



## Causes and consequences of variability in the timing of spring phytoplankton blooms

DAVID W. TOWNSEND,\* LEON M. CAMMEN,† PATRICK M. HOLLIGAN,‡  
DANIEL E. CAMPBELL§ and NEAL R. PETTIGREW\*

(Received 12 April 1993; in revised form 30 August 1993; accepted 28 September 1993)

**Abstract**—Established conceptual models of the initiation and progression of spring phytoplankton blooms are reconsidered in light of recent observations. We use biological simulation modelling as a tool for the analysis of spring plankton blooms in shallow, coastal waters in temperate latitudes of the North Atlantic. The model shows that interannual variability in the timing of bloom initiation arises from year-to-year differences in incident irradiation, as determined by weather (cloudiness). This variability in timing results in some years when the spring bloom occurs in cold water temperatures near 0°C. Model results suggest that due to low temperature inhibition of heterotrophic consumption, more fresh organic material is delivered to the benthos in these cold-water blooms than when the bloom occurs in waters only 3°C warmer. Thus we suggest that variable bloom timing can be important to the trophodynamic fate of bloom products.

We suggest that variability in timing of spring phytoplankton blooms in offshore and open ocean waters is also related to weather, through controls on the light field and wind mixing. Our analyses of wind-driven vertical mixing demonstrate such blooms can begin following the winter period of deep convection, and prior to the vernal development of stratification, provided that wind speed is below a certain, predictable threshold, which we estimate. In such cases, there may be several spring bloom pulses, each interrupted by self-shading light limitation or vertical mixing events. Eventually the seasonal thermocline develops and nutrient exhaustion curtails bloom production. This means that the spring phytoplankton bloom in offshore and open ocean areas may be significantly more productive, result in more export production, and be more important to the carbon cycle, than has been previously assumed. Furthermore, these features of temperate marine planktonic ecosystems are not only sensitive to annual variations in weather, but also any trends that might result from greenhouse warming or other factors that affect the climate system.

### INTRODUCTION

THE spring phytoplankton bloom is important to the economy of the oceans, with respect to trophodynamics and fisheries, and to global biogeochemical cycles. Much of the overall productivity at higher trophic levels in temperate latitude oceans is dependent on the relatively short period of time associated with the spring plankton bloom. The bloom can

---

\*Department of Oceanography and Center for Marine Studies, University of Maine, Orono, ME 04469, U.S.A.

†National Sea Grant College Program, NOAA, 1335 East-West Highway, Silver Spring, MD 20910, U.S.A.

‡Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, U.K.

§University of Rhode Island, Graduate School of Oceanography, Narragansett, RI 02882, U.S.A.

amount to one-third of the annual phytoplankton production in some areas, and may represent more than half the total annual input of organic matter to the benthos (PARSONS *et al.*, 1984; SMETACEK *et al.*, 1978; SMETACEK, 1980; PEINERT *et al.*, 1982; FORSSKÄHL *et al.*, 1982). In addition to its trophodynamic significance, there has been a growing appreciation for the significance of the spring bloom to the global carbon cycle (BREWER, 1986; BERGER and WEFER, 1990; BERGER *et al.*, 1989; WATSON *et al.*, 1991; DUCKLOW and HARRIS, 1993). However, the timing of onset of the spring bloom, its subsequent duration, and the magnitude and fate of organic production during the bloom, are not well understood.

We present here the results of biological simulation modelling, and scale analyses of wind-driven vertical water column mixing under conditions of neutral stability, to examine the environmental factors that can lead to year-to-year variations in the timing and productivity of the spring phytoplankton bloom. We go on to assess the possible ecological and biogeochemical outcomes of such variations. We focus our attention on two types of hydrographic situations in temperate latitudes: (1) shallow, cold, well-mixed waters for which the temperature at the time of the spring phytoplankton bloom varies significantly, and (2) oceanic, temperate latitude waters in which intermittent mixing events during the spring can exert considerable influence on annual primary productivity.

In both cases, the timing of initiation of the bloom is variable from year to year. In the case of spring phytoplankton blooms in inshore coastal waters we show that that variability is tied to incident light as determined by weather (cloudiness). Our model predicts that consumption of the coastal bloom material by planktonic heterotrophs is much reduced in years when the bloom occurs in waters near 0°C vs years when the bloom occurs in waters only 3°C warmer. In the case of spring blooms in offshore and open ocean waters, we dispel the pervasive notion that a deep mixed layer implies that phytoplankton are continually being mixed to great (light-limiting) depths, and we show that in the absence of active convection, downward dispersal of phytoplankton through a deep, neutrally stable (unstratified) surface layer will be determined by wind and wave mixing. Thus we find that the spring bloom can begin following the winter period of convective mixing, and prior to the vernal development of vertical water column stability, provided that wind speeds are below a certain, predictable threshold, which we estimate. In such cases, offshore phytoplankton bloom production may not exhaust the supply of nutrients prior to the development of the seasonal thermocline. Rather, there may be several spring bloom pulses, each interrupted by self-shading light limitation or vertical mixing events. Eventually the seasonal thermocline develops and nutrient exhaustion curtails bloom production. This possibility of a succession of episodic blooms means that the spring bloom in offshore and open ocean areas may be significantly more productive, result in more export production, and be more important to the carbon cycle than has been previously assumed.

## BLOOMS IN INSHORE WATERS

### *Bloom timing*

Factors contributing to the onset of the spring phytoplankton bloom have been recognized in a descriptive sense for decades (ATKINS, 1928; GRAN and BRAARUD, 1935), and were quantified by SVERDRUP (1953). The year-to-year variability of the timing of onset of the bloom is also well established (e.g. BIGELOW *et al.*, 1940), and more recently, the

possible significance of this variability has been discussed with respect to benthic productivity (e.g. TOWNSEND and CAMMEN, 1988). In short, the initiation and evolution of the spring phytoplankton bloom is determined by a combination of events that reflect the balance between the amount of solar radiation received by a phytoplankton population, the availability of dissolved inorganic nutrients, and phytoplankton biomass losses associated with respiration, grazing and sedimentation (SMETACEK and PASSOW, 1990; PLATT *et al.*, 1991).

In shallow inshore areas of the temperate Northwest Atlantic, the spring phytoplankton bloom can begin anytime from late winter to early spring (BIGELOW *et al.*, 1940; HITCHCOCK and SMAYDA, 1977; CURA, 1981; SMETACEK and PASSOW, 1990; TOWNSEND and SPINRAD, 1986). The principal factor triggering the onset of these early blooms is the increasing solar radiation, which is modulated by cloud cover. Decreases in the water turbidity and increases in vertical water column stabilization related to river input of fresh water, for example from a winter thaw, can also be important (e.g. PINGREE *et al.*, 1986; TOWNSEND and SPINRAD, 1986). Concentrations of inorganic nutrients are generally high at this time of year. RILEY (1957, 1967) suggested that the critical light intensity triggering the bloom was reached when the depth averaged, vertically integrated irradiance within the mixed layer increased to *ca* 40 Ly day<sup>-1</sup> (20.9 W m<sup>-2</sup>). This empirically determined light value, as a practical indicator of the critical depth, has been corroborated by a number of subsequent reports (BARLOW, 1958; GIESKES and KRAAY, 1975; PINGREE *et al.*, 1976; HITCHCOCK and SMAYDA, 1977; CURA, 1981; HORN and PAUL, 1984; TOWNSEND and SPINRAD, 1986). Although the depth of the upper mixed layer is often defined by the depth of the seasonal thermocline, which isolates phytoplankton in the well-illuminated surface layers, in inshore areas it can be determined solely by bottom depth, thus leading to blooms in vertically isothermal and isopycnal waters (e.g. HITCHCOCK and SMAYDA, 1977).

Because of year-to-year variability in cloud cover, there will be some years (with more cloud-free days) when sufficient light for a spring bloom occurs prior to vernal warming. Therefore, water temperatures at the time of the spring bloom can be very cold (about 0°C) and, as we will show, this can retard significantly the metabolic rates of consumers of the plant material. It has been hypothesized earlier that variability in benthic-pelagic coupling and subsequent recruitment of demersal fishes might result from this interplay between variable timing of the spring phytoplankton bloom and ambient water temperatures (TOWNSEND and CAMMEN, 1988). Specifically, hindcasts predicted that the onset of the spring bloom in coastal waters of the Gulf of Maine varied by about 6 weeks over a 16-year period from 1971 to 1986, and that water temperatures at the time of the bloom varied from *ca* -1 to 5°C (TOWNSEND and CAMMEN, 1988; and unpublished data). An example of such an inshore bloom in cold waters is given in Fig. 1, which shows phytoplankton chlorophyll concentrations >5 µg L<sup>-1</sup> in Linekin Bay on the Maine coast (*ca* 44°N) in waters only slightly above 0°C.

### *Simulation modelling of coastal blooms and the effects of water temperature*

In order to critically evaluate the effects of cold water temperatures on the fate of phytoplankton production during early blooms, we developed a numerical simulation model that describes the inter-relationship between variable environmental factors and the pelagic ecosystem. Basically, the model includes processes in the water column and calculates a flux of material that sediments to the benthos. We assumed there was no

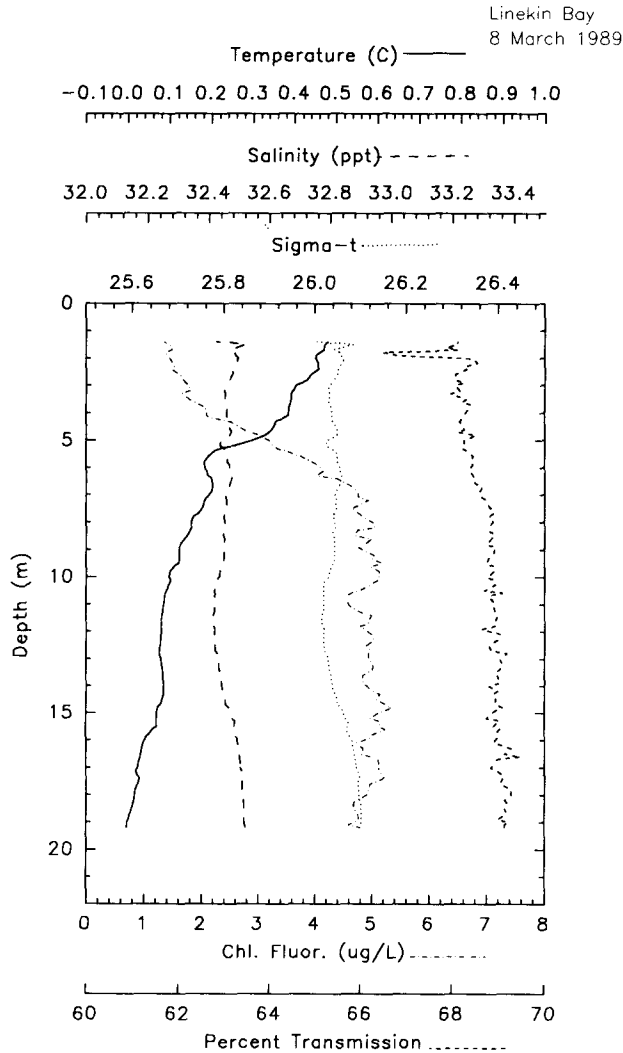


Fig. 1. Linekin Bay, Maine, 8 March 1989, as an example of a winter-spring phytoplankton bloom proceeding at temperatures  $0.4^{\circ}\text{C}$  in shallow unstratified waters. Plotted are continuous profiles of temperature, salinity, density ( $\sigma_t$ ), *in situ* chlorophyll fluorescence and percent light transmission, collected with a Neil Brown Smart CTD with a Sea Tech *in situ* fluorometer and transmissometer.

benthic regeneration of nitrogen to the water column. Inputs to the model are 16 years of water temperature and solar insolation data measured near Boothbay Harbor, Maine. The model is described in Tables 1 and 2 and Fig. 2.

The model assumes an unstratified water column with a depth of 50 m. Sunlight  $J_1$ , surface water temperature,  $T$ , and a source of inorganic nitrogen,  $J_N$ , are the external forcing functions that control the pelagic ecosystem. Nitrogen flux,  $J_N$ , enters the water column as the result of mixing during the first 120 days of the year. This flux was set so that

Table 1. Definitions of the coastal spring bloom simulation model forcing functions, storages, constants, and coefficients for pathway flows on 1 January for the coastal waters of the Gulf of Maine

Symbol	Definition
<i>Forcing functions</i>	
$J_I$	Daily solar insolation
$J_R$	Daily solar radiation available to phytoplankton
$J_N$	Daily input of nitrogen
$T$	Water temperature
$AN$	Ratio of phytoplankton gross production to phytoplankton biomass
<i>Storages</i>	
$N$	Inorganic nitrogen
$P$	Phytoplankton
$Z$	Zooplankton
<i>Constants</i>	
$a$	Arrhenius coefficient for phytoplankton and zooplankton growth and respiration (0.07)
$A_{chl}$	Specific attenuation of phytoplankton [ $0.02 \text{ m}^{-1} (\text{mg chl } a \text{ m}^{-3})^{-1}$ ]
$A_w$	Specific attenuation of water, inorganic and organic particles
$S_{max}$	Maximum settling rate of phytoplankton cells ( $5.0 \text{ m day}^{-1}$ ) - 0.5
$S_{min}$	Minimum settling rate of phytoplankton cells ( $0.5 \text{ m day}^{-1}$ )
$SR$	Scaling factor for settling rate of phytoplankton cells (13)
$T_z$	Temperature of zooplankton $Q_{10}$ switch ( $3^\circ\text{C}$ )
<i>Scaling coefficients for pathway flows on 1 January</i>	
$k_{chl}$	Light absorbed by phytoplankton
$k_w$	Light attenuated by other than phytoplankton
$k_1$	Phytoplankton gross production
$k_2$	Phytoplankton settling
$k_3$	Phytoplankton respiration
$k_4$	Zooplankton grazing
$k_6$	The effect of feeding rate on assimilation
$k_7$	Zooplankton assimilation
$k_8$	Zooplankton passive respiration
$k_9$	Zooplankton active respiration
$k_{10}$	Predation on zooplankton
$k_{11}$	Phytoplankton $N$ leakage
$k_{12}$	Zooplankton active remineralization
$k_{13}$	Zooplankton passive remineralization
$k_{14}$	Phytoplankton $N$ uptake

Table 2. The equations describing the coastal spring bloom simulation model

$$J_R = J_I/[1 + k_{chl}PN \exp(aT) + k_w \exp(A_{chl}P + A_w)]$$

$$AN = k_1NJ_R \exp(aT)$$

$$dP/dt = k_1PNJ_R \exp(aT) - k_2P[S_{max} \exp(-SRAN) + S_{min}] - k_3P \exp(aT) - k_4PZ \exp(aT_z)$$

$$dZ/dt = (k_7 - k_9)(PZ \exp(aT_z)\{1 - k_6[k_4PZ \exp(aT_z)/Z]\}) - k_8 \exp(aT_z)Z - k_{10}Z$$

$$dN/dt = k_{11}P \exp(bT) + k_{12}Z \exp(dT_z) + k_{13}PZ \exp(cT_z)\{1 - k_6[k_4PZ \exp(cT_z)/Z]\} - k_{14}PNJ_R \exp(aT)$$

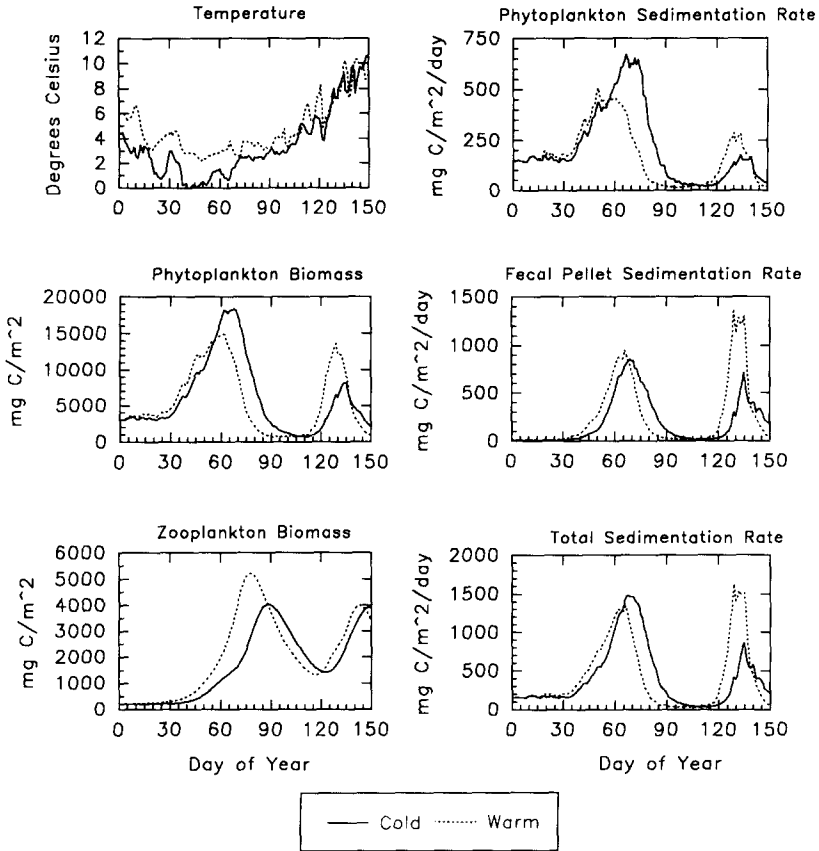


Fig. 2. Spring bloom simulation model output, using light data received at Boothbay Harbor for the year 1974, and temperature data for 1974 (a warm year) and 1978 (a cold year). The equations used in the model are given in Table 2. The model demonstrates different "export" of phytoplankton carbon in "cold" vs "warm" water spring blooms in shallow inshore waters of the Gulf of Maine. The double phytoplankton and zooplankton peaks result from the collapse of the first phytoplankton pulse due to light limitation by self-shading; this was followed by a subsequent recovery and a second peak.

nitrogen concentration in the water would remain undiminished over the first 60 days of the year to enable the model to conform to field observations. The water column contains storages of phytoplankton,  $P$ , zooplankton,  $Z$ , and nitrogen,  $N$ . Both catabolic and anabolic processes of phytoplankton and zooplankton are mediated by water temperature,  $T$ .

Phytoplankton production is driven by the external environmental variables, sunlight and water temperature. The phytoplankton temperature response is modelled by an Arrhenius function with a  $Q_{10}$  of 2 between 0 and 10°C. In addition, grazing pressure, phytoplankton biomass, and nitrogen supply act to modify primary production within the model. Phytoplankton biomass also affects production through self-shading which decreases the light available for photosynthesis,  $J_R$ . Self-shading is included in the model by making light attenuation a function of phytoplankton biomass.

Zooplankton feed on phytoplankton and produce fast settling fecal pellets. Zooplankton ingestion is determined by temperature, phytoplankton biomass, and zooplankton biomass, with assimilation efficiency an inverse function of the specific feeding rate. Nitrogen is recycled primarily by zooplankton while phytoplankton store nitrogen, leaking only a small amount into the water column. Zooplankton respiration is divided into an active component associated with feeding and a passive component including the energy used for maintenance, digestion and growth. In keeping with results in the literature discussed below, zooplankton respiration and growth, unlike photosynthesis, are assumed to be insensitive to temperature below 3°C and to have a  $Q_{10}$  of 2 above 3°C.

Phytoplankton cells and zooplankton fecal material settle from the water column and constitute a flux of material to the benthic ecosystem. Settling rate of phytoplankton cells is a function of the physiological state of the phytoplankton as reflected by  $AN$ , the ratio of gross primary production to phytoplankton biomass. Settling reaches a maximum,  $S_{\max}$ , of 4.5 m day<sup>-1</sup> when  $AN$  approached zero and reaches a minimum,  $S_{\min}$ , of 0.5 m day<sup>-1</sup> when  $AN$  is large.

*Model results.* We compared two runs of the model, the first with water temperatures from 1974, a relatively cold year (water temperatures during the bloom ranged from 0 to 2°C) and the second with water temperatures from 1978, a relatively warm year (water temperatures ranged from 2 to 4°C during the bloom) (Fig. 2); light was kept constant by using only the light data from 1978 for both model runs. In the “cold” version, the peak of the modelled phytoplankton bloom occurred about 1 week later than in the “warm” version, and the zooplankton bloom was delayed by about 2 weeks compared with the “warm” version. Net phytoplankton production during the early bloom (up to day 90) was 7% greater during the “cold” year than during the “warm” year, zooplankton grazing was 11% less, and the result was that the amount of phytoplankton cells settling out of the water column during the early bloom was about 30% greater during the “cold” year than during the “warm” year; there was little difference between the 2 years in zooplankton fecal production. Given the increased input of intact phytoplankton cells to the benthos, representing a high-quality food source relative to the other major pools of detrital organic matter available to benthic consumers, the “cold” year would be expected to result in a greater production of benthic macrofauna.

Our modelling results support a number of earlier works which show that, at water temperatures near 0°C, the metabolism of heterotrophs is greatly slowed relative to the rate of photosynthesis (POMEROY and DEIBEL, 1986; WALSH and MCROY, 1986; KUPARINEN, 1987), suggesting that the proportion of organic matter consumed by heterotrophic organisms during early, cold-water blooms should be significantly less than during later, warmer-water blooms. KUPARINEN (1987), for example, showed that water column respiration prior to and during the spring diatom bloom in the Gulf of Finland was due primarily to phytoplankton, and that bacterial respiration did not become significant until after the phytoplankton maximum when the water temperature rose from 1.25 to 5°C. POMEROY and DEIBEL (1986) maintained that high secondary production in colder waters may result because the inhibition of bacterial decomposition allows the herbivores to utilize a greater fraction of the primary production. However, the role of the metazoan heterotrophs, in particular the herbivorous copepods, remains largely unknown with respect to their impact on early spring blooms in cold water.

There is an extensive body of research on the metabolism of zooplankton as a function of

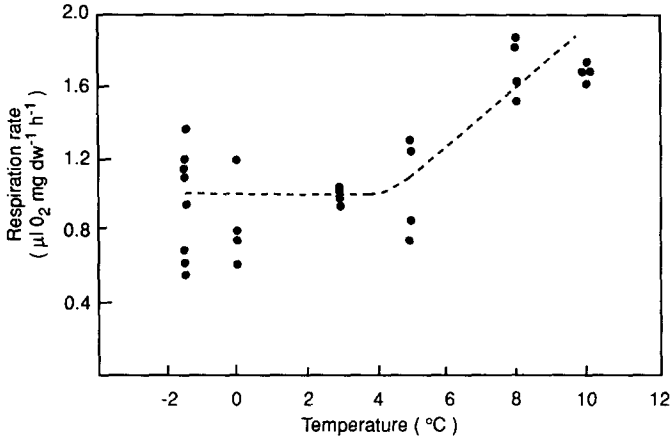


Fig. 3. Oxygen consumption rate versus temperature for *Calanus glacialis*, redrawn after TANDE (1988); the dotted line has been added, and fitted by eye. Note the flat response in oxygen consumption with increasing temperatures between  $-1.7^{\circ}\text{C}$  and  $3^{\circ}\text{C}$  (or between  $-1.7^{\circ}\text{C}$  and  $5^{\circ}\text{C}$ ), which may represent lack of a metabolic response over this low temperature range.

temperature (e.g. ANRAKU, 1964; CONOVER and CORNER, 1968; CORKETT and McLAREN, 1978; IKEDA, 1985; and many others), but few studies have dealt with temperate-latitude, cold water environments ( $<3^{\circ}\text{C}$ ); rather, most are for high latitude, polar waters (e.g. BIGGS, 1982; IKEDA and MITCHELL, 1982; HIRCHE, 1987; IKEDA and BRUCE, 1986; TANDE, 1988; BÄMSTEDT and TANDE, 1988; IKEDA and SKJOLDAL, 1989). Results indicate that the metabolism and grazing of herbivorous copepods may be inhibited at temperatures near  $0^{\circ}\text{C}$ , in a manner similar to that shown for microheterotrophs. In a study of *Calanus glacialis* in the Barents Sea, TANDE (1988) reported that for temperatures in the range  $-1.7$  to  $+5^{\circ}\text{C}$ , grazing was independent of food concentration and oxygen consumption was relatively constant; above  $5^{\circ}\text{C}$ , respiration increased linearly with temperature (Fig. 3). In a study of the respiration of copepods from the Greenland Sea, HIRCHE (1987) reported  $Q_{10}$ s from 2.05 to 4.5 over the temperature range  $0$ – $15^{\circ}\text{C}$ . However, Hirche's plots of the natural logarithm of oxygen uptake as a function of temperature (his Fig. 2, reproduced here as Fig. 4) show some scatter and departure from linearity at the lowest temperatures, and it is possible that rate of respiration changes little between  $0^{\circ}\text{C}$  and  $3$ – $5^{\circ}\text{C}$ .

These earlier studies of microheterotrophs and copepods, in conjunction with our modelling results, suggest that a reduced metabolic temperature response at low temperature ( $<3$ – $5^{\circ}\text{C}$ ) is a general property of consumer organisms in marine ecosystems. This reduced temperature response, or nonlinearity in the metabolic-temperature relation at very low temperatures, has not, to our knowledge, been explicitly described or discussed in the literature. However, other more indirect support in the literature for low temperature inhibition of zooplankton abounds. For example, a lowered metabolic rate in copepods in later winter and early spring in temperate regions is a well known phenomenon and is believed to reflect one of several overwintering strategies for energy conservation during the low productivity winter period (CONOVER and CORNER, 1968; SMITH and LANE, 1987). Furthermore, there are several accounts of suppressed grazing



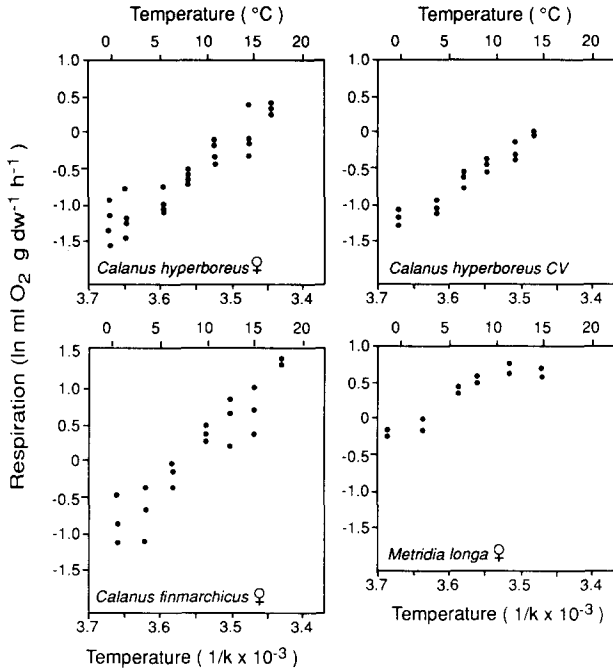


Fig. 4. Natural logarithm of oxygen consumption versus temperature for copepods from the Greenland Sea, redrawn from HIRCHE (1987). Note the scatter in points at lowest temperatures (near 0°C) which may represent a departure from a logarithmic respiration–temperature relationship.

activity during the early stages of winter–spring phytoplankton blooms in cold water (e.g. in Narragansett Bay; PRATT, 1965; MARTIN, 1965; DEASON, 1980).

#### BLOOMS IN OFFSHORE WATERS

It is generally accepted that the establishment of the seasonal thermocline is a prerequisite for the development of the spring phytoplankton bloom in offshore and open ocean waters, but not all data are consistent with this hypothesis (TOWNSEND *et al.*, 1992; GARSIDE and GARSIDE, 1993). Studies in the open North Atlantic Ocean provide evidence both for variable bloom timing, and for commencement of blooms prior to stratification. COLEBROOK (1979) showed that the timing of onset of the spring phytoplankton bloom for the North Atlantic region as a whole varies by several weeks, from mid-April to early May, and that this variability cannot be correlated with annual differences in the timing of warming of the surface waters and the development of the seasonal thermocline. This inconsistency suggests that other factors affect bloom initiation. Indeed, COLEBROOK's (1982) data (his Fig. 2) showed more clearly that the bloom appears to begin in the open North Atlantic in the absence of thermal stratification, and he repeated his earlier suggestion that only very weak, or even transient periods of vertical stability may suffice to initiate the spring bloom. Williams and co-workers (WILLIAMS and ROBINSON, 1971; WILLIAMS, 1972; WILLIAMS and HOPKINS, 1973, 1974; and WILLIAMS and WALLACE, 1975) presented temperature, nutrient and phytoplankton chlorophyll data collected from 1971

to 1975 at Ocean Weather Station INDIA in the North Atlantic (50°N, 19°W); these data can also be interpreted to show that the spring bloom may begin before the clear development of vertical stratification.

GARSDIE and GARSDIE (1993) inferred from nutrient analyses during the JGOFS North Atlantic bloom study in 1989, that phytoplankton growth started prior to the development of thermal stratification. TOWNSEND *et al.* (1992) provided direct evidence that phytoplankton blooms in the offshore waters of the Gulf of Maine can occur without the development of a thermocline or pycnocline, and they suggested that earlier bloom studies in the open North Atlantic might represent a similar phenomenon: blooms may commence in a neutrally stable water column provided that vertical mixing is insufficient to produce light limitation, and that the growth rates of the phytoplankton population exceed other losses.

The modelling studies of WOODS and ONKEN (1982) and TAYLOR and STEPHENS (1993) have shown that daytime solar inhibition of convective mixing may be one mechanism by which blooms can develop in the absence of mean water column stratification. Cells grow in a relatively shallow mixed layer during the day and are subsequently mixed downwards by convection at night; this could give rise after several diurnal cycles to relatively high concentrations of chlorophyll from the surface to considerable depths (>50 m) as observed by WILLIAMS and co-workers (*op. cit.*) and by TOWNSEND *et al.* (1992). Such daily variations in mixing depth will also entrain back toward the surface any subsurface layers of diatoms that tend to form when the cells sink, provided they do not drop below the maximum depth of nocturnal mixing (WOODS and ONKEN, 1982). It is important to note that surface mixing processes in the spring are likely to be sensitive to annual and longer term changes in climatic conditions except in continental shelf waters where strong tidal mixing has a dominating effect on water column stability and the timing of the establishment of the seasonal thermocline (PINGREE *et al.*, 1976).

If bloom initiation can occur independent of vertical water column stratification, then the conceptual framework upon which phytoplankton bloom simulation models are built must be reconsidered. For example, simulation models of spring phytoplankton production in the North Atlantic (e.g. WROBLEWSKI *et al.*, 1988; WROBLEWSKI, 1989) have been structured by effectively allowing a thermocline to cap off a surface layer; the available nutrient load in that upper mixed layer determines the level of primary production. Furthermore, the models assume that an unstratified surface layer does indeed vertically mix; that is, when the mixed layer is deep, phytoplankton production will be light limited. It would then follow that a temporal model run of a bloom would mimic the seasonal development of stratification and the shoaling of the upper mixed layer from south to north, and indeed WROBLEWSKI'S (1989) model shows that the bloom develops in the southern portion of the North Atlantic and advances northward as the mixed layer shoals to 100 m or less.

In apparent contrast to this modelling scenario, the data of WILLIAMS and co-workers (*op. cit.*) show evidence in some years of one or more episodic phytoplankton pulses before the main bloom, with each pulse occurring in the absence of significant and persistent thermal stratification, followed by a replenishment of the surface nutrient field. In 1974, for example, their data show two separate phytoplankton pulses in mid-April to early May, before the third and main bloom in mid-May (Fig. 5). Both bloom pulses were characterized by reduction, but not exhaustion of surface nutrients, and were followed by a replenished nutrient field (presumably the result of vertical mixing), only to become

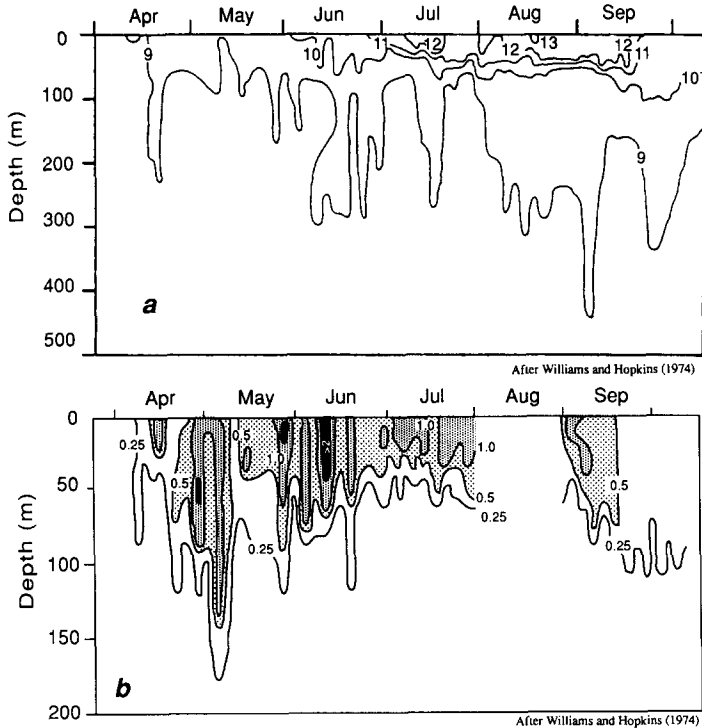


Fig. 5. Data from Ocean Weather Station INDIA in the North Atlantic Ocean 59°N 10°W, redrawn from WILLIAMS and HOPKINS (1974). (a) Contours of temperature in upper 500 m of the water column from 1 April to 10 October, 1974; contour interval is 1°C. (b) Contours of chlorophyll *a* in the upper 200 m, from 6 April to 9 October 1974; contour intervals are 0.25, 0.5, 1.0 and 2.0  $\mu\text{g} \cdot \text{L}^{-1}$ .

depleted following the third main bloom (WILLIAMS and HOPKINS, 1974). Although the data in WILLIAMS and HOPKINS (1974) were collected daily from a stationary ship, an inherent weakness is that they give no indication of spatial variability or the influence of eddies. For example, SAVIDGE *et al.* (1992) showed in their study of the 1989 North Atlantic bloom that mesoscale eddies significantly affect the distribution of phytoplankton abundance, with productivity being positively correlated with stratification. On the other hand, it appears unlikely that the data in WILLIAMS and HOPKINS (1974) were similarly affected, because there were no clear variations in the vertical temperature structure during the period of interest (Fig. 5).

#### *Vertical wind mixing and light limitation*

Each spring, following the winter period of buoyancy extraction, which produces deep convective mixing of the water column, and prior to springtime warming of the surface waters, there is a period when the daily average heat flux across the air–sea interface tends to zero. The water column then is neutrally stable from the surface to the depth of winter convective mixing. It would then follow that blooms occurring during this transitional period of limited convective vertical mixing (TAYLOR and STEPHENS, 1993) would be more

likely to be continually supplied with nutrients, as may have been the case in the North Atlantic in 1974 (Fig. 5). Apart from nocturnal periods of convective mixing, the only other source of energy for deep vertical mixing during this transitional period is the wind. And if the wind is incapable of mixing the neutrally-stable water column to a depth greater than the critical depth, a phytoplankton bloom can commence and be sustained.

Figure 6 illustrates the point for two example areas: the offshore Gulf of Maine (42°N) and the open North Atlantic (60°N). The depth-averaged, vertically integrated irradiances ( $E^*$ ) reaching various depths in the water column are presented in Fig. 6A and B. As we have already discussed, the bloom can begin if  $E^*$  is greater than  $40 \text{ Ly}\cdot\text{day}^{-1}$  (an empirically-determined critical light intensity) in the actively mixing layer. The dates at which this occurs (in the absence of cloud cover) are shown in Fig. 6A and B for 42°N and 60°N for various mixed layer depths. Thus, for example, with a mixing layer of 90 m (e.g. SVERDRUP, 1953) in the North Atlantic (Fig. 6B) we would expect the bloom to begin after Day No. 110 (late April). Figure 6C presents the same principle another way, where the seasonal increase in the critical depth is shown for 42°N and 60°N. If wind mixing is insufficient to actively stir a neutrally stable water column to a depth greater than the critical depth, a spring phytoplankton bloom begins. If wind stress subsequently increases so that active mixing extends below the critical depth, the bloom will collapse and nutrients will be replenished, thus setting the stage for additional blooms of this nature, or upon the development of stratification, the main spring bloom.

We have estimated the depth of wind mixing under conditions of neutral stability using the classical Ekman layer model, where the depth of wind (or frictional) influence is traditionally (and arbitrarily) defined as the depth at which wind-driven currents have decayed to *ca* 5% ( $e^{-\pi}$ ) of their surface magnitude, or approximately three Ekman depths (Fig. 7). The decay scale (Ekman depth) of the turbulent Ekman layer can be estimated by

$$D_E \sim 0.1 U^*/f$$

(CSANADY, 1982), where  $U^*$  is the friction velocity, which is given by the square root of the applied stress divided by a constant water density,

$$U^* = (\tau/\rho_w)^{1/2}$$

and  $f$  is the Coriolis parameter, written as

$$f = 2\Omega \sin \varphi$$

where  $\Omega$  is the angular speed of Earth's rotation and  $\varphi$  is the latitude. Thus, it can be seen that the Ekman depth varies as the square root of the applied stress, and inversely with the sine of the latitude (Fig. 7). The vector wind stress, needed to estimate Ekman depth at a particular location, is often parameterized in terms of a quadratic drag law

$$\tau = C_D(w)\rho_a \mathbf{W}\mathbf{W}$$

(e.g. GILL, 1982) where  $\rho_a$  is the air density ( $1.2 \text{ kg m}^{-3}$ ),  $\mathbf{W}$  is the wind velocity,  $W$  is the wind speed, and we have allowed the drag coefficient [ $C_D(w)$ ] to depend upon the wind speed. For the vertical mixing problem at hand are not concerned with the direction of the applied stress and can express the stress magnitude as

$$\tau = C_D(w)\rho_a W^2.$$

The functional dependence of the drag coefficient upon wind speed has been the subject of

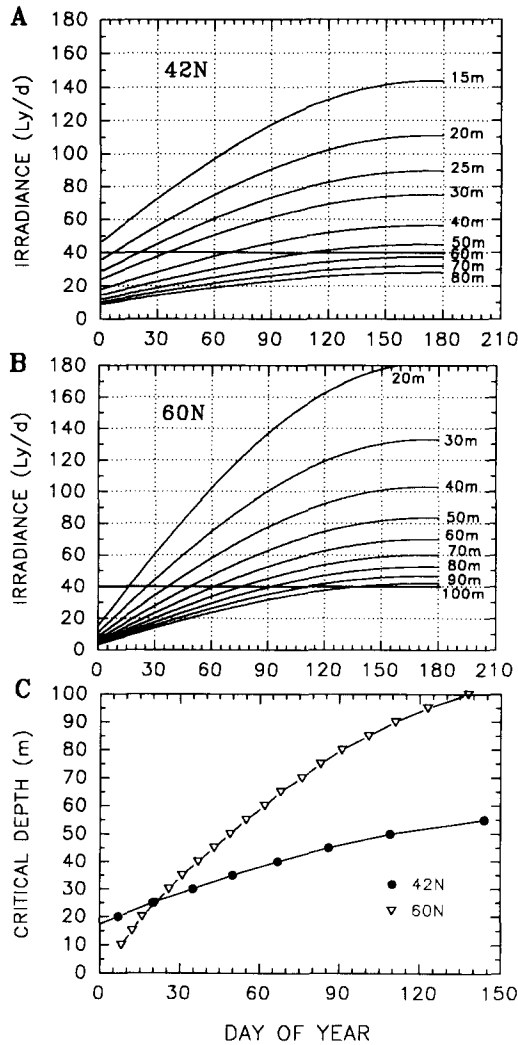


Fig. 6. (A) Plots of depth-averaged, vertically integrated irradiance in the Gulf of Maine (42°N) and (B) the North Atlantic Ocean (60°N), calculated as

$$E^* = 1/kzE_0(1 - \exp(-kz))$$

$$E_0 = \alpha + \beta \sin(\omega t)$$

where  $k$  = the diffuse attenuation coefficient;  $z$  = depth (m);  $\alpha$  = the solar irradiance at the sea surface on the winter solstice;  $\beta$  = the difference in solar irradiance at the sea surface between the winter and summer solstice;  $\omega = \pi/365$ ; and  $t$  = day number after the winter solstice. Values of  $k$  are assumed to be  $0.1 \text{ m}^{-1}$  for the North Atlantic (SVERDRUP, 1953), and  $0.21$  for the Gulf of Maine. Values of  $\alpha$  are  $2.9 \text{ Ly} \cdot \text{day}^{-1}$  for the North Atlantic and  $124 \text{ Ly} \cdot \text{day}^{-1}$  for the Gulf of Maine;  $\beta = 417 \text{ Ly} \cdot \text{day}^{-1}$  for the North Atlantic and  $349 \text{ Ly} \cdot \text{day}^{-1}$  for the Gulf of Maine (SVERDRUP *et al.*, 1942). (C) Solutions of  $E^*$  (depth-averaged vertically integrated irradiance) =  $40 \text{ Ly} \cdot \text{day}^{-1}$  during the winter-spring season for the Gulf of Maine (42°N) and the North Atlantic (60°N). Day number is corrected to correspond to 1 on January 1 in these plots.

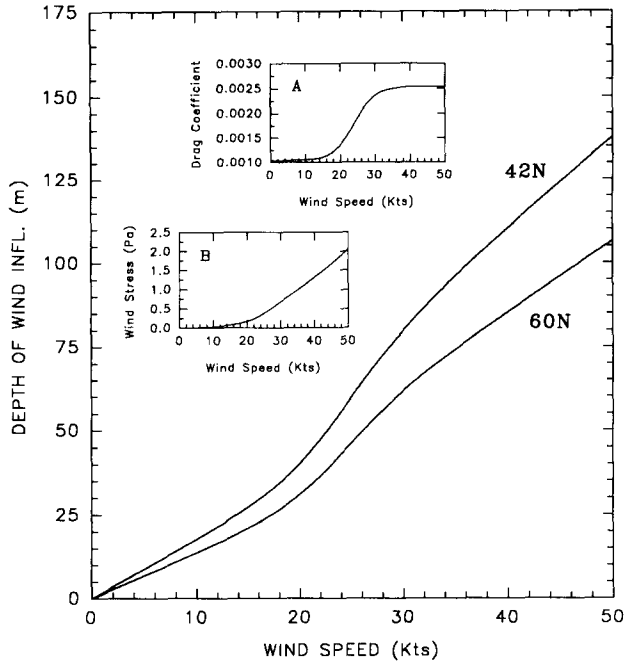


Fig. 7. Maximum depth of wind mixing as a function of wind speed for 42°N (the Gulf of Maine) and 60°N (the North Atlantic) assuming the depth of wind influence is approximated by three Ekman depths (see text). Insert panel (A) gives the dependence of the drag coefficient (dimensionless) upon wind speed (kts), using the empirically-derived formula of AMOROCHO and DEVRIES (1979); insert panel (B) gives the dependence of surface wind stress (Pascals) on wind speed (kts) using the quadratic drag law (e.g. GILL, 1982).

numerous recent studies. Based upon the analysis of an extensive data set, AMOROCHO and DEVRIES (1980) offered an empirically-derived formula:

$$C_D(w) = 0.0015\{1 + \exp [(12.5 - W)/(1.56)]\}^{-1} + 0.00104$$

where  $w$  is the wind speed ( $\text{m s}^{-1}$ ) at 10 m above the sea surface. Figure 7A shows the dependence of the drag coefficient on wind speed.

The maximum depth of wind stirring in an unstratified fluid, which we estimated here by three Ekman depths, as a function of wind speed is shown in Fig. 7. For example, Fig. 7 shows that for a critical depth of 90 m (e.g. SVERDRUP, 1953) in the North Atlantic in late April, a bloom can commence provided the wind speed is on the order of 40 kts or less; likewise, for a critical depth of 40 m in the Gulf of Maine (e.g. TOWNSEND *et al.*, 1992), the wind speed would need to be on the order of 20 kts or less. Thus, given the rapidly increasing solar radiation during spring, and deep penetration of light in the relatively clear late-winter waters, a phytoplankton bloom can begin in the upper water column, despite the absence of vertical stratification, and despite considerably large wind speeds. This appears to have been the case as demonstrated by TOWNSEND *et al.* (1992) in the Gulf of Maine, and may have been the case in the North Atlantic in April of 1974 (Fig. 4). Rather than being dependent on the timing of vertical water column stratification, the

onset of the spring bloom in open ocean waters would, as in coastal waters, be dependent on weather, particularly cloud cover and wind speed.

## DISCUSSION AND CONCLUSIONS

The timing of spring phytoplankton blooms is variable among years in coastal waters where the depth of the mixed layer extends to the bottom, and thus bloom initiation is triggered by the vernal increase in solar radiation. This allows for inter-annual variation to be induced by differences in weather, in particular, cloud cover. The effect is that blooms may occur in some years in very cold waters, where the metabolism of the heterotrophic consumers may be significantly reduced, thus facilitating a more efficient flux of carbon to the benthos.

Our modelling results and earlier published studies would suggest that overwintering zooplankton populations in temperate waters may not be particularly well-adapted to seasonally cold environments, and thus they are less able to graze winter–spring phytoplankton blooms in years when they occur in relatively cold water. The model results emphasize the potential significance of this lack of cold-water adaptation in leading to more efficient benthic–pelagic coupling during relatively cold years. The end result should be that a greater fraction of primary production goes into export production (BERGER and WEFER, 1990), with the potential of increasing benthic productivity. It can be argued that zooplankton metabolic rates may be essentially independent of temperature at very cold temperatures, thus preventing zooplankton from responding effectively, in terms of reproduction, to cold water blooms until the waters warm to some critical temperature. Above this critical temperature, metabolism becomes more sensitive to temperature changes, and zooplankton grazing and respiration rates begin to increase in a regular fashion. It is possible that such a temperature control, or “ $Q_{10}$  switch”, on metabolic processes of herbivorous copepods in temperate regions would lend a selective advantage by tending to prevent propagation in response to “false starts” of the winter–spring phytoplankton blooms.

The onset of offshore and open ocean spring blooms is probably also subject to inter-annual variability in weather, and early blooms that occur prior to stratification as a result of favorable weather conditions (i.e. clear and calm) may be a source of primary production that has been overlooked by production models controlled primarily by water column stratification. That is, following the uptake of some portion, or all, of the available nutrients in the upper water column, a subsequent vertical mixing event could cause the bloom to crash, due to deep mixing and light limitation, and at the same time serve to replenish the surface nutrient field to previous levels, thus allowing a subsequent bloom to occur. The energy required to produce such vertical mixing would be much less for a neutrally stable water column than for one in which a thermocline has formed. The data presented in WILLIAMS and HOPKINS (1974) for the North Atlantic bloom in 1974 show that production resulting from the two brief blooms in mid-April and late April–early May was of similar magnitude to that of the main bloom that developed in mid- to late May, with high production continuing into June and July. Thus, the spring bloom in some years could be on the order of twice as productive as existing simulation models might predict. Furthermore, blooms preceding the development of vertical water column stratification may be commonplace so that twice as much organic carbon is being exported to deep waters than has been previously assumed.

Spring phytoplankton blooms in temperate latitude coastal and ocean waters tend to occur earlier than predicted by many models, and their timing is apparently influenced by variations in climatic forcing. Variations in mean wind speed, cloudiness (which affects surface irradiance as well as night convection), and air temperature will all affect the hydrographic conditions controlling phytoplankton growth. Changes in wind strength and direction over decadal time scales have been previously identified by VENRICK *et al.* (1987), DICKSON *et al.* (1988) and LANGE *et al.* (1990) as possible causes for significant variations in phytoplankton abundance within both coastal and oceanic waters.

The potential impacts on marine pelagic ecosystems of climate change induced by human activities remain uncertain. However, in the context of greenhouse warming and any associated modification of wind fields (see BAKUN, 1991), it is likely that both the intensity and timing of spring phytoplankton blooms will be altered in some regions. For example, BAKUN (1991) postulated that a greater temperature contrast between the continents and the oceans will increase the intensity of coastal upwelling, and FRANK *et al.* (1990) concluded that changes in plankton productivity associated with greater stratification of the water column may favor pelagic as opposed to demersal fish communities since less organic matter is likely to reach the bottom. In neither study were the effects of climate change on spring blooms discussed specifically, but the implications within this context are clear.

The difficulties of predicting the effects of natural or anthropogenic variations in climatic factors on marine plankton communities (see SCHEFFER, 1991; STEELE and HENDERSON, 1992) severely limit our capacity to assess their significance for ecological or biogeochemical processes. However, concerning the two situations discussed in this paper, it appears that conditions at the time of the onset of the spring bloom are especially sensitive to climatic perturbation, and that any effects on the dynamics of plankton populations above the level of the seasonal thermocline will modify the fluxes of materials, including carbon, to deep water and the sediments. In particular it is noted that earlier blooms will tend to enhance productivity in the spring (and possibly total annual production) and to cause a greater proportion of organic matter to be lost from the surface layer. The latter effect may be related to reduced herbivory at low temperatures and/or to loss of synchrony between primary and secondary producers, and clearly has important implications for ocean geochemical cycles.

*Acknowledgements*—The ideas expressed here benefitted from various discussions with Steven Ackleson, Michael Lesser, Maureen Keller and Michael Sieracki. Portions of the modelling work were carried out under NSF grant OCE-8800532 to LMC, DWT and DEC at the Bigelow Laboratory for Ocean Sciences. This work was also funded in part by NSF grant OCE-9202061 to D. W. Townsend.

## REFERENCES

- AMOROCHO J. and J. J. DEVRIES (1980) A new evaluation of the wind stress coefficient over water surfaces. *Journal of Geophysical Research*, **85**, 433–442.
- ANRAKU M. (1964) Influence of the Cape Cod canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. Respiration and feeding. *Limnology and Oceanography*, **9**, 195–206.
- ATKINS W. R. G. (1928) Seasonal variations in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton standing crop. *Journal of the Marine Biological Association of the United Kingdom*, **15**, 191–205.
- BAKUN A. (1991) Global climate change and intensification of coastal upwelling. *Science*, **247**, 198–201.



- BÄMSTEDT U and K. TANDE (1988) Physiological responses of *Calanus finmarchicus* and *Metridia longa* (Copepoda: Calanoida) during the winter–spring transition. *Marine Biology*, **99**, 31–38.
- BARLOW J. P. (1958) Spring changes in phytoplankton abundance in a deep estuary, Hood Canal, Washington. *Journal of Marine Research*, **17**, 53–67.
- BERGER W. H. and G. WEFER (1990) Export production: seasonality and intermittency, and paleoceanographic implications. *Paleogeography, Paleoclimatology, Paleoecology (Global and Planetary Change Sec.)*, **89**, 245–254.
- BERGER W. H., V. S. SMETACEK and G. WEFER (eds) (1989) *Productivity of the ocean: present and past*, Wiley, Chichester, 471 pp.
- BIGELOW H. B., L. C. LILLICK and M. SEARS (1940) Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. Part I. Numerical distribution. *Transactions of the American Philosophical Society*, **21**, 149–191.
- BIGGS D. C. (1982) Zooplankton excretion and NH<sub>4</sub> cycling in near-surface waters of the Southern Ocean. I. Ross Sea, austral summer 1977–78. *Polar Biology*, **1**, 55–67.
- BREWER P. G. (1986) What controls the variability of carbon dioxide in the surface ocean? A plea for complete information. In: *Dynamic processes in the chemistry of the upper ocean*, J. D. BURTON, P. G. BREWER and R. CHESSELET, editors, NATO Conference Series IV, 17. Plenum, London, 1986, pp. 215–231.
- 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. (1982) Continuous plankton records: Seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *Journal of Plankton Research*, **4**, 435–462.
- CONOVER R. J. and E. D. C. CORNER (1968) Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. *Journal of the Marine Biological Association of the United Kingdom*, **48**, 49–75.
- CORKETT C. J. and I. A. MCLAREN (1978) The biology of *Pseudocalanus*. *Advances in Marine Biology*, **15**, 1–248.
- CSANADY G. T. (1982) *Circulation in the coastal ocean*. D. Reidel, Holland, 279 pp.
- CURA J. J. (1981) Physical and biological factors affecting the phytoplankton growth and seasonal secession in the Damariscotta River estuary. Ph.D. Dissertation, University of Maine. 119 pp.
- DEASON E. E. (1980) Grazing of *Acartia hudsonica* (*A. clausi*) on *Skeletonema costatum* in Narragansett Bay (USA): Influence of food concentration and temperature. *Marine Biology*, **60**, 101–113.
- DICKSON R. R., P. M. KELLY, J. M. COLEBROOK, W. S. WOOSTER and D. H. CUSHING (1988) North winds and production in the eastern North Atlantic. *Journal of Plankton Research*, **10**, 151–169.
- DUCKLOW H. W. and R. P. HARRIS (1993) Introduction to the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 1–8.
- FORSSKÄHL M., A. LAAKKONEN, J. -M. LEPPÄNEN, A. NIEMI, A. SUNDBERG and G. TAMELANDER (1982) Seasonal cycle of production and sedimentation of organic matter at the entrance to the Gulf of Finland. *Netherlands Journal of Sea Research*, **16**, 290–299.
- FRANK K. T., R. I. PERRY and K. F. DRINKWATER (1990) The predicted response of Northwest Atlantic invertebrate and fish stocks to CO<sub>2</sub>-induced climate change. *Transactions of the American Fisheries Society*, **119**, 353–365.
- GARSDIE C. and J. C. GARSIDE (1993) The “*f*-ratio” on 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 75–90.
- GIESKES W. W. C. and G. W. KRAAY (1975) The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Netherlands Journal of Sea Research*, **9**, 166–196.
- GILL A. E. (1982) *Atmosphere–ocean dynamics*. International Geophysics Series, Volume 30, Academic Press, New York.
- GRAN H. H. and T. BRAARUD (1935) A quantitative study of the phytoplankton of the Bay of Fundy and Gulf of Maine (including observations on hydrography, chemistry and turbidity). *Journal of the Biological Board of Canada*, **1**, 279–467.
- HIRCHE H. -J. (1987) Temperature and plankton. II. Effect on respiration and swimming activity in copepods from the Greenland Sea. *Marine Biology*, **94**, 347–356.
- HITCHCOCK G. L. and T. J. SMAYDA (1977) The importance of light in the initiation of the 1972–1973 winter–spring diatom bloom in Narragansett Bay. *Limnology and Oceanography*, **22**, 126–131.
- HORN H. and L. PAUL (1984) Interactions between light situation, depth of mixing and phytoplankton growth during the spring period of full circulation. *International Revue ges. Hydrobiologie*, **69**, 507–519.

- IKEDA T. (1985) Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Marine Biology*, **85**, 1–11.
- IKEDA T. and B. BRUCE (1986) Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November–December). *Marine Biology*, **92**, 545–555.
- IKEDA T. and A. W. MITCHELL (1982) Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to body size and chemical composition. *Marine Biology*, **71**, 283–298.
- IKEDA T. and H. R. SKJOLDAL (1989) Metabolism and elemental composition of zooplankton from the Barents Sea during the early Arctic summer. *Marine Biology*, **100**, 173–183.
- KUPARINEN J. (1987) Production and respiration of overall plankton and ultraplankton communities at the entrance to the Gulf of Finland in the Baltic Sea. *Marine Biology*, **93**, 591–607.
- LANGE C. C., S. K. BURKE and W. H. BERGER (1990) Biological production off Southern California is linked to climate change. *Climate Change*, **16**, 319–329.
- MARTIN J. H. (1965) Phytoplankton–zooplankton relationships in Narragansett Bay. *Limnology and Oceanography*, **10**, 185–191.
- PARSONS T. R., M. TAKAHASHI and B. HARGRAVE (1984) *Biological oceanographic processes*, 3rd Edition, Pergamon Press, Oxford, 330 pp.
- PEINERT R., A. SAURE, P. STEGMAN, C. STEINEN, H. HAARDT and V. SMETACEK (1982) Dynamics of primary production and sedimentation in a coastal ecosystem. *Netherlands Journal of Sea Research*, **16**, 276–289.
- PINGREE R. D., P. M. HOLLIGAN, G. T. MARDELL and R. N. HEAD (1976) The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom*, **56**, 845–873.
- PINGREE R. D., G. T. MARDELL, P. C. REID and A. W. G. JOHN (1986) The influence of tidal mixing on the timing of the spring phytoplankton development in the Southern Bight of the North Sea, the English Channel and on the northern Armorican Shelf. In: *Lecture notes on coastal and estuarine studies, Vol. 17, tidal mixing and plankton dynamics*, M. J. BOWMAN, C. M. YENTSCH and W. T. PETERSON, editors, Springer-Verlag, Berlin, pp. 164–192.
- PLATT T., D. F. BIRD and S. SATHYENDRANATH (1991) Critical depth and marine production. *Proceedings of the Royal Society of London, B*, **246**, 205–217.
- POMEROY L. R. and D. DEIBEL (1986) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science*, **233**, 359–361.
- PRATT D. M. (1965) The winter–spring diatom flowering in Narragansett Bay. *Limnology and Oceanography*, **10**, 177–184.
- RILEY G. A. (1957) Phytoplankton of the North Central Sargasso Sea, 19502. *Limnology and Oceanography*, **2**, 252–270.
- RILEY G. A. (1967) The plankton of estuaries. In: *Estuaries*, G. H. LAUFF, editor, American Association for the Advancement of Science Publication 83, Washington, D.C., pp. 316–326.
- SAVIDGE G., D. R. TURNER, P. H. BURKILL, A. J. WATSON, M. V. ANGEL, R. D. PINGREE, H. LEACH and K. J. RICHARDS (1992) The BOFS 1990 spring bloom experiment: Temporal evolution and spatial variability of the hydrographic field. *Progress in Oceanography*, **29**, 235–281.
- SCHAFFER M. (1991) Should we expect strange attractors behind plankton dynamics and if so, should we bother? *Journal of Plankton Research*, **13**, 1291–1305.
- SMETACEK V. (1980) Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. *Ophelia*, **1**, (Suppl.), 65–76.
- SMETACEK V., K. VON BROCKEL, B. ZEITSCHEL and W. ZENK (1978) Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. *Marine Biology*, **47**, 211–226.
- SMETACEK V. and U. PASSOW (1990) Spring bloom initiation and Sverdrup's critical-depth model. *Limnology and Oceanography*, **35**, 228–234.
- SMITH S. L. and P. V. Z. LANE (1987) On the life history of *Centropages typicus*: responses to a fall diatom bloom in the New York Bight. *Marine Biology*, **95**, 305–313.
- STEELE J. H. and E. W. HENDERSON (1992) The role of predation in plankton models. *Journal of Plankton Research*, **14**, 157–172.
- SVERDRUP H. U. (1953) On conditions for the vernal blooming of phytoplankton. *Journal du Conseil*, **18**, 287–295.
- SVERDRUP H. U., M. W. JOHNSON and R. H. FLEMING (1942) *The oceans: their physics, chemistry and general biology*, Prentice-Hall, Englewood Cliffs, NJ, 1087 pp.

- TANDE K. S. (1988) The effects of temperature on metabolic rates of different life stages of *Calanus glacialis* in the Barents Sea. *Polar Biology*, **8**, 457–461.
- TAYLOR A. J. and J. A. STEPHENS (1993) Diurnal variations of convective mixing and the spring bloom of phytoplankton. *Deep-Sea Research II*, **40**, 389–408.
- TOWNSEND D. W. and L. M. CAMMEN (1988) Potential importance of the timing of spring plankton blooms to recruitment of juvenile demersal fishes. *Biological Oceanography*, **5**, 215–229.
- TOWNSEND D. W. and R. W. SPINRAD (1986) Early spring phytoplankton blooms in the Gulf of Maine. *Continental Shelf Research*, **6**, 515–529.
- TOWNSEND D. W., M. D. KELLER, M. E. SIERACKI and S. G. ACKLESON (1992) Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature*, **360**, 59–62.
- VENRICK E. I., J. A. MCGOWAN, D. R. CAYAN and T. L. HAYWARD (1987) Climate and chlorophyll: Long-term trends in the central North Pacific Ocean. *Science*, **238**, 70–72.
- WALSH J. J. and C. P. MCROY (1986) Ecosystem analysis in the southeastern Bering Sea. *Continental Shelf Research*, **5**, 259–288.
- WATSON A. J., C. ROBINSON, J. E. ROBINSON, P. J. LE B. WILLIAMS and M. J. R. FASHAM (1991) Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic. *Nature*, **350**, 503.
- WILLIAMS R. (1972) Biological sampling at Ocean Weather Station INDIA (59°00'N 19°00'W) in 1972. *Annales Biologiques, Copenhagen*, **29**, 41–44.
- WILLIAMS R. and G. A. ROBINSON (1971) Biological sampling at Ocean Weather Station INDIA (59°00'N 19°00'W) in 1971. *Annales Biologiques, Copenhagen*, **28**, 579.
- WILLIAMS R. and C. C. HOPKINS (1973) Sampling at Ocean Weather Station INDIA (59°00'N 19°00'W) in 1973. *Annales Biologiques, Copenhagen*, **30**, 60–62.
- WILLIAMS R. and C. C. HOPKINS (1974) Sampling at Ocean Weather Station INDIA (59°00'N 19°00'W) in 1974. *Annales Biologiques, Copenhagen*, **31**, 57–60.
- WILLIAMS R. and M. A. WALLACE (1975) Sampling at Ocean Weather Station INDIA (59°00'N 19°00'W) in 1975. *Annales Biologiques, Copenhagen*, **32**, 62–64.
- WOODS J. D. and R. ONKEN (1982) Diurnal variation and primary production in the ocean. *Journal of Plankton Research*, **4**, 735–756.
- WROBLEWSKI J. S. (1989) A model of the spring bloom in the North Atlantic and its impact on ocean optics. *Limnology and Oceanography*, **34**, 1563–1571.
- WROBLEWSKI J. S., J. L. SARMIENTO and G. L. FLIERL (1988) An ocean basin scale model of plankton dynamics in the North Atlantic. 1. Solutions for the climatological oceanographic conditions in May. *Global Biogeochemical Cycles*, **2**, 199–218.