1 The spring phytoplankton bloom

Let us begin with the upper pelagic environment, the layer of ocean water illuminated by sunlight where plants can carry out photosynthesis. Much of biological oceanography has been concerned with explaining the seasonal cycle of plant stock variations occurring in this "euphotic" layer, especially in coastal areas and across the temperate North Atlantic. These cycles include a strong spring increase, then decrease, in phytoplankton stock known as the spring bloom. Establishment of the earliest marine laboratories on the shores of the North Atlantic gave study and explanation of the spring bloom strong impetus. Once you understand the basic explanation of the spring bloom, you will be well into the basic observations and theory of biological oceanography. However, it is important to state even before we begin that spring blooms do not occur over all of the world's oceans, or even over very much of them. There are alternative relationships among illumination, water column mixing, plant growth, plant nutrient availability, and herbivore grazing which pertain over large ocean areas. Study of these different ecosystem patterns constitutes much of current biological oceanography. We will cover other patterns later.

Pelagic plants are small

Oceans contrast sharply with the land by the absence of large, complex plants. Sargassum weed suspended from gas bladders in the subtropical gyre of the North Atlantic is a special and localized exception. However, it provides a model that it is a little surprising not to find everywhere; designs exist for large, floating plants, they just are not typical. Instead, almost all plants in the water itself, as opposed to attached to the bottom, that is plants in **pelagic** habitats, are small, unicellular algae known as **phytoplankton**. The word plankton comes from Greek (πλαγκτος) and implies a necessity to drift with the currents. Clytemnestra, in Aeschylus's *Agamemnon*, used it in denying her thoughts were wandering (planktos). A classical scholar suggested it to Victor Henson, a founder of planktology, to describe relatively passive swimmers. Phytoplankton range in cell diameter from about 1 μm to about 70 μm with a few representatives up to 1 mm. It is important to form a mental sense of this size range. Typical bacteria are 1 μm diameter; red blood cells are 7 μm; an object of 50 μm is just visible to the naked eye if contrast is high. Most algal cells in the sea are at the lower end of this range (Box 1.1).

Why are pelagic ocean plants so small? Biological oceanographic dogma, which will not be contradicted here, says they are small because it provides large surface area relative to their biomass in order to absorb nutrients like nitrate, phosphate, and iron from extremely dilute solution. Soil water in land habitats provides somewhat higher levels of nutrients (Table 1.1). The modest difference is augmented in the soil water case, however, by rapid resupply from the closely adjacent mineral phase; nutrients do not become so thoroughly depleted in soil water. Thus, rootlets and root hairs over a small fraction of the plant's surface can supply nutrients for growth and maintenance of very

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Box 1.1

Several sets of prefixes have been proposed to distinguish size classes of plankton. We seem to have settled on those proposed by Sieburth *et al.* (1978):

Characteristic length	Term (examples)
< 0.2 µm	Femtoplankton (viruses)
0.2–2 µm	Picoplankton (bacteria, very small eukaryotes)
2–20 µm	Nanoplankton (diatoms, dinoflagellates, protozoa)
20–200 µm	Microplankton (diatoms, dinoflagellates, protozoa, copepod nauplii, etc.)
0.2–20 mm	Mesoplankton (mostly zooplankton)
2–20 cm	Macroplankton

Table 1.1 Relatively low values of major nutrient concentration in surface waters compared to natural (as opposed to fertilized) soil water values. Units are micromoles liter^{-1} (µM).

	NO$_3$	PO$_4$
Upper ocean concentrations in winter		
North Atlantic subarctic	6	0.3
North Pacific subarctic	16–20	1.1
Natural soil water	5–100*	5–30**

* Soil and agricultural chemists use strange units like kg NO$_3$ hectare^{-1} to 20 cm soil depth. They rarely attempt to extract soil water *per se*, which is difficult because soil is relatively dry and much of the water is associated with organic matter.
** Also hard to characterize. This range came from a soil science text, but do not put much faith in it (units were 0.05 to 3.0 ppm, a usual unit in that field). Most published data are µg PO$_4$(g soil)$^{-1}$.

large structures. In the sea, the rate of supply is limited by diffusion to the absorbing plant surface from dilute solution, so plant surface must be maximized relative to plant bulk. This is achieved by being small. For example, diatoms are an abundant group among the phytoplankton. Many of them are cylindrical, and if we fix the length/diameter ratio at 1, then the surface area to volume ratio varies as 6/length, increasing strongly as size gets smaller. The surface area of a 30 µm diatom of this shape is 4241 µm^2, while that of a 15 µm one is a quarter of that, 1060 µm^2. However, the smaller one has twice the **surface per unit volume**. Surface to volume (*S/V*) ratios of spheres vary similarly as 6/diameter. The effect of size on *S/V* is stronger for more elongate shapes (prove that to yourself by doing the calculations).

It is not surface *per se* that matters, since phytoplankton cells only cover a small fraction of their surface with transport enzymes to move nutrients from outside to inside. The importance of small size is to provide a large **relative** surface toward which diffusion can move nutrients; it is the rate of diffusion that is limiting at low concentrations. At the size scale of the phytoplankton, fluid surface boundary layers are large relative to the plants, inhibiting fluid exchange next to the boundary. Turbulent shear is mostly at larger scales than the size of cells (Lazier & Mann 1989), so effectively the water next to a cell exchanges only slowly. Although sinking and turbulence can increase nearby nutrient availability, supply is effectively limited to molecular diffusion. The diffusive flux of a dissolved solute, such as nitrate, toward an absorbing surface of area A is given by Fick's Law, which Fick derived (Cussler 1984) by analogy to Fourier's Law for heat conduction:

flux (amount arriving/time) $= -AD \ \delta C/\delta x$,

where D is the substance-specific diffusion coefficient and $\delta C/\delta x$ is the gradient of concentration (amount/volume) away (hence the minus sign) from the surface. Fick proved the physical reality

of this relation by simple, elegant experiments. Experimental determinations of D (units in the form $-l^2 t^{-1}$) for small solutes in water are all close to -10^{-5} cm^2 s^{-1}: nitrate -1.90×10^{-5}, ammonia -1.64×10^{-5}, chloride -2.03×10^{-5}, glycine -1.06×10^{-5}, oxygen -2.10×10^{-5}. This indicates that strong imbalances in supply of substrates to a cell will rarely be due to differences in diffusivity of the substrates. The only evolutionary strategy available to increase flux per unit biomass is to increase A/V, that is, to reduce size. That is why phytoplankton are small. This effect is also our best explanation for differences in the typical sizes of phytoplankton cells during different seasons or between different pelagic ecosystems (e.g. Morel *et al.* 1991). Diffusion is slow enough that only a small fraction of the cell surface need be occupied by transport enzymes to acquire the specific molecules the cell must absorb. Estimates by Berg and Purcell (1977), based on rates of diffusion and handling time per molecule, can be interpreted to imply that only a few percent of the cell surface needs to be devoted to transport enzymes for any required solute. More would not be useful, due to limitation of diffusive supply to the surface. This claim would be more convincing if someone would develop a direct demonstration that transport molecules occupy a small area on the surface of cells.

Because phytoplankton are small, they are also ephemeral compared to terrestrial plants or to algae attached along the shore. Grazing terrestrial animals typically take a bite from a plant, which then heals; pelagic grazers typically ingest the entire plant, so it is gone. Therefore, maintenance of a population of cells, a **phytoplankton stock**, depends upon their rapid reproduction. And repro-

duction can be rapid. Many (not all) phytoplankton can double once or more times per day. Thus, if grazers are few and growth conditions (light, nutrients, temperature) are good, then stocks can grow exponentially. Doubling once per day, they can increase 1000-fold in 10 days. Rapidly growing diatoms can increase twice that fast. This rapid growth is the basis for phytoplankton population outbursts or "blooms", which most commonly occur (where they occur) in the spring. Phytoplankton blooms have been and remain a central interest in biological oceanography, and we will consider them in some detail. Even more detail is available in the literature.

The seasonal cycle of phytoplankton stocks

Phytoplankton growth rates depend upon irradiance to drive photosynthesis, which is incorporation of carbon into new organic matter, and upon nutrient availability to supply elements other than carbon. Those factors influence the *per capita* growth rates of the plants. They are important to the individual plant cell. However, the bulk production of new phytoplankton biomass (**stock**, Box 1.2) at any given site depends more importantly upon what the stock is. Unless there are many plants to photosynthesize, there will be very little total photosynthesis, known in ecological parlance as **primary productivity**. That can be surprisingly hard to keep in mind: total productivity (carbon fixed as organic matter/area/time) depends upon the plant stock. There is a nice regional proof of this for the southern California Current by

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Box 1.2

Chlorophyll *a* is the key light-absorbing pigment involved in photosynthesis, so the amount of it in the water column is a reasonable, if imperfect, measure of the available photosynthetic capacity, that is a functional measure of plant stock. Moreover, chlorophyll concentration is relatively easy to measure. Phytoplankton are removed from a known volume of water with a suitably fine filter (glass-fiber mesh is most common), then chlorophyll is extracted with acetone and quantified by spectrophotometer, chromatography or, since it shows red fluorescence in blue illumination, with a fluorometer. You will find typical recipes for these techniques in Parsons *et al.* (1984).

Hayward and Venrick (1982). They cruised about the area in May–June of 1981, measuring the vertical integrals of primary productivity and of chlorophyll (again, a **stock** measure) down to the bottom of the **euphotic** zone, the near-surface layer in which light is sufficient for net photosynthesis (Fig. 1.1). The correlation is about as strong as we see in ecology. Plant stock depends upon the past history of productivity and also upon the history of the plant death rate. "Death" (or at least loss to the surface layer stock) comes from (i) grazing, (ii) mixing out of the euphotic zone, (iii) sinking, or (iv) disease. The latter has largely been ignored until fairly recently. It has now been shown that marine waters contain viruses that are capable of lysing phytoplankton cells (Suttle *et al.* 1990), which is discussed in Chapter 5.

The interactions among seasonally varying light, nutrient availability, and losses to mixing and grazing have long been credited with generating the seasonal cycle of phytoplankton stock abundance. Seasonal cycles vary markedly between places, but there is a classic cycle that is observed in coastal Atlantic waters, such as the North Sea or off Cape Cod, and all across the high-temperate Atlantic. Because these sites are near important marine laboratories, their phytoplankton stock cycle has received considerable scrutiny. Its explanation is a major goal of biological oceanography. In places where cycles are strongly different (the tropics, the subarctic Pacific, the Southern Ocean), they are usually discussed in contrast to

the spring bloom cycle. Characteristically, textbooks show this cycle in a schematic way (Fig. 1.2). That is symptomatic of a problem of the discipline. Because getting out to sea on a regular or sustained basis is difficult, we still have no single time series quantifying the progression of a spring bloom with good (daily, or near daily) resolution of required variables, although some data series from moorings supply part of what is required (e.g. Stramska and Dickey 1993, and papers cited by them). Measurements needed are phytoplankton stock, irradiance, water column density structure, and nutrients, all from well before the stock increase until it has subsided again. Evaluation of exactly which kinds of plants make up the phytoplankton stock during the progress of the bloom would also be useful; we do know that the overall bloom can be constituted of several, sequential blooms of different species. Estimates of grazing and phytoplankton sinking would also be good, but harder to obtain. As we shall see, all of this will be more useful from a site deep enough that the bottom does not provide a sort of "artificial" lower limit to vertical mixing.

The standard explanation of the schematic (Fig. 1.2) goes as follows. In winter, mixing increases surface layer nutrients to their seasonal high, setting the stage for phytoplankton growth in spring. However, persistence of low winter light prevents rapid growth, and the deep mixing keeps loss rates high. In spring, illumination increases and warms the surface so that mixing is inhibited by stratifica-

Fig. 1.1 The relationship in May–June 1981 between phytoplankton growth rate measured by ^{14}C-uptake (mgC m^{-2}h^{-1}) plotted against available chlorophyll *a* (mg m^{-2}). The line is fitted between medians of the upper and lower thirds. Both variables are integrated over depth from 0 to 50 m. Inset: station positions for points in the regression. (After Hayward & Venrick 1982.)
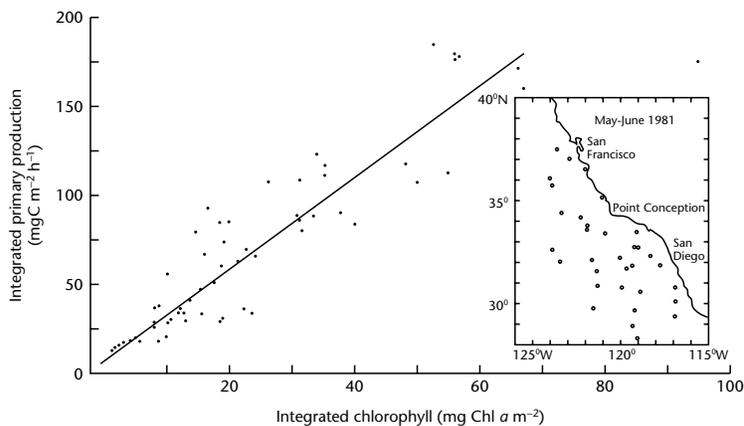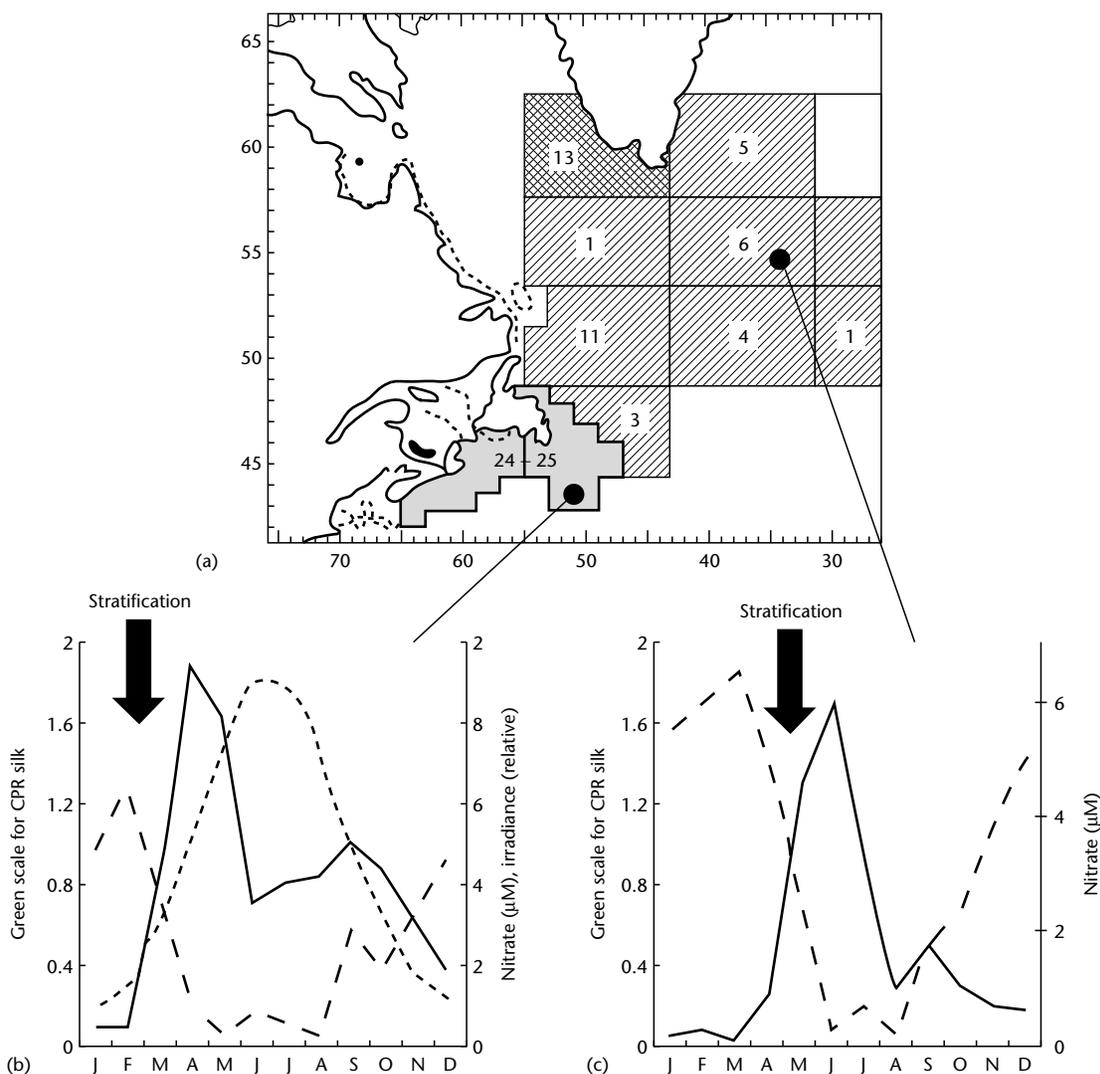
Fig. 1.2 Average annual cycling of phytoplankton biomass (solid line) at two North Atlantic sites. Cycles include a spring bloom, fall bloom, and extreme winter low. Estimates are from color of 240 μm continuous plankton recorder "silks" after towing through the regions neighboring the points indicated in all seasons of many different years (based on Robinson 1970). Peak stock at the more northern site occurs later. Relative irradiance (short dashes) and nitrate (long dashes) curves are hypothetical.

tion of the water column. It also raises the phytoplankton growth rate. Thus, stock can accumulate, producing a "spring bloom". By late spring or summer, nutrients become exhausted in the surface layer, growth slows, and loss to increasing grazer stocks reduces the phytoplankton stock to a low but varying level. Summer variations come from intermittent injections of nutrients from depth (storms). In autumn illumination is still good, many of the grazers have gone into resting phases in anticipation of winter (or because late summer–autumn water temperatures are the highest of the year), and nutrients begin to be supplied to the surface by strengthening winds. The result often

is a fall bloom. The onset of winter winds mixes this away and returns the system to low winter stocks and low winter activity rates. That explanation is basically right. For sites that exhibit such blooms, it holds up under quantitative investigation. There are many details to consider, since investigation of blooms has been a major focus of biological ocean-ography throughout the 20th century.

Critical depth theory

It is not uncommon for the onset of the spring bloom to be explained with only passing reference to the grazing process. This produced the "critical depth" theory of Gran and Braarud (1935) and Sverdrup (1953). As originally formulated, grazing **was** incorporated in a vague way. The notion is that the relative rate of plant growth, that is stock increase (dP/dt) per unit stock (1/P), equals

gross photosynthesis − respiration:
$$1/P(dP/dt) = PS - R.$$

Sverdrup suggested that photosynthesis, PS, de-creases with depth in proportion to the exponential decrease of irradiance, while respiration, R, might be **roughly** constant with depth. He took respir-ation to be "community metabolism", that is, all removals including both plant respiration and stock reductions by grazers (as emphasized in a comment by Smetacek and Passow 1990). Several different vertical levels are defined by the inter-actions of PS and R (Fig. 1.3). The community **"photosynthetic compensation depth"** is the verti-cal level at which the local value of (PS − R) = 0. Again, this definition applies to the metabolic activity of the whole community, not just of plants. A plant physiologist would define a photosynthetic compensation depth as the level where net primary production (photosynthesis less **plant** respiration) = 0. That would be somewhat below the level intended by Sverdrup, because grazing increases the loss term. Well below either version of compen-sation depth is the **"critical depth"**, the level at which the vertical integral of (PS − R) = 0. The only losses involved in this original definition of

Fig. 1.3   Features of Sverdrup's (1953) critical depth model for spring bloom initiation. Gross photosynthesis decays exponentially downward in response to progressive dimin-ution of irradiance according to Beer's Law ($I_Z = I_O e^{-kZ}$, where k is the coefficient of extinction due to absorbance and scattering, and Z is the depth). Net photosynthsis is shifted left by the assumed depth-invariant community respiration. Shaded areas show zones of positive (above the **compensa-tion depth**) and negative (below) net photosynthesis down to the **critical depth** where the integrals are equal. (After Sverdrup 1953.)

critical depth are from community metabolism of photosynthate. In addition, however, there will be losses from the upper, lighted layer through vertical mixing. In general, mixing **above** the first signifi-cant thermal step in the water column is rapid, for all practical purposes instantaneous. Mixing **through** this thermal step is slow. Sverdrup predicted that spring blooms would get under way at the time in the heating of the water column when the thermocline rose above the critical depth. Before that time, mixing would make 1/P(dP/dt) negative for the euphotic zone overall. Afterward, mixing losses would be small and stock would accumulate above the thermocline.

This critical depth theory works, roughly. Sverdrup (1953) showed data (Fig. 1.4) from a weathership stationed in the high-temperate

Fig. 1.4 Data for 1949 from Weathership "M" (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate k values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April–May, when critical depth exceeded the mixing depth. While these data are crude, the observation set has never been duplicated. (After Sverdrup 1953.)

North Atlantic (66°N, 2°E) where phytoplankton increase did closely coincide in timing with water column stratification. In general, blooms, where they are important, occur shortly after the first, non-transient establishment of the seasonal thermocline. Bloom timing varies between years according to variation in the surface heating. Where grazer stocks are very low in winter and early spring, the theory works well because grazing is such a minor part of "community" respiration. Grazing is difficult to measure, so the theory can be applied more readily if it is negligible. This is approximately true in the mid-latitude North Atlantic close to the coast (that is, in **neritic** waters), so the theory works well for the "classical" seasonal cycle problem. In other regions, the mixing depth remains important, but it sometimes works in a

somewhat different fashion (e.g. see Nelson and Smith 1991).

Critical depth and mixing combine differently in shelf seas, since the bottom acts as a lower limit to vertical mixing. A study by van Haren *et al.* (1998) provides high-resolution time series of chlorophyll, temperature, irradiance, and wind speed gathered by automatic instruments mounted on a tower sited at 45 m depth in the central North Sea. They measured phytoplankton stock as chlorophyll concentration using a fluorometer (Box 1.3). Chlorophyll increased (Fig. 1.5) from the mid-winter level of 0.5 mg m^{-3} as soon as **photosynthetically active radiation** (PAR) exceeded 6.5 µE m^{-2} s^{-1}, an approximation of the physiologic compensation (PS − R ≥ 0) intensity in these waters (Tett 1990). That occurred in the later half of February. Stock

Box 1.3

Because they contain chlorophyll, phytoplankton can be quantified *in situ* by exciting, then measuring, their fluorescence. Water adjacent to a small window on an *in situ* **fluorometer** (Box Fig. 1.3.1) is flashed with a xenon lamp filtered at 455 nm, and the resulting fluorescence due to chlorophyll at 685 nm is measured with a photomultiplier circuit. Corrections for light source

variation are made by reporting the ratio of fluorescence to light intensity measured internally in the housing. Van Haren *et al.* (1998) made periodic calibrations of this signal by filtering plants from the vicinity of the sensor and extracting chlorophyll for determination by high-performance liquid chromatography (HPLC). Fluorescence measured in this way varies strongly with external illumination, since chlorophyll decouples in the dark from the energy transfer system in the chloroplasts of the plant and fluoresces more strongly. Thus, there is artifactual day–night and depth variation (Box Fig. 1.3.2). Careful accounting for such effects must be incorporated in field studies with fluorometers. These instruments are deployed as vertical water column profilers and as moored recorders.
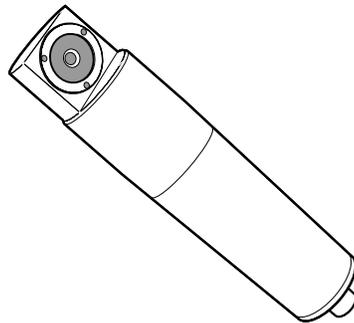
Theory of operation
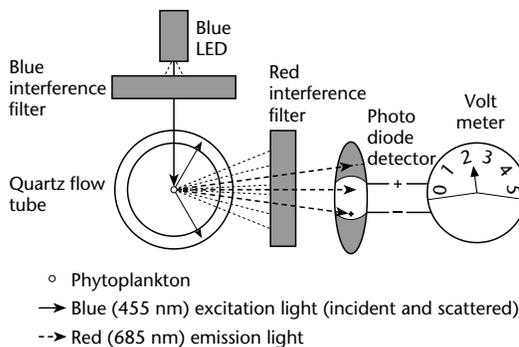
Box Fig. 1.3.1 A commercial fluorometric chlorophyll *a* recording device with a diagram of its operating principle. Blue light is beamed into an observation space and the resulting red fluorescence is measured by a detector and recorded. (Chelsea Instruments.)
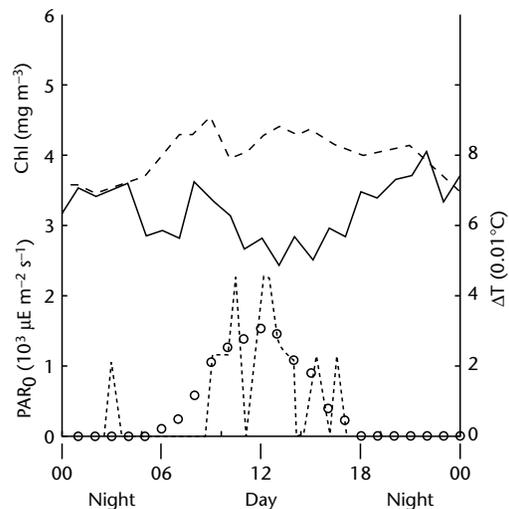
Box Fig. 1.3.2 One day of hourly data from van Haren *et al.* (1998), showing the "artifactual" effect by which greater illumination (at 11 m vs. 23 m) reduces fluorescence of chlorophyll.

increased from there, the bloom showing some recurring peaks between 3 and 6 mg Chl m^{-3} from about 10 March through mid-April. Peaks were associated with lapses in wind speed (shown as the cube of wind speed, $|W|^3$, a measure of mixing power). Stratification within the 45 m

water column, shown as a temperature difference measured by thermistors at 11 and 23 m, only set in about 20 April, after the bloom had passed.

Clearly, losses due to mixing downward in the shallow North Sea ecosystem are not fatal to phytoplankton, which are returned upward by
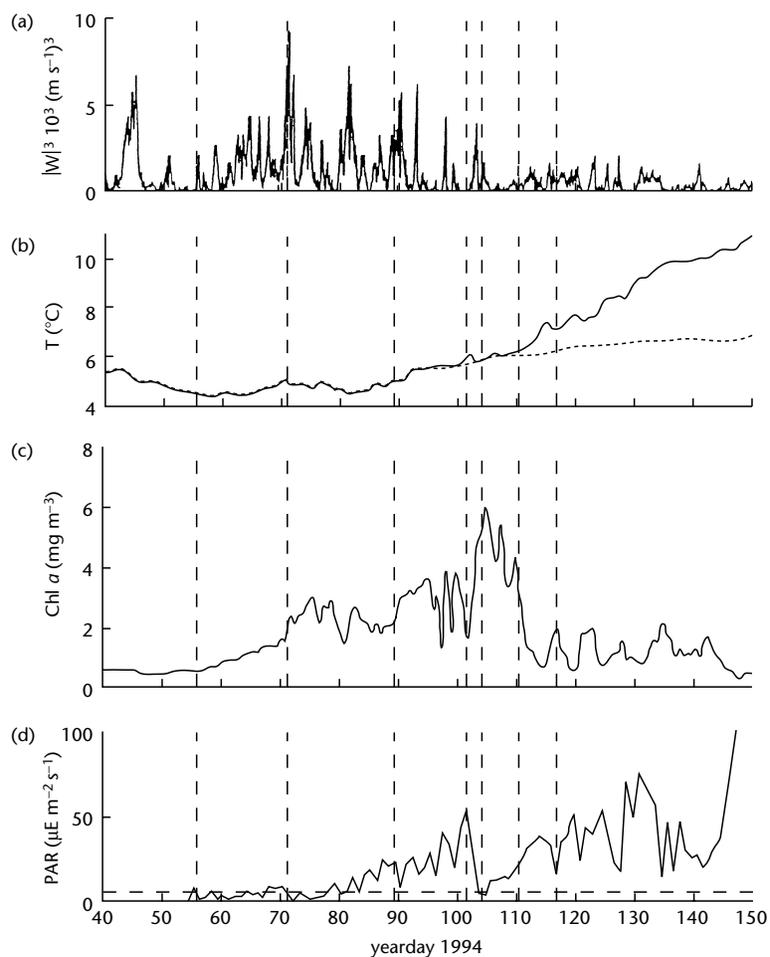
Fig. 1.5 Time series from a shallow mooring site in the North Sea of (a) wind-mixing force, (b) temperature at 11 m (solid) and 43 m (dashed), (c) chlorophyll *a*, and (d) photosynthetically active radiation (PAR) at $Z = 11$ m. Chlorophyll *a* began to increase as soon as PAR exceeded $6.5 \, \mu E \, m^{-2} s^{-1}$, an approximation of the physiological compensation $(PS - R \geq 0)$ intensity in these waters (Tett 1990), shown by the flat dashed line in (d). Note that chlorophll increased long before water column stratification, indicated by separation of temperature curves for 11 m and 43 m. The bottom at 45 m limits mixing to within the euphotic zone after year day 57. (After van Haren *et al*. 1998.)

mixing. A critical depth model is useful here, but only in the sense that it predicts a bloom will start when the critical depth is driven below the seafloor by increasing light. After 20 April, chlorophyll at 11 m oscillated between 0.5 and 2 mg m^{-3}, possibly responding to nutrient pulses from the bottom. Light alone appears to control the onset of the bloom. Nutrient limitation presumably stops it; nitrate and silicate moved from winter values of 6.5 and 2.5 μM, respectively, to values in April of 0.5 and 0.3 μM. Those levels should not be limiting to all phytoplankton, but certainly would be to larger cells such as the diatom *Guinardia flaccida*, which is the dominant phytoplankter of the bloom period. Nothing can be said from

these data about how phytoplankton are removed from the stock over the course of the bloom. Such early season blooms are reported for many shallow, coastal sites including Georges Bank and Narragansett Bay.

The JGOFS North Atlantic bloom experiment

Oceanic, as opposed to neritic, means well out to sea, where influences of the bottom and of inputs from the coast, like river inflow, are small. The oceanic Atlantic north of 45°N, particularly on the eastern side, mixes to depths exceeding 250 m

in winter (Glover & Brewer 1988). Deep mixing brings abundant major nutrients to the surface, with nitrate exceeding 6 μM, and it flushes most of the phytoplankton out of the illuminated upper strata. Chlorophyll is reduced to less than 0.05 mg m^{-3}. Stratification re-establishes in late March or April, sometimes May, and a bloom ensues lasting about 50 days. This was studied in 1989 by a cooperative international program, the Joint Global Ocean Flux Study (JGOFS). Further work was done in the Biogeochemical Ocean Flux Study (BOFS) by European oceanographers in

1990. One of the most intensely studied areas encompassed three stations ranging from 46° to 49°N along about 18°W, well out to sea due west of Cornwall. By the time all the ships and scientists arrived on April 25, 1989, stratification was just setting in (Fig. 1.6) and phytoplankton stocks were still low (0.5 mg m^{-3}). A bloom ensued, raising chlorophyll to 2.6 mg m^{-3}, and lowering major nutrients (Fig. 1.6). Similarly, at 49°N, 18°W in 1990, stocks increased until mid-May, when there was a peak at about 2.8 mg m^{-3}, a typical peak for the spring bloom in this region. Most of the
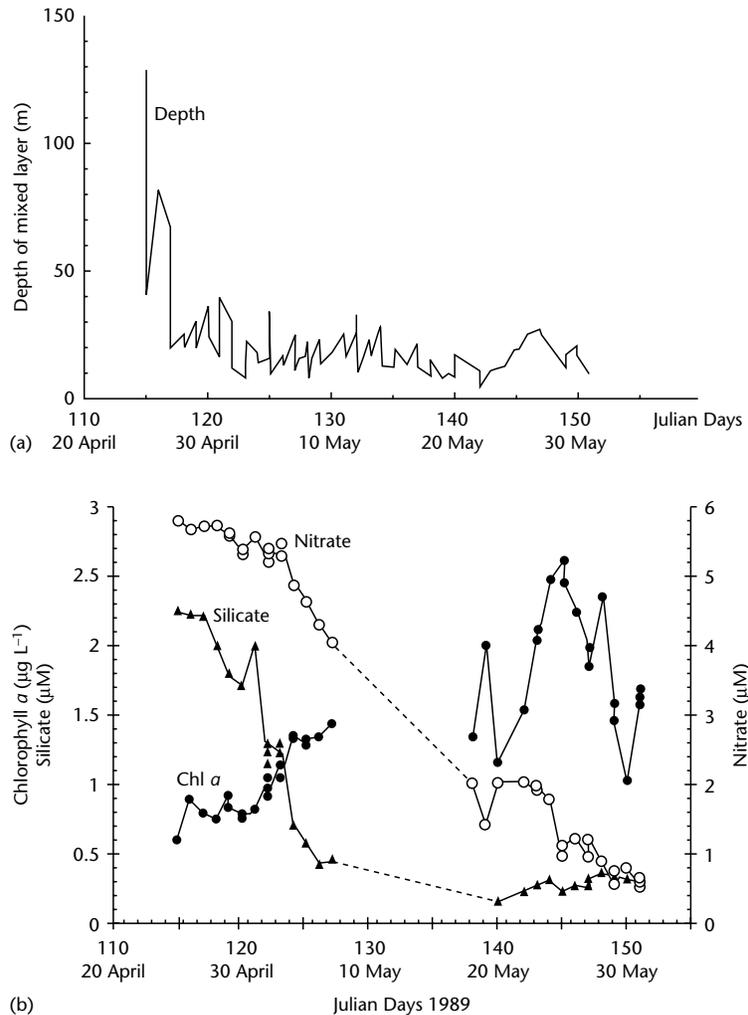
Fig. 1.6 (a) Time series of mixed layer depth at 47°N, 20°W, April–May 1989. Observations began just before sharp shoaling of the seasonal thermocline. (After Lochte et al. 1993.) (b) Time series of chlorophyll, nitrate, and silicate at 46°N, 18°W in April–May 1989. (After Sieracki et al. 1993.)

enhanced stock was very close to the surface, only extending below about 25 m at the very peak of the bloom (Savidge *et al.* 1992). In both studies, nitrate came down as phytoplankton went up. Plotting chlorophyll vs. nitrate for the 1990 data (Fig. 1.7) shows the inverse correlation is strong, and the connection is certainly direct: the growing phytoplankton reduce the fixed nitrogen, incorporating it in their organic constituents (principally proteins, but also DNA and other compounds with amine groups). When the nitrate, phosphate, silicate, and other nutrients are reduced, phytoplankton growth slows.

Over this entire region on any given date, the bloom appears to be extremely patchy, to occur in **mesoscale** (a few 10s to 100 km) blobs. This is evident from satellite observations even when lots of individual satellite images must be combined over a fairly long period to get a complete picture (Esaias *et al.* 1986). The JGOFS North Atlantic bloom experiment showed that this is an effect of mesoscale eddies, which are always scattered over this region (Robinson *et al.* 1993). There were three cyclonic (anticlockwise in the northern hemisphere) eddies (Fig. 1.8) evident from satellite altimetry in the region of the observational study during April–May 1989. The sea surface of a cyclonic eddy slopes up from the middle to the rim due to the Coriolis effect. This height difference can be estimated by radar ranging from a satellite, and eddy velocity approximated geostrophically from the slope (Fig. 1.8, right inset). The eddies evolved
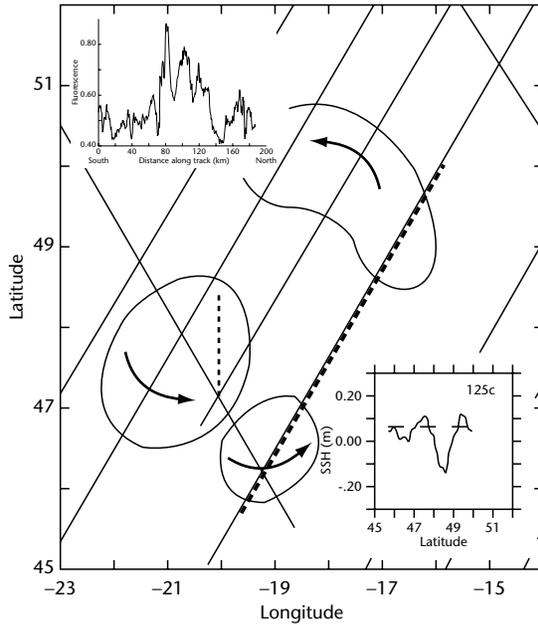
Fig. 1.8 Outlines of three cyclonic eddies identified by satellite altimetry in the JGOFS North Atlantic bloom observation area. Thin, oblique lines are the tracks of the satellite. The heavy dashes indicate the portion of satellite track for which sea surface height (SSH) is shown in the right inset. (After Robinson *et al.* 1993.) The dashed line in the middle eddy is the track of a LIDAR-carrying aircraft. The left inset shows along-track chlorophyll estimated by flash fluorometry. A downward directed, blue laser (LIDAR) is pulsed downward from an airplane. A detector quantifies the red fluorescent return, which is converted with calibration data to estimates of near-surface chlorophyll *a*. (After Yoder *et al.* 1993.)
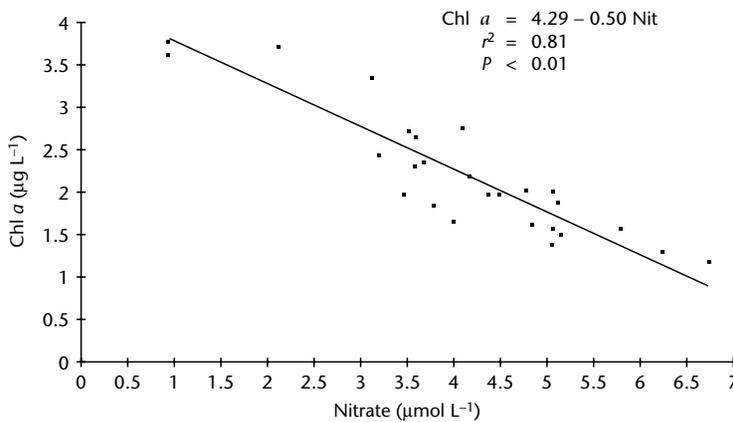
Fig. 1.7 Scatter diagram showing the relation between chlorophyll *a* and nitrate concentrations during the BOFS observations at 47°N, 20°W in 1990. Effectively this is a time series from lower right to upper left during the increase phase of the bloom. Subsequent points would drop vertically to the abscissa. (After Barlow *et al.* 1993.)

in shape, but were persistent. Cyclonic eddies are regions of greater vertical stabilization of the water column, and the spring bloom tends to advance in them earlier or faster so that they become high-chlorophyll patches (Fig. 1.8, top left inset).

Similar patterns also occur in the phytoplankton distributions after the main spring bloom, as seen in June to the south of Iceland (Fig. 1.9) by photographing reflections from phytoplankton carrying tiny, reflective calcite plates. The importance of the mesoscale eddy field to oceanic phytoplankton is evident from this picture. Moreover, coastal waters exhibit similar patchiness for different dynamic reasons. Chlorophyll concentrations estimated at stations over the continental shelf in the New York bight (Fig. 1.10) show that phytoplankton stock during the spring bloom varies in swirling, active patterns. These are not entirely aligned with the flow, because complex interactions of growth patterns and horizontal mixing establish the pattern at any given moment.
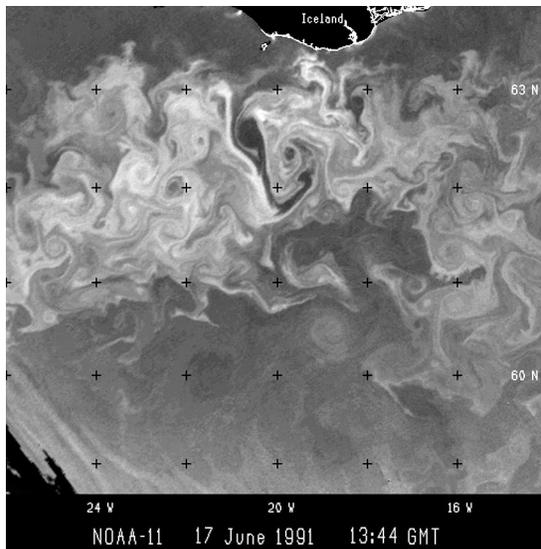
Fig. 1.9 Advanced very high-resolution radiometer (AVHRR) image from the visible spectral band of the Atlantic Ocean south of Iceland. Lighter colors are from higher reflectance of sunlight caused by blooming phytoplankton (*Emiliania huxleyi*) bearing plaques of calcite (coccoliths) on the cell surface. (Courtesy of Steve Groom, Plymouth Marine Laboratory, similar to fig. 2 in Robertson *et al*. 1994.)

Species successions in the spring bloom

No floristic analysis was included in the JGOFS North Atlantic bloom study. Microscopic identification of phytoplankton has almost become a thing of the past. To get an idea of the diversity of plant community development during blooms, we will have to look at data decades old (which is not in itself a problem). However, Barlow *et al*. (1993) did examine this question indirectly in the JGOFS project. As we will consider later in some detail, different algal groups have differing complexes of chloroplast pigments other than chlorophyll *a*. In particular, diatoms (which are non-motile in opal shells) carry fucoxanthin while prymnesiophytes (small flagellated cells) carry 19′-butanoyloxyfucoxanthin, both of which are photoprotective pigments preventing damage to the chloroplast at high irradiance. At a so-called Langrangian station following a drifter with a drogue at 20 m from 49°N, 19°W along a southeasterly track, the relative pigment composition changed (Fig. 1.11), from predominantly fucoxanthin to predominantly 19′-butanoyloxyfucoxanthin, implying a shift in phytoplankton from mainly diatoms to a preponderance of prymnesiophytes. This happened in less than 10 days, after the peak of chlorophyll *a* but while it remained relatively high ($> 1.5\,\mathrm{mg\,m^{-3}}$). Thus, the spring bloom is not driven by just the production needed to raise stock levels once. The plants are turning over rapidly and an initially dominant species can be replaced by another. Shifts of this sort, from diatoms to flagellates, can be caused by slowing of diatom growth due to silicate depletion occurring before nitrate or phosphate depletion limits growth rates for all phytoplankton (Sieracki *et al*. 1993). Shifts of this kind can also be due to water flow and horizontal mixing, so it should not be immediately interpreted as a strictly biological replacement process. Langrangian tracers do not fully guarantee that a study will be looking solely at the biological aspects of change. Different mesoscale features can be promoting different types of phytoplankton. Those can be mixed and drifters can slip from one into another. Sorting out the effects of flow from those of biological
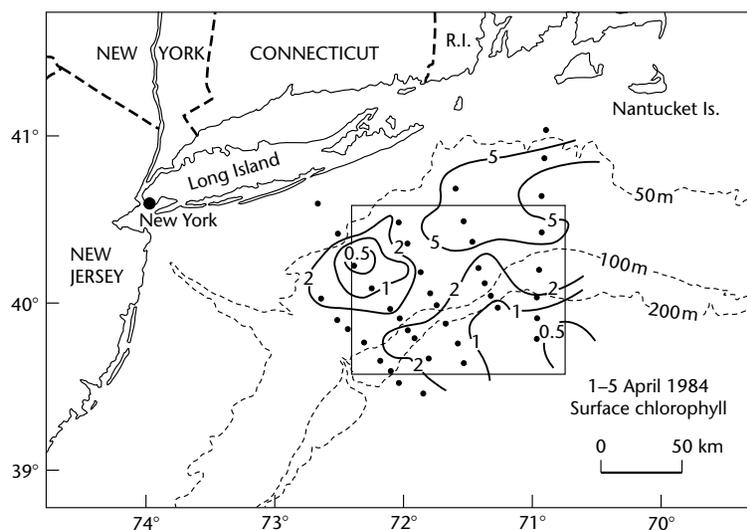
Fig. 1.10 Chlorophyll contours ($mg\,m^{-3}$) over the continental shelf and slope in the New York bight as measured from a ship. (After Walsh *et al*. 1988.)

change is the most bedeviling problem in biological oceanography.

Many, although not all, of the older studies were based on tows of fine mesh nets (see Box 1.4). Thus, a large part of the phytoplankton, the nano- and picoplankton, was lost through the pores. For example, nets of approximately $60\,\mu m$ mesh were towed fairly frequently from weatherships at
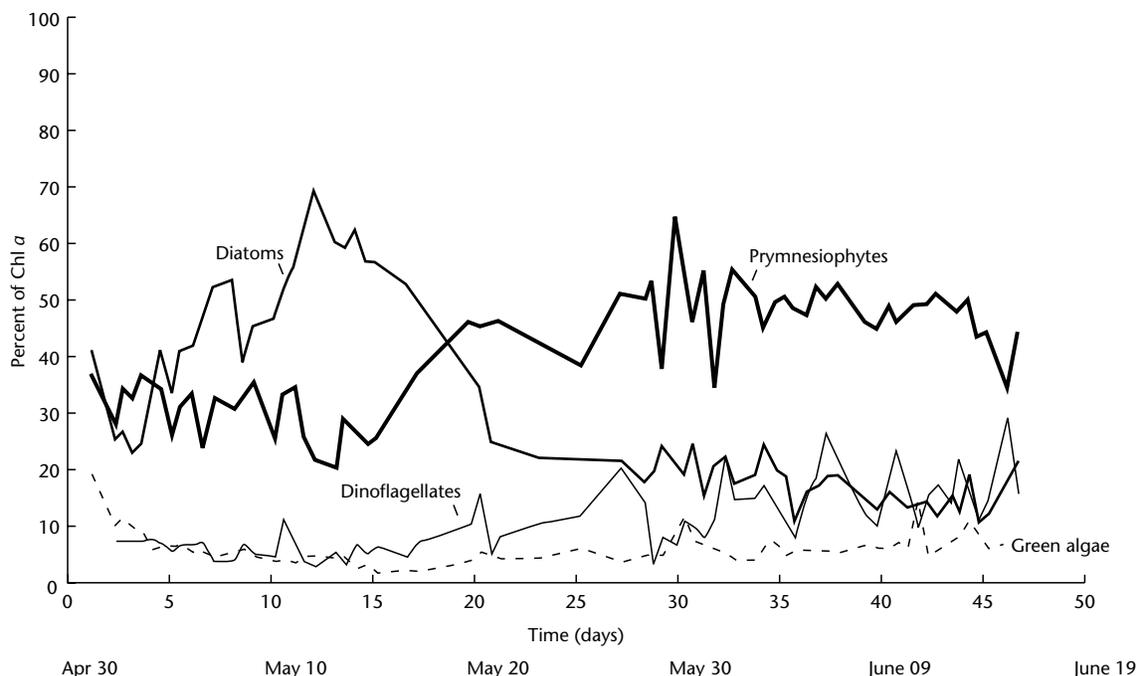
Fig. 1.11 Fractions of chlorophyll *a* associated with accessory pigments from different phytoplankton groups (as labeled) during the course of the spring bloom at approximately 49°N, 20°W in 1990. (After Barlow *et al*. 1993.)

Box 1.4

Biological oceanography is very dependent upon filtration processes to concentrate and separate particles and organisms from the main constituent of oceans, seawater. Filters used range from the tiniest submicron porosities (to 0.025 μm) to about a decimeter in large trawls. Fine filters include paper (now little used), glass-fiber pads, porous silver, and products of several schemes for making minute pores in plastic disks. For example, the round pores produced by neutron bombardment of thin, polycarbonate or polyester sheets can be precisely sized and very uniform (©Nucleopore or, generally, ''particle track etch'' filters). Similar uniformity has recently become available in honeycomb structures of aluminum oxide (to 0.02 μm) offering high relative pore area and, thus, flow rates. Nets for capture of plankton are usually cones of loosely woven fabric. Originally made from silk, modern netting is precisely woven of nylon melted together at the thread crossings. The holes are square and mesh size is specified as the length along the sides of the holes.

Smallest holes are about 5 μm, the largest in common use are 1 mm. Since fabric can twist and stretch, mesh sizes should be selected so the diagonal measure is shorter than the narrowest axis of the target organism. Phytoplankton nets are usually 20−60 μm; zooplankton nets are commonly 50−1000 μm.
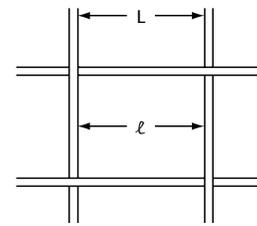
"Mesh size" = l Porosity (%) = $100 \, (l^2/L^2)$

Station "I" in the Irminger Sea at (60°N, 20°W) in the late 1940s (Corlett 1953). That means that most of the phytoplankton went through the meshes, while phytoplankton large enough to be retained were either diatoms or dinoflagellates. These do show a definite succession: diatoms bloom first, dinoflagellates later (Fig. 1.12). That is considered, on the basis of modest oceanic data, to be typical. While the date of the diatom peak differed by as much as a month over just three years, the dominant diatoms at the abundance peak were the same each year. They were *Chaetoceros laciniosus* and *Chaetoceros affinis,* chain-forming, centric species. The autumn bloom, which is quite definite and prolonged at this site, was dominated by *Rhizosolenia alata*, a needle-like diatom. Dominant dinoflagellates were all *Ceratium* species: *tripos*, *fusus*, and *furca*, all abundant in all three years after the initial diatom outburst. Given sufficient silicic acid in the euphotic zone, diatoms grow faster than dinoflagellates, so they bloom first. Dinoflagellates come along later, when diatoms have depleted the silicic acid and lost stock to sinking and grazing.

A nearshore, weekly time series from Long Island Sound by Conover (1956) shows another feature of spring blooms. In shallow water the spring bloom can be superimposed over chlorophyll levels that are greater than 2 μg L^{-1} (mostly 5 μg L^{-1}) throughout the year, levels that would be bloom maxima in oceanic areas. The cyclic pattern is the same, it just occurs against a higher background. As in the North Sea case examined earlier, the bottom is above the critical depth, so the "spring" bloom can begin with only a slight increase in day length and sun angle (Fig. 1.13). Nutrients, particularly nitrate, were used very rapidly during the diatom bloom and nitrate stayed low until September. During the bloom peak, diatoms, mostly *Skeletonema costatum*, made up the majority of cells counted in formalin-preserved samples. They were replaced by much lower numbers of dinoflagellates, mostly *Ceratium*, in summer. Conover was aware that microflagellates were also present – phytoplankton smaller than 5 μm diameter from several, distinct algal divisions. They carry most of the chlorophyll from May through December, but they were not preserved by Conover's technique. The original
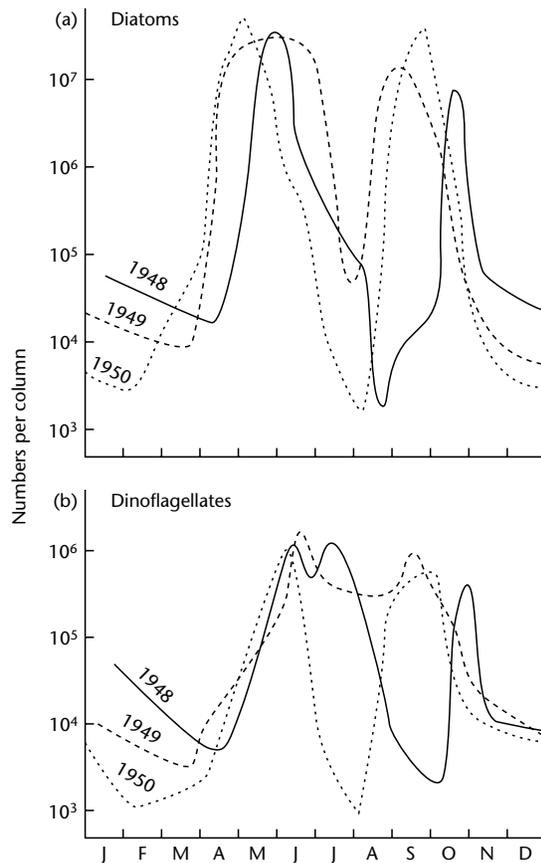
Fig. 1.12   Seasonal cycles of (a) diatoms and (b) dinoflagellates at Station "I" (60°N, 20°W) in the North Atlantic. Diatoms bloom, and then are replaced by dinoflagellates. Bloom timing varies among years by a month or more. Cells were counted with a microscope. (After Corlett 1953.)

data ran to 95 weekly samples, a standard we need in more oceanic studies.

A simpler demonstration of the importance of small cells in late stages of the seasonal succession can be obtained with filters by comparing amounts of chlorophyll passing and retained by some arbitrary pore sizes. At the end of the spring bloom in the Gulf of St. Lawrence (Tamigneaux *et al.* 1999), cells > 5 μm (most of them probably considerably larger than that) contained 78% of chlorophyll, while a month later 95% of chlorophyll passed through a 5 μm filter. Most phytoplankton biomass

after nutrient depletion by the spring bloom is ultraphytoplankton. In general, the lower the phytoplankton biomass, the greater the proportion that will be in very tiny cells (Fig. 1.14). This lesson, that blooms are constituted of microphytoplankton while ultraplankton sustain lower and more constant stocks, appears to fit everywhere in the oceans. It is probably attributable to a difference in the grazing regime to which each is subject. This will be covered in more detail later, but the basic explanation is that tiny plants cannot build up large biomass because they are subject to grazing by protozoans. Heterotrophic ciliated and flagellated protozoa can have maximum rates of population increase even greater than those of their phytoplankton prey. Thus, their stocks and grazing potential can rapidly overtake any increase in the nanoplankton or ultraphytoplankton. Phytoplankton greater than $20-30$ μm are only prey to larger, metazoan grazers with long life cycles and, thus, slow response times. The resulting lag in grazing response allows stocks of larger phytoplankton to "bloom".

The fate of bloom phytoplankton

A key aspect of spring bloom dynamics is the fate of phytoplankton once they have grown. Most often the phytoplankton increasing dramatically in spring bloom are diatoms, cells of intermediate to large size (> 10 to 70 μm or more in diameter) with opal cell walls (Chapter 2). They have a large central, water-filled vacuole with electrolytes modified relative to seawater so as to maintain nearly neutral buoyancy. This capability fails under nutrient stress, and the cells become "senescent" and begin to sink. In both coastal waters and the oceanic North Atlantic the spring bloom terminates by sinking-out of these relatively large cells (Smetacek 1985). They progressively flocculate on the way down and reach the bottom in a few days or weeks as a major pulse of organic "particle flux". Throughout the course of the bloom, however, substantial amounts of phytoplankton are eaten by so-called mesozooplankton, a mixture of small, but not microscopic, animals (appendicularians,
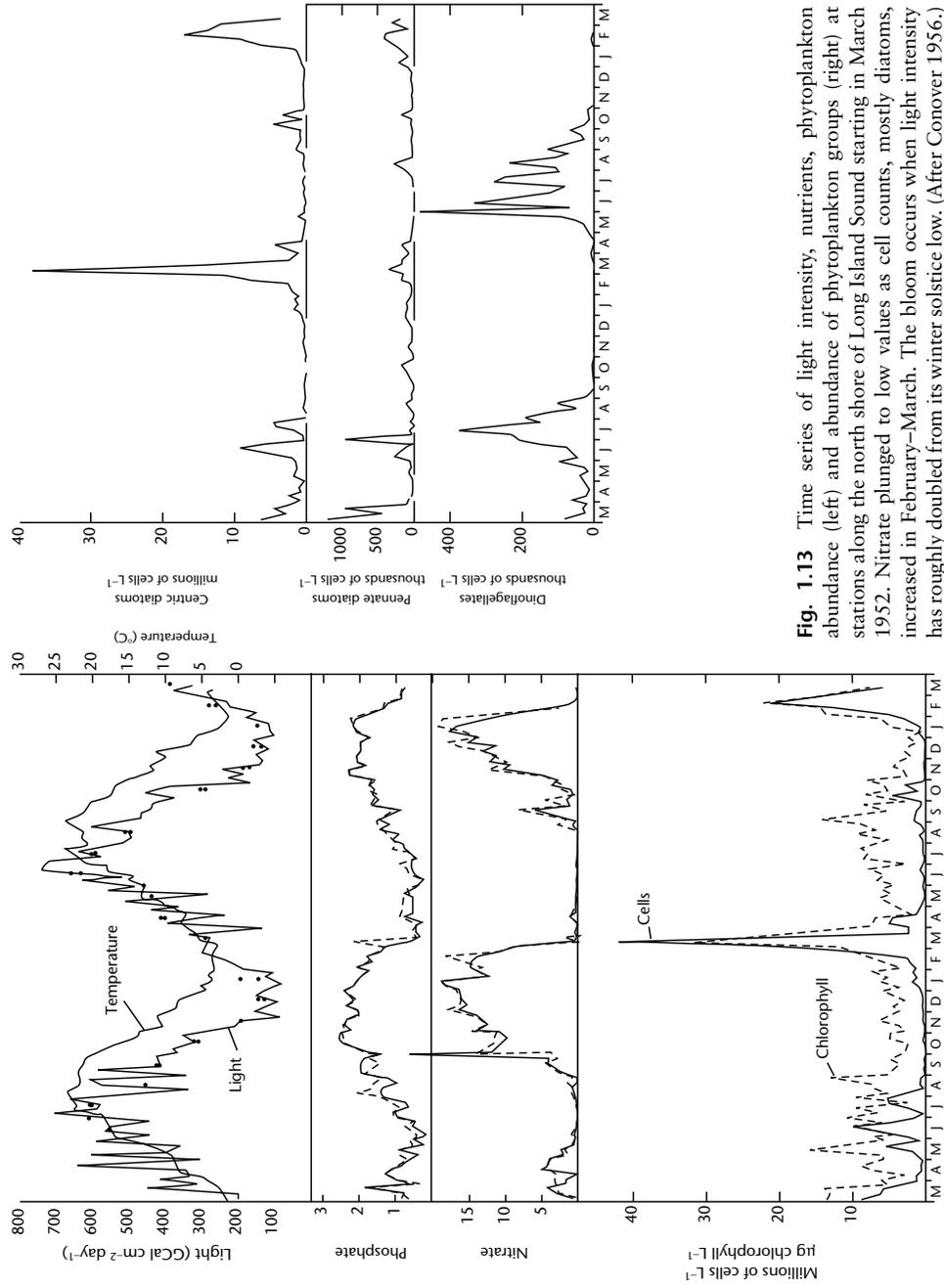
Fig. 1.13 Time series of light intensity, nutrients, phytoplankton abundance (left) and abundance of phytoplankton groups (right) at stations along the north shore of Long Island Sound starting in March 1952. Nitrate plunged to low values as cell counts, mostly diatoms, increased in February–March. The bloom occurs when light intensity has roughly doubled from its winter solstice low. (After Conover 1956.)
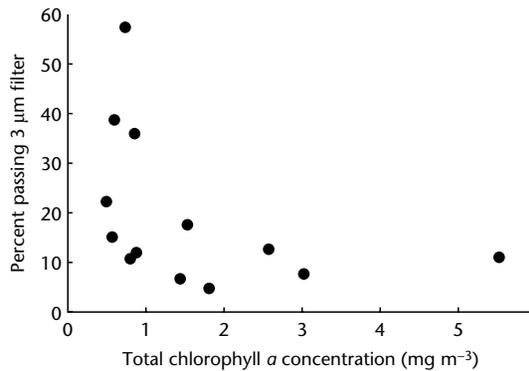
Fig. 1.14 Relation in the southern North Sea between phytoplankton standing stock as chlorophyll and the fraction of chlorophyll passing a 3 μm filter. (After Iriarte & Purdie 1993.)

copepods, euphausiids, and others). We will meet them later. The exact grazing rates during the bloom are a continuing issue, but grazing creates considerable phytoplankton stock turnover well before nutrients are depleted. The grazers return some of the elements in the phytoplankton they eat to the water as excretory products. These are then once more available for reuse by phytoplankton. They are said to be "regenerated nutrients".

Critical depth theory, again

If critical depth theory works anywhere, it must work in the oceanic North Atlantic (Smetacek & Passow 1990). The North Atlantic is a strongly seasonal ocean that mixes deeply enough in winter for vertical exchange to keep phytoplankton stocks low until stratification sets in during spring. Platt *et al.* (1991) reformulated Sverdrup's theory to take account of modern data describing rates of photosynthesis as a function of available light (the "P vs. I" relation). The reformulation was mathematically abstruse, and they showed it differed by a maximum of about 10% from Sverdrup's simple linear P vs. I relation (which gives a simple exponential decay in photosynthesis vs. depth). Next, Platt *et al.* guessed at the loss terms:

- phytoplankton respiration (4% biomass day^{-1} plus a fraction varying with photosynthesis);
- excretion of unrespired organic matter (set at 5% of photosynthesis);
- grazing by mesozooplankton (4% of biomass day^{-1}) and protozoa (5% of biomass day^{-1}); and
- cell sinking (set at 1 m day^{-1} at all depths).

They found no information upon which to estimate the variation of these losses with depth, so they stuck with the constant vertical profile adopted by Sverdrup. Fractional losses of biomass were "assumed independent of depth". That is radically unsatisfactory, but Platt *et al.* were quite right that we do not have the data to do much better. They then proceeded to calculate the critical depths for specific dates and latitudes. Their table is reduced here (Table 1.2) to show the trends.

Table 1.2   Critical depths as a function of date and latitude. (From Platt *et al.* 1991.)

		Critical depth (m)	
Date	Latitude (°N)	With just phytoplankton respiration	With all losses included
1 February	40	361	131
	50	274	97
1 March	40	447	164
	50	385	141
1 April	40	551	193
	50	521	238
1 May	40	635	237
	50	639	238
1 June	40	691	258
	50	723	270

The result approximately predicts bloom dates in the North Atlantic, for example in the venerable data from Station "M" (Fig. 1.4). The key point is that the greater the daily irradiance (that is the lower the latitude and the later in the spring) the deeper the critical depth. Increasing plant growth rates near the surface increase the vertical integral of production, driving the critical depth down. Spring blooms do not occur in this ocean until significant stratification sets in above the levels calculated. Roughly, the theory works.

Alternate scenarios

The critical depth mechanism probably operates in most spring blooms. However, those relationships are not the only possibility. Townsend *et al.* (1994) have suggested that the key aspect of vertical water column structure is not stratification but actual mixing. In the absence of recurring winds, mixing can slow to the modest rates of diel convection. Thus, a very calm period could lead to a near-surface bloom without stratification, simply because the phytoplankton growth rate is maximal near the surface. They produced a summary of examples from the literature showing that timing of "spring" blooms is variable in the temperate North Atlantic, with first events as early as February and as late as the end of April. Often subsequent windstorms will disperse such initial blooms and replenish the nutrients they use, setting up the surface layer for new blooms. Thus, for example, the JGOFS North Atlantic bloom experiment may have been looking at only the last of several pulses of high phytoplankton stock. Overall production would be much higher than just one bloom would generate.

Further, this opens the possibility that an established plant stock will intercept more light in the upper water column, thus enhancing upper layer warmth and establishing thermal stratification. In other words, the order of events (and causation) can be calm → bloom → stratification, rather than stratification → bloom. Townsend

et al. (1994) also argued that early blooms may be enabled by the greater inhibition of grazing by cold temperature than of photosynthesis. The data they adduce in this regard are suspect, but the idea may have some validity. Stramska and Dickey (1993) showed chlorophyll and temperature data from fluorometers and thermistors moored in deep water south of Iceland during April–May 1989. A bloom, which eventually reached 4 mg Chl a m^{-3}, was underway, if still incipient, a week prior to measurable stratification above 100 m (which is, however, well above the critical depth; Table 1.2). Stratification then set in immediately. This seems to fit the alternate causal order. However, Stramska and Dickey's convincing model of the interactions among available irradiance, enhancement of absorbance by phytoplankton pigments, and mixing (a function of measured wind speed) suggests that the effect of pigment on stratification is at most a one day acceleration in the bloom, an acceleration requiring wind speeds of less than 10 m s^{-1} (20 kts). However, at the peak of the bloom the model suggests that light absorption by phytoplankton could have shoaled the bottom of the mixed layer by about 5 m. Eventual shoaling of the heated layer is probably a larger, more important effect than acceleration of the bloom. Concentration of heat produces higher surface temperatures.

Seasonal phytoplankton cycles in other regions

As stated at the outset, seasonal cycles of phytoplankton standing stock that include a spring bloom are characteristic of most temperate coastal waters and occur across the northern North Atlantic. These cycles have attracted great interest because of their proximity to very active laboratories. In a way, the interactions of changes in illumination, mixing, and nutrients with phytoplankton growth and zooplankton grazing that produce, then diminish, the spring bloom constitute the fundamental dogma of biological oceanography. They are the subjects of vigorous efforts to model their

dynamics. We will examine the components of the interactions and the models in some detail. However, these dynamics do not pertain over most of the world's oceans. Seasonal cycles in the vast subtropical gyres, the equatorial zone, upwelling areas, and high-temperate oceanic regions of the Pacific are different. Each of these systems exhibits cycles of different form, and in each case for different reasons. Some of that is understood. Much of that understanding is through contrasts to pelagic ecosystems with spring blooms.