton succession, blooms, and community dynamics. Much of this variability is trivial and transitory, without major impact; some is more significant, and still other perturbations are symptomatic of major transitions. Variability in habitat properties and plankton responses therefore signals the status and trends of the interactive habitat–plankton relationship. The problem is to interpret these signals. One approach is to treat variability in habitat properties and plankton processes as “events”. An event may be good for some organisms, trophic compartments or processes, but bad for others; e.g. events can be “crises” or “beneficial”. Harmful algal blooms, for example, are more likely to be “crisis” events, or disrupt *in situ* processes, than diatom blooms.

Events have differing frequencies of occurrence and duration. A given event may be a single, isolated occurrence and, therefore, rare and even unique. An example is the novel, 1985 harmful “brown tide” of *A. anophagefferens*, which lasted 5 months in Narragansett Bay (Smayda and Villareal, 1989), never having been recorded previously, nor since. Alternatively, a given type of physical, chemical, or biological event can be common, and even recur with high frequency. Examples include: the annual spring (upwelling) diatom blooms, species’ successions, wind-induced mixing, nutrient cycles, etc. Whether rare or common, events which are embedded within long-term trends or cycles (Figs 1, 4) are probably driven by factor interactions which differ from those responsible for the basic trend or cycle.

Induced and reflected events

Although events are dissimilar and their causes and impacts vary, they generally fall into one of two major types: the observed variability is either an induced or a reflected event (Raup, 1981). Since at any given time all niche properties are in a variable state subject to continuous modification, induced and reflected events can occur concurrently. Induced events generally are responses to abiotic (i.e. physical, chemical) factors, often as the result of linear processes. They may represent either a modest transitory stage, or signal that a more fundamental change is occurring. An example

of the latter is the takeover of the phytoplankton community in the Dutch Wadden Sea by *P. pouchetii*, apparently in response to increased anthropogenic phosphorus levels (Riegman *et al.*, 1992). Red tide outbreaks which frequently follow excessive rainfall and run-off are well documented. These irregular blooms are also induced events; but their modification of ecosystem bloom dynamics is usually temporary. In marked contrast, variability occurring as a reflected event may be signalling that a fundamental change in the ecosystem is either in progress or has occurred. Analyses of reflected events are very difficult. They are often the outcome of a complex series of non-linear processes accompanied by parallel trends in several physical, chemical, and trophic properties. Reflected events can result when an induced event (i.e. abiotic induction of a biotic change) leads to cascading biotic changes. For example, the inverse relationship noted by Dickson *et al.* (1988) between westerly winds and phytoplankton abundance leading to a long-term decline in zooplankton illustrates an upper level biotic change reflective of an abiotic/biotic interaction. Reflected events may also result from biotic/biotic interactions, and include effects of over-fishing. Examples of interactions among phytoplankton, zooplankton, macrofauna, fishes, and birds symptomatic of reflected events and fundamental changes in the ecosystem are provided by Aebischer *et al.* (1990) and Lindeboom *et al.* (1995).

Point and threshold events

Whether induced or reflected, variable events are more than responses and departures from baseline dynamics, they are also “turning points”, either transitory or prolonged, which temporarily or permanently influence subsequent variability and dynamics. When viewed as turning points, the various episodes of variability can serve as quasi-ecological indicators of ecosystem condition. There are two types of turning points: point events and threshold events (Raup, 1981).

Point events tend to be stochastic, unpredictable variations of variable duration. They are not part of the regular cycle (i.e. seasonal, annual, etc.), and their consequences are temporary. Much of the day-to-day variability encountered in the plankton habitat and in planktonic behaviour is of this “chance” type, and often occurring in response to physical disruptions of the habitat. Point events do not abort diel, seasonal, annual, and inter-annual cycles and trends, but they may influence the rates and processes typical of these patterns.

Threshold events, in contrast, typically are deterministic and often unique (i.e. non-recurrent). They signal that a fundamental, permanent change has occurred in habitat, plankton structure, dynamics and/or trophic processes; for instance, as a result of the progressive

increase in nutrient loading up to a critical level (threshold). The persistent blooms of *P. pouchetii* and its takeover as a keystone species in the Dutch Wadden Sea, while initially a reflected event, apparently have evolved into a threshold event in response to continued eutrophication.

Monitoring

The ability to identify whether the observed variability is induced, reflected, or a point or threshold event, and whether it is significant is influenced by the sampling protocol. The duration and classification of an event, for example, are relative to the time-period under consideration. Weatherhead (1986) examined the question of how unusual are unusual events? based on a review of 380 time series (mostly terrestrial), which lasted from 1 to 15 years. Unusual was defined as an event that had a 5% probability of occurring by chance in a given year. Two contradictory, unresolved viewpoints resulted. One view holds that short-term studies are more likely to miss infrequent, random, and unusual events, and lead to erroneous conclusions. The opposing view is that short-term time series record too many events as unusual. Thus, sampling frequency influences the ability to discern the type of variability event observed, as does the duration over which measurements are made. The spatial scale of the analyses also appears to be a factor. Short-term variations generally appear to occur on small spatial scales, whereas long-lived fluctuations tend to be spatially extensive. These space-time relationships indicate the need to consider both site-specific and regional factors as determinants of the interactive habitat-plankton variability.

The level of insight expected from a monitoring programme, e.g. observational, quantitative, or predictive awareness, obviously influences its design (Smayda, 1995). Monitoring, as usually carried out, can warn of, or document changes, but can indicate neither their causes nor the actual importance of the physical, chemical, and biological processes contributing to the observed variability. Almost all time series are descriptive, with statistical correlations frequently based on proxy variables (invariably temperature) which exhibit parallel trends with the unknown factor(s) actually regulating plankton behaviour. The traditional monitoring strategy is clearly inadequate in dealing with habitat-plankton variability. Habitat-plankton variability occurs as a set of events of different types and impacts subject to short- and long-term temporal scales, and to on-site and far-field spatial effects. Its properties of scale, multiple varieties, differing periods, amplitudes, response times, and biological interactions make it difficult to quantify the causes and effects of plankton variability based on static measurements. This makes

derived predictions problematical. Temporal variations in bloom cycles and related dynamics are persistent, intrinsic characteristics around which energy-flow and foodweb dynamics are structured. Since variability impacts many core issues within biological oceanography, conceptual and methodological approaches to plankton variability must be placed within an oceanographic context, i.e. trophodynamically, rather than focused upon as expressions of local, site-specific variability. A combination of observational and process-oriented, *in situ* rate measurements is needed to establish cause and effects. The descriptive examples of the regional and site-specific patterns of habitat and plankton variability presented in this volume (Colijn *et al.*, 1998) should facilitate the much needed research to quantify habitat-plankton variability. The need to carry out quantitative long-term observations is essential if we are to model global change, to hindcast its causes, to forecast its consequences, to quantify the patterns of variability, its trends and cycles, and to sort out the natural, inherent variability of the plankton and their habitat from that induced by anthropogenic modification.

References

- Aebischer, N. J., Coulson, J. C., and Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature*, 347: 753–755.
- Anderson, D. M. 1989. Toxic algal blooms: a global perspective. *In* Red tides: biology, environmental science and toxicology, pp. 11–16. Ed. by T. Okaichi, D. Anderson, and T. Nemoto. Elsevier, Amsterdam. 489 pp.
- Ascioti, F., Beltrami, E., Carroll, T. O., and Creighton, W. 1993. Is there chaos in plankton dynamics? *Journal of Plankton Research*, 15: 603–617.
- Baar, H. J. W. de 1994. von Liebig's Law of the Minimum and plankton ecology (1899–1991). *Progress in Oceanography*, 33: 347–386.
- Boalch, G. T. 1987. Changes in the phytoplankton of the western English Channel in recent years. *British Phycology Journal*, 22: 225–235.
- Boalch, G. T., and Harbour, D. S. 1977. Unusual diatom off the coast of south-west England and its effect on fishing. *Nature*, 269: 687–688.
- Borkman, D. G., and Smayda, T. J. 1998. Long-term trends (1972–1996) in water clarity revealed by Secchi disk measurements in lower Narragansett Bay, Rhode Island, USA. *ICES Journal of Marine Science*, 55 (this volume).
- Braarud, T., and Heimdal, B. R. 1970. Brown water on the Norwegian coast in autumn 1966. *Nytt Magasin for Botanik*, 17: 91–97.
- Bricelj, M., and Lonsdale, D. 1997. *Aureococcus anophagefferens*: causes and ecological consequences of brown tides in U.S. mid-Atlantic coastal waters. *Limnology and Oceanography*, 42: 1023–1038.
- Cadée, G. C. 1986. Recurrent and changing patterns in phytoplankton of the westernmost inlet of the Dutch Wadden Sea from 1969–1980. *Marine Biology*, 93: 281–289.

- Cadée, G. C., and Hegeman, J. 1986. Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophyceae) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. *Netherlands Journal of Sea Research*, 20: 29–36.
- Colebrook, J. M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955–59. *Fishery Bulletin, United States*, 75: 357–368.
- Colebrook, J. M. 1979. Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Marine Biology*, 51: 23–32.
- Colebrook, J. M. 1986. Environmental influences on long-term variability in marine plankton. *Hydrobiologia*, 142: 309–325.
- Colijn, F., Tillmann, U., and Smayda, T. J. (Eds.). 1998. The temporal variability of plankton and their physico-chemical environment. *ICES Journal of Marine Science*, 55 (this volume).
- Currie, R. 1984. Evidence for 18.6-year lunar nodal drought in western North America during the past millennium. *Journal of Geophysical Research*, 89: 1295–1308.
- Cushing, D. H. 1978. Biological effects of climatic change. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 173: 107–116.
- Cushing, D. H. 1982. *Climate and fisheries*. Academic Press, New York. 373 pp.
- Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., and Cushing, D. H. 1988. North winds and production in the eastern North Atlantic. *Journal of Plankton Research*, 10: 151–169.
- Droop, M. R. 1973. Some thoughts on nutrient limitation in algae. *Journal of Phycology*, 9: 264–272.
- Durbin, E. G., Durbin, A. G., and Campbell, R. G. 1992. Body size and changes in egg production in the marine copepod *Acartia hudsonica* during a winter–spring bloom in Narragansett Bay. *Limnology and Oceanography* 37: 342–360.
- Eikrem, W., and Thronsen, J. 1993. Toxic prymnesiophytes identified from Norwegian coastal waters. In *Toxic phytoplankton blooms in the sea*, pp. 687–692. Ed. by T. J. Smayda and Y. Shimizu. Elsevier, Amsterdam. 952 pp.
- Gieskes, W. W. C., and Kraay, G. W. 1977. Continuous plankton records: changes in the plankton of the North Sea and its eutrophic southern bight from 1948 to 1975. *Netherlands Journal of Sea Research*, 11: 334–364.
- Granéli, E., Paasche, E., and Maestrini, S. Y. 1993. Three years after the *Chrysochromulina polylepsis* bloom in Scandinavian waters in 1988: some conclusions of recent research monitoring. In *Toxic phytoplankton blooms in the sea*, pp. 23–32. Ed. by T. J. Smayda and Y. Shimizu. Elsevier, Amsterdam. 952 pp.
- Gray, J. S., and Christie, H. 1983. Predicting long-term changes in marine benthic communities. *Marine Ecology Progress Series*, 13: 87–94.
- Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia*, 32: 79–99.
- Harris, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models and management. *Canadian Journal of Fisheries and Aquatic Science*, 37: 877–890.
- Hickel, W., Mangelsdorf, P., and Berg, J. 1993. The human impact in the German Bight: eutrophication during three decades (1962–1991). *Helgoländer Meeresuntersuchungen*, 47: 243–263.
- Hitchcock, G. L., and Smayda, T. J. 1977. The importance of light in the initiation of the 1972–1973 winter–spring bloom in Narragansett Bay. *Limnology and Oceanography*, 22: 126–131.
- Honjo, T. 1992. Harmful red tides of *Heterosigma akashiwo*. NOAA Technical Report, National Marine Fishery Service, 111: 27–32.
- Horne, E. P. W., and Platt, T. 1984. The dominant space and time scales of variability in the physical and biological fields on continental shelves. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 183: 8–19.
- Jahnke, J., and Baumann, M. E. M. 1987. Differentiation between *Phaeocystis pouchetii* (Har.) Lagerheim and *Phaeocystis globosa* Scherffel. I. Colony shapes and temperature tolerances. *Hydrobiological Bulletin*, 21: 141–147.
- Johnstone, J. A., Scott, A., and Chadwick, H. C. 1928. *The marine plankton*. University Press, Liverpool. 194 pp.
- Joint, I., Jordan, M. B., and Carr, M. R. 1997. Is phosphate part of the Russell cycle? *Journal of the Marine Biological Association of the United Kingdom*, 77: 625–633.
- Karentz, D., and Smayda, T. J. 1984. Temperature and the seasonal occurrence pattern of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period (1959–1980). *Marine Ecology Progress Series*, 18: 277–293.
- Karentz, D., and Smayda, T. J. 1998. Temporal patterns and variations in phytoplankton community organization and abundance in Narragansett Bay during 1959–1980. *Journal of Plankton Research*, 20: 145–168.
- Lange, C., Hasle, G. R., and Syvertsen, E. 1992. Seasonal cycle of diatoms in the Skagerrak, North Atlantic, with emphasis on the period 1980–1990. *Sarsia*, 77: 173–187.
- Li, Y., and Smayda, T. J. 1998. Temporal variability of chlorophyll in Narragansett Bay, 1973–1990. *ICES Journal of Marine Science*, 55 (this volume).
- Lindeboom, H. J., van Raaphorst, W., Beukema, J. J., Cadée, G. C., and Swennen, C. 1995. (Sudden) changes in the North Sea and Wadden Sea: oceanic influences underestimated? *Scientific Symposium on the 1993 North Sea Quality Status Report*, pp. 79–85.
- Maddock, L., Harbour, D. S., and Boalch, G. T. 1989. Seasonal and year-to-year changes in the phytoplankton from the Plymouth area, 1963–1986. *Journal of the Marine Biological Association of the United Kingdom*, 69: 229–244.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, 1: 493–509.
- Martin, J. H. 1965. Phytoplankton–zooplankton relationships in Narragansett Bay. *Limnology and Oceanography*, 10: 185–191.
- Martin, J. H. 1970. Phytoplankton–zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. *Limnology and Oceanography*, 15: 413–418.
- Medlin, L. K., Lange, M., and Baumann, M. E. M. 1994. Genetic differentiation among three colony-forming species of *Phaeocystis*: further evidence for the phylogeny of the Prymnesiophyta. *Phycologia*, 33: 199–212.
- Partensky, F., and Sournia, A. 1986. Le dinoflagellé *Gyrodinium* cf. *aureolum* dans le plancton de l'Atlantique nord: identification, écologie, toxicité. *Cryptogamie Algologie*, 7: 251–276.
- Pratt, D. M. 1965. The winter–spring flowering in Narragansett Bay. *Limnology and Oceanography*, 10: 173–184.
- Raup, D. M. 1981. Introduction: What is a crisis? In *Biotic crises in ecological and evolutionary time*, pp. 1–12. Ed. by M. H. Nitecki. Academic Press, New York. 293 pp.
- Reid, P. C., Robinson, G. A., and Hunt, H. G. 1987. Spatial and temporal patterns of marine blooms in the northeastern Atlantic and North Sea from the Continuous Plankton Recorder survey. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 187: 27–37.

- Reynolds, C. S. 1990. Temporal scales of variability in pelagic environments and the response of phytoplankton. *Freshwater Biology*, 23: 25–53.
- Riegman, R., and Kuipers, B. R. 1994. Resource competition and selective grazing of plankton in a multispecies pelagic food web mode. *P.S.Z.N.I. Marine Ecology*, 15: 153–164.
- Riegman, R., Noordeloos, A. A. M., and Cadée, G. 1992. *Phaeocystis* blooms and eutrophication of the continental coastal zones of the North Sea. *Marine Biology*, 112: 479–484.
- Riley, G. A. 1955. Review of the oceanography of Long Island Sound. *Deep-Sea Research*, 3 (Suppl.): 224–238.
- Riley, G. A. 1967. The plankton of estuaries. *In Estuaries*, pp. 316–326. Ed. by G. H. Lauff. AAAS Publ. 83, Washington, D.C., 757 pp.
- Russell, F. S., Southward, A. J., Boalch, G. T., and Butler, E. I. 1971. Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature*, 234: 468–470.
- Smayda, T. J. 1973. The growth of *Skeletonema costatum* during a winter–spring bloom in Narragansett Bay. *Norwegian Journal of Botany*, 20: 219–247.
- Smayda, T. J. 1976. Plankton processes in mid-Atlantic near-shore and shelf waters and energy-related activities. *In Effects of energy-related activities on the Atlantic Continental Shelf*, pp. 70–94. Ed. by B. Manowitz. Proc. Conf. Brookhaven National Laboratory, BNL. 260 pp.
- Smayda, T. J. 1984. Variations and long-term changes in Narragansett Bay, a phytoplankton-based coastal marine ecosystem: relevance to field monitoring for pollution assessment. *In Concepts in marine pollution measurements*, pp. 663–679. Ed. by H. White. University of Maryland, College Park, Maryland. 743 pp.
- Smayda, T. J. 1989. Primary production and the global epidemic of phytoplankton blooms in the sea: a linkage? *In Novel phytoplankton blooms*, pp. 449–483. Ed. by E. M. Coper, V. M. Bricelj, and E. J. Carpenter. Springer Verlag, Berlin. 799 pp.
- Smayda, T. J. 1990. Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. *In Toxic marine phytoplankton*, pp. 29–40. Ed. by E. Granéli, B. Sundström, L. Edler, and D. M. Anderson. Elsevier, Amsterdam. 554 pp.
- Smayda, T. J. 1995. Environmental monitoring. *In Manual on harmful marine microalgae*, pp. 405–431. Ed. by G. M. Hallegraeff, D. M. Anderson, and A. D. Cembella. IOC Manuals and Guides, No. 33, UNESCO. 551 pp.
- Smayda, T. J. 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography*, 42: 1137–1153.
- Smayda, T. J., and Villareal, T. 1989. The 1985 “brown tide” and the open phytoplankton niche in Narragansett Bay during summer. *In Novel phytoplankton blooms*, pp. 159–187. Ed. by E. M. Coper, V. M. Bricelj, and E. J. Carpenter. Springer Verlag, Berlin. 799 pp.
- Stockwell, D. S. A., Buskey, E. J., and Whitley, T. E. 1993. Studies on conditions conducive to the development and maintenance of a persistent “brown tide” in Laguna Madre, Texas. *In Toxic phytoplankton blooms in the sea*, pp. 693–698. Ed. by T. J. Smayda and Y. Shimizu. Elsevier, Amsterdam. 952 pp.
- Townsend, D. W., and Cammen, L. M. 1988. Potential importance of the timing of spring plankton blooms to benthic–pelagic coupling and recruitment of juvenile demersal fishes. *Biological Oceanography*, 5: 215–229.
- Weatherhead, P. J. 1986. How unusual are unusual events? *American Naturalist*, 128: 150–154.

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