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Reviewed work(s):
Source: *Annual Review of Ecology and Systematics*, Vol. 19 (1988), pp. 19-38
Published by: Annual Reviews
Stable URL: http://www.jstor.org/stable/2097146
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Ann. Rev. Ecol. Syst. 1988. 19:19–38
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MARINE PLANKTON FOOD CHAINS

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INTRODUCTION: THE CLASSICAL VIEW OF PLANKTON FOOD CHAINS

The view on the ecology of marine plankton has changed significantly within the last decade. In some respects the change is sufficiently dramatic to make some authors speak about a "change in paradigm" (84). The new picture of plankton dynamics includes the recognition that phototrophic and heterotrophic microorganisms play a substantial and sometimes dominating role in the cycling of matter in the sea, that plankton food chains include a higher number of trophic levels than hitherto believed, and that a large fraction of the primary production is not consumed directly by herbivorous consumers but is channelled through a pool of dead organic matter before it becomes available—via bacterial production—to phagotrophic organisms. In this latter respect the structure of planktonic systems resembles benthic and terrestrial systems.

This changing view is remarkable for more than one reason. Among different types of ecosystems, that of the open sea was long considered the simplest and best understood. Many ecology textbooks used marine plankton to introduce the concept of food chains. A graphical presentation might be in the form of a pyramid with its base representing primary producers; above them two horizontal layers represented zooplankton and fish, respectively; and at the top a fisherman (or a whale) represented the highest trophic level. While this essentially remains correct, it has certainly proven to be an incomplete picture of pelagic food chains.

Modern biological oceanography began at the turn of the century. During the following decades it developed into an established discipline which successfully explained fundamental aspects of plankton dynamics. Organic

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production in the sea depends on phytoplankton, in particular, diatoms and dinoflagellates. These organisms are consumed by zooplankton such as copepods, which in turn serve as food for small fish which end up as prey for larger fish. While the species diversity of zooplankton was recognized, the concept of pelagic food chains was a very simple one, illustrating the point that food chains cannot include more than about five levels because of the limited efficiency in the transfer of organic carbon from one trophic level to the next. Early on it was recognized that photosynthetic productivity is usually limited by the availability of mineral salts and in particular by nitrogen. Since particulate organic material tends to sink to the bottom and become mineralized there, regenerated mineral nutrients accumulate in deeper waters beneath the photic zone. In waters permanently stratified thermally, the photic zone becomes depleted of nutrient salts, and this explains the low productivity of most tropical seas. In temperate seas where the thermal stratification breaks down seasonally, mineral nutrients are returned to the surface waters. This results in a much higher productivity, and also explains the characteristic seasonal plankton succession in temperate waters as well as the enhanced productivity of upwelling zones.

Data eventually showed that the spatial scale of heterogeneity in plankton communities seems to be tens or hundreds of kilometers, and the temporal scale, weeks or months. With the advent of methods for the quantification of primary productivity (in particular the C-14 method which was developed around 1950), a general understanding of the pelagic ecosystem appeared to have been achieved. It also seemed feasible to make quantitative predictions, for example, of fish productivity in different seas. An account of the early history of biological oceanography is given by Mills (61). Steele's book on the North Sea (78) represents a relatively recent attempt to analyze the structure and flow of materials in the open sea according to the classical picture of the planktonic food web.

The aim of the present review is to present a picture of the planktonic food web as that picture has evolved during recent years. I then continue to discuss some aspects in more detail; particular emphasis is placed on the physiological and physical constraints of plankton organisms which explain the recent findings of biological oceanography. I conclude with a few remarks on current and future problems in plankton research.

A NEW PICTURE OF PLANKTON COMMUNITIES

The Composition of Plankton Communities

From a historical point of view our revised view of plankton food chains is largely due to the discovery that microbes (in a wide sense) play a considerably larger quantitative role in seawater than was previously recognized (7,

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67), although Lohmann (60) early in the century drew attention to the presence of organisms which were not retained by the plankton nets and filters used by his contemporary planktologists. Thus, this review begins with an inventory of planktonic communities.

Size is one possible way to classify plankton organisms, and the terminology of Sieburth (72) is useful and has become widely accepted. Organisms are classified according to logarithmic size classes, so that those measuring 0.2–2 μm are referred to as "picoplankton," those measuring 2–20 μm are "nanoplankton," those measuring 20–200 μm are "microplankton," and those exceeding 200 μm are "mesoplankton."

The principal constituents of the picoplankton are prokaryotes, although a few eukaryote, photosynthetic organisms (notably representatives of the chlorophytes) are small enough to be included in this group. The presence of heterotrophic bacteria in seawater was established long ago, but the introduction of direct counts using fluorescence microscopy increased previous estimates, based on plate counts, by about two orders of magnitude (30, 40). Numbers of bacteria range from about 10^5 in very oligotrophic or deep waters to about 5×10^6 ml^{-1} in eutrophic coastal waters. The coccoid cyanobacteria have recently proven to be a ubiquitous component of seawater. Particularly in oligotrophic waters, they may be responsible for the largest part of the photosynthetic activity (43, 47, 65, 80).

The nanoplankton includes photosynthetic as well as phagotrophic forms. Some flagellates, notably among the chrysomonads and the dinoflagellates, possess chloroplasts and also are phagotrophs. This well-known phenomenon seems to be quite common among marine nanoplankters (23). The photosynthetic nanoplankton includes a variety of pigmented flagellates (cryptomonads, chrysophytes, haptophytes, prasinophytes, and some euglenoids and dinoflagellates) as well as chlorophytes and some tiny diatoms. The phagotrophic component of the nanoplankton is composed of a variety of nonpigmented flagellates (choanoflagellates, cryptomonads, chrysomonads, bicoecids, and helioflagellates, in addition to some poorly studied types with unknown systematic affinities). Amoeboid forms also occur, but they are probably confined to the surface of suspended detrital particles and the surface film. Although ciliates and dinoflagellates mainly belong to the microplankton, some forms are smaller than 20 μm and so formally belong to the nanoplankton. The typical concentration of nanoplankton in surface waters is around 10^3 cells ml^{-1} and can range perhaps from 500 to 10^4 ml^{-1} (27). Quantification of these forms is based mainly on epifluorescence microscopy as it is used for direct enumeration of bacteria. This technique also reveals the presence of chlorophyll in individual cells and has recently been refined in various ways (e.g. 15, 37).

The photosynthetic microplankton includes the "classical" phytoplank-

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ters—first of all the diatoms and the dinoflagellates. The phagotrophs include ciliates—among which the aloricate and the loricate (tintinnid) oligotrichs dominate—dinoflagellates, radiolaria and achantharia, and some of the smallest metazoan zooplankton. One ml of seawater typically contains 1–10 microplankton organisms. Plankton organisms which exceed the size of microplankton include some giant protozoa and, of course, a variety of metazoa such as the copepods, cladocera, rotifera, etc, and larval forms of benthic invertebrates. Even larger pelagic forms are usually referred to as "nekton" and include anything from euphausiid shrimp, fish, and squids up to whales.

Pelagial life thus spans more than seven orders of magnitude in length (from <1 μm bacteria to >10 m whales). While pelagic organisms represent a tremendous diversity with respect to form and function, the great variation in size allows for some generalizations concerning the structure and function of planktonic food chains, generalizations which are based solely on considerations of scaling.

Plankton Food Chains and the Microbial Loop

While the classical picture of plankton food chains remains essentially correct, the fact that bacteria and protists typically make up about half the total biomass suggests that this description is incomplete. This is even more obvious when it is recognized that rates of potential growth and of weight specific metabolism are more or less inversely proportional to length. Consequently "microbes" are responsible for by far the largest part of the energy flow in the pelagic ecosystem.

In addition to mere quantification of microorganisms, some other early observations contributed to our contemporary view of the planktonic food web. It was found that photosynthetic nano- or picoplankton is often responsible for a large part of the entire primary production, and this is especially so in oligotrophic oceanic waters (43, 66, 81). Yet the zooplankton species do not, in general, seem capable of retaining such small food particles (48).

Another discovery was that phytoplankton cells tend to excrete a substantial fraction of the photosynthate in the form of dissolved organic material. Although accurate estimates of this are difficult to obtain, values for laboratory cultures and for field populations are typically within the range of 10–50% of the primary production (32, 54, 56).

The finding that heterotrophic bacteria constitute a substantial biomass led to the development of methods for estimating bacterial production in the sea. Most of these methods (e.g. quantification of the uptake of radioactively labelled organic compounds) could not easily be converted into estimates of bacterial generation time in situ. One reason for this is that utilizable organic compounds occur in concentrations too low to be quantified, although a very

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rapid turnover of such compounds could be demonstrated (5, 41). Yet these methods did indicate a very high bacterial activity. Among the methods currently most accepted for the quantification of bacterial growth, one is based on the frequency of dividing cells in samples of natural populations and another on the incorporation of radioactively labelled thymidine (which is assumed to be proportional to DNA-synthesis of bacteria) in incubated water samples (33, 38). These endeavors have shown that bacterial generation times in seawater typically range from a few hours to more than 24 hours, according to temperature and other conditions. Together with data on bacterial biomass this suggests that bacterial production as measured with the C-14 method may be around 20% of the primary production. Since bacterial growth efficiency is not likely to exceed 50%, apparently about half of the primary production is consumed by bacteria. Actually bacterial growth to a large extent depends on algal exudates and correlates with algal biomass (55, 56). However, since small heterotrophic cells (including the bacteria themselves) are also likely to excrete dissolved organics the fraction of the primary production directly utilized by bacteria may not be as large as suggested above.

Since bacterial numbers remain relatively stable a sink for bacterial production must exist. With very few exceptions, filter feeding zooplankters are not capable of retaining particles of bacterial size, and this also applies to the types of ciliates commonly encountered in marine plankton (26). It has been shown that consumption by heterotrophic nanoflagellates accounts for the disappearance of the bacterial production. This result is based on studies of the concentration of nanoflagellates in seawater, in conjunction with laboratory studies measuring nanoflagellate growth rates and their ability to clear bacterial suspensions (17, 24, 25). Thus, the flagellates may typically clear the entire water column of bacteria at rates ranging from 0.5 to 2 times per day. This picture is supported by experiments in which certain size fractions of the plankton are removed from seawater samples and incubated for short times. Relieving the bacteria from predation by removing nanoplankters, or the nanoplankters from predation by removing the microplankton, leads to population growth. Links of planktonic food chains are established, and production of the different components of the plankton can be estimated (3, 68, 71). Heterotrophic nanoflagellates seem also largely to be responsible for the consumption of cyanobacteria and the smallest eukaryote primary producers.

The nanoplankton forms, in turn, fall victim to the phagotrophic microplankton, among which ciliates and heterotrophic dinoflagellates may be the most important components (4, 12, 14, 58, 74). These forms together with the larger phytoplankters then enter the "classical" plankton food chain.

To describe this addition to the classical picture of planktonic food chains, the term *microbial loop* was coined by Azam et al (6), and the graphical

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presentation in Figure 1 explains the term. The model of plankton food chains assumes that (*a*) considerable variation exists in the cell sizes of primary producers, (*b*) these excrete a substantial part of the photosynthate in the form of dissolved organic material which is utilized efficiently only by heterotrophic bacteria, and (*c*) size ratios between predator and prey are constrained within certain limits. There is no doubt that it gives a qualitatively correct picture of what goes on; in addition to the evidence already presented, direct observations on successional patterns in natural waters demonstrate the microbial loop directly (e.g. 4, 25, 77).

Plankton food chains now seem to resemble terrestrial and benthic communities much more in that a substantial part of the carbon flow is channelled through detrital material and heterotrophic microorganisms. What remains is a discussion of why the food chains take this form, based on the properties of the environment and of the individual organisms, the circumstances under which the microbial loop plays a greater or smaller role, and the implications for marine productivity from the viewpoint of human exploitation of the sea—for mineral cycling and some other aspects. The second part of this review is devoted to these problems.

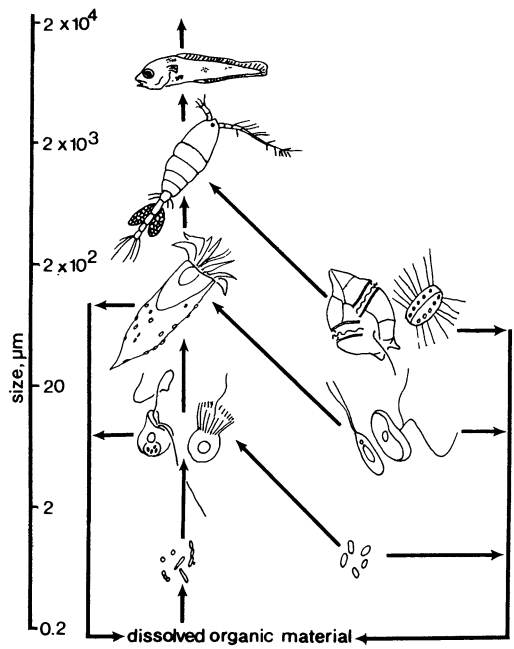

Figure 1 A schematic presentation of the microbial loop and its relation to the classical plankton food chain. The left column represents heterotrophs and the right column the photoautotrophs.

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PROPERTIES OF PLANKTON ORGANISMS AND FOOD CHAINS

Steady State Phagotrophic Food Chains

Photosynthetic organisms depend on light as a source of energy and dissolved compounds as building blocks for growth, while bacteria (other than photosynthetic ones) depend on dissolved compounds for their assimilatory as well as for their dissimilatory metabolism. All other important constituents of the plankton are phagotrophs depending on particulate organic material, that is, other organisms for food. Due to mechanical and physiological constraints, food chains formed by phagotrophic organisms have certain characteristic properties.

One reason for this is that the size ratios between predator and prey are fixed within certain limits. It is trivial to state that prey species rarely exceed their predators in size. For any predator of a given size there is also a minimum size of prey below which capture is inefficient. Three principal methods of concentrating or catching suspended prey organisms exist: *raptorial feeding* which depends on the random encounter between an individual prey organism and its predator; *filter feeding* in which prey organisms are concentrated by sieving through a (ciliary or pseudopodial) filter; and *diffusion feeding* which means that motile prey accidentally collide with a sticky part of the body surface of the predator. These three basic mechanisms have their analogies in fishing methods, viz, fish spearing, trawling, and using fish traps, respectively. In each case scaling arguments show that predator efficiency decreases with a decreasing prey: predator size ratio (26). Although such arguments are based on simplified assumptions, the basic conclusion is not affected much by the complexities of real organisms.

Empirically, typical length ratios between prey and predator turn out to be around 1 : 10; they are very rarely less than 1 : 100 or more than 1 : 1. Furthermore, this generalization seems invariant with absolute size. Thus, a 10 m baleen whale eating 10 cm long fish and a 50 μm ciliate filtering 0.5μm long bacteria both represent prey:predator length ratios of 1 : 100. The most extreme example of the use of small food particles is provided by planktonic tunicates; their mucus filters can retain particles of bacterial dimensions (31, 52). At the other extreme some protozoa phagocytize particles of their own size. Parasitism may constitute an important exception; circumstantial evidence suggests that certain parasites are important in plankton communities, but knowledge is limited because this is a neglected field. Generalizing, pelagic communities include organisms spanning about seven orders of magnitude in length and prey:predator ratios are fixed and take values around 1 : 10.

Another important relationship is between metabolic rate and growth rate

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on the one hand and body size on the other. It is an empirical fact that when organisms spanning a large range in sizes are compared, weight specific metabolic rate is proportional to weight$^{-1/4}$. Net growth efficiency for unicellular organisms and for small invertebrates is approximately 60%. Efficiency of digestion may vary according to food quality, but it is not likely to be size dependent, whereas loss of dissolved organics may be relatively larger in small organisms. Nevertheless, it is a reasonable generalization that growth efficiency is invariant with size (13, 29). A consequence of this is that the rate of increase in biomass (population growth rate) varies with the same power function of weight as does the weight specific metabolic rate.

With these assumptions it is possible to predict the size structure of a steady state pelagic food web (51, 64). In principle these models equate the (size dependent) growth rate of prey organisms with the energy demands (growth + dissimilatory metabolism, divided by growth efficiency) for the next trophic levels. Models differ regarding details in the assumptions, but the basic result is the same: each logarithmic size class should represent about the same biomass or rather, the biomass of each logarithmic size class should decrease slightly with increasing size. A consequence of this model is also that while the biomass spectrum of the community is invariant with body size, the energy flow and the rate of transfer of materials (carbon, nitrogen, and so on) decreases monotonously with size due both to metabolic losses and to the decrease in weight-specific metabolism with increasing body size.

Oceanic planktonic communities represent approximations of a steady state situation. In this case the predictions of the models have been supported by data (70): from bacteria to whales the number of individuals per unit volume of water is approximately inversely proportional to their body weight with a slight tendency to decrease with increasing size. According to productivity each logarithmic size class of plankton organisms constitutes a volume fraction of seawater ranging from about 10^{-8} to 10^{-7}.

In coastal or more productive seas the planktonic communities cannot at any time be described as in a steady state. Seasonal events including periodic additions of mineral nutrients trigger population oscillations, the succession of which reflects the structure of food chains (4, 27, 28, 74, 77). This type of population oscillation, from a qualitative point of view, can be predicted by Lotka-Volterra type equations for prey-predator systems which then suggest that more productive systems show greater amplitudes of the oscillations (27). This oscillatory behavior reflects another aspect of the size structure of planktonic communities because the time period of predator-prey cycles is approximately inversely proportional to the population growth rates of the involved species. Therefore, while population oscillations of diatoms and copepods occur on the order of a month, those of bacteria and their protozoan predators can be measured in days. The temporal patchiness of planktonic systems may therefore be of a finer scale than has been previously assumed.

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Uptake and Excretion of Dissolved Materials

The photosynthetic organisms and the heterotrophic bacteria depend on the uptake of dissolved compounds which often occur in an extremely diluted form, and it is generally accepted that the availability of one or more such substances limits productivity in the sea. A large body of literature exists which treats the limiting role of various mineral nutrients for the primary producers. Here I restrict the discussion to considerations of scaling, and this throws some light on the size structure of planktonic communities under different conditions.

A cell takes up dissolved material from the surrounding water by active transport at certain sites on the cell membrane. The substance is brought to the cell by the diffusion gradient surrounding the cell which is created by the uptake at the surface. At one extreme, when substrate concentration is very low the concentration at the cell surface is zero (that is, the membrane has an excess uptake capacity relative to the limitation due to the diffusion rate of the substance). In this diffusion-limited case, uptake is simply proportional to the bulk concentration of the compound in question, to its diffusion constant, and to the diameter of the cell; but it is independent of the transport capacity of the cell membrane. Since the metabolic demands of a cell are approximately proportional to its surface, it is obvious that under intense competition for a dissolved substrate, small cells are at an advantage relative to larger ones.

At the other extreme, when bulk substrate concentrations are very high and not very different from that close to the cell surface, the active transport capacity of the cell membrane becomes limiting, and everything else being equal, uptake becomes proportional to surface area (second power of the diameter). In this case there is no particular advantage in being small (26, 44, 53).

Seawater contains about 1 mg of dissolved organic material per liter; however, only a small proportion of this represents low molecular compounds readily utilized by bacteria. According to Azam & Cho (5) 1 ml contains about 50 ng of utilizable organic carbon which, assuming 10^6 bacteria ml^{-1}, represents about twice the amount of carbon contained in the bacteria. Thus, without a continuous input of dissolved organics, seawater could sustain one to two cell divisions. These figures suggest that the pool of useable carbon may turn over several times per day. Seawater is a very dilute substrate for bacteria, and given the above considerations, it is highly improbable that any organisms larger than bacteria use dissolved organic material efficiently.

Much consideration has been given to whether bulk concentrations of dissolved organics are sufficient to explain observed bacterial growth rates. A variety of mechanisms that would enable bacteria to use spatial heterogeneity (such as chemosensory attraction to algal cells) have been suggested (5). As discussed below these ideas are problematic. However, if we assume the diffusion limited case, the uptake of a spherical bacterium is given by

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$V = 4\pi DRS$, where D is the diffusion coefficient, R is the radius of the cell and S is bulk concentration. Assuming that $S = 50$ ng C ml^{-1}, $D = 10^{-5}$ cm^2 sec^{-1}, and $R = 0.5$ μm, then the uptake of the cell is about 20 fg C h^{-1}, which would allow for a doubling every second hour. While the theoretical uptake rate at low concentrations may not be quite realistic (53) and while substrate concentrations probably vary and are not precisely known, the considerations show that use of microscale spatial heterogeneity may not be necessary for explaining bacterial growth rates observed in the sea.

Photosynthetic cells are often limited by the availability of mineral nutrients and in particular by nitrogen and phosphorus. In the photic layers of oligotrophic seas, concentrations of orthophosphate and useable forms of nitrogen may be at the limit of detection. Since primary production does take place, mineral salts must have a very rapid turnover under these circumstances. Again the above considerations suggest that the smallest cells, that is, the photosynthetic pico- and nanoplankton will be competitively superior, relative to larger cells. However, where there is an import of mineral nutrients to the photic zone, bulk concentrations may remain high in spite of a considerable production of cells. Such an import of nutrient salts takes place at upwelling zones and fronts and seasonally in temperate seas. Under these conditions larger phytoplankters such as diatoms and dinoflagellates become competitive and may dominate among the primary producers.

Data confirm these predictions: in oligotrophic waters pico- and nanoplankters predominate as primary producers, but whenever there is an input of "new" nutrients, larger phytoplankters become important. This is also reflected in the seasonal cycle of temperate waters: during spring when nutrient levels are high, a diatom bloom is responsible for the bulk of the production, and later, during the summer when mineral nutrients are scarce, tiny phytoflagellates and cyanobacteria predominate (42, 49, 74, 81). In oligotrophic waters, the base of the food chain is composed of very small cells; the microbial loop dominates the pelagic food web; and unicellular organisms are responsible for almost the entire energy flow and the mineralization processes in the water column. Conversely, when an import of mineral nutrient takes place, the base of the food chains is constituted by large phytoplankton cells to a much higher degree. These are eaten by zooplankters such a copepods, or they sediment to the bottom, thus adding organic matter to the benthic communities. Under these conditions food chains consist of fewer levels, and a much larger part of the primary production is channelled to larger organisms such as fish or is exported to the benthos.

The excretion of dissolved organics from living cells constitutes the basis for bacterial production. Various studies suggest that as much as 20–50% of the primary production of phytoplankton cells is excreted and thus represents a loss to the organisms (32, 54). Various attempts to explain this have argued

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some sort of adaptive value to phytoplankton cells, but none of these seems very convincing. The subject has most recently been reviewed by Bjørnsen (11). Calculations which take into account published values on the permeability of cell membranes, the diffusivity of low molecular compounds, and the dimensions of phytoplankters, taken together, suggest that loss of dissolved organics is an inevitable aspect of being a small organism. This view is supported by the fact that excretion of organics is not coupled to the rate of photosynthesis and also takes place in the dark and that heterotrophic nanoplankters excrete comparable amounts of dissolved organics (2).

Remineralization and Mineral Cycling

In the classical picture of the pelagic ecosystem, remineralization is in part due to the zooplankton and in part takes place in the sediments through microbial decomposition of particulate material which sinks to the bottom. A large fraction of the mineralization takes place in the water column, and the smallest sized organisms are largely responsible for this process. Dugdale & Goering (22) distinguish between "regenerated" mineral nutrients and "new" nutrients which are imported to the photic zone from the underlying water masses by physical processes. In the case of nitrogren, locally regenerated nutrients are mainly in the form of ammonia, whereas new nutrients predominantly consist of nitrate due to microbial nitrification in the sediments or deeper water layers.

Regarding phagotrophic food chains, mineralization is a relatively simple concept because the relative composition with respect to the elements is almost invariant among plankton organisms (although large phytoplankton cells tend to have somewhat higher C : N and C : P ratios than do other forms). In phagotrophs part of the ingested organic carbon is oxidized through dissimilatory metabolism, rather than incorporated into cells. The amount of nitrogen or phosphorus mineralized corresponds to the amount of oxidized carbon, and so in principle, e.g., the rate of nitrogen mineralization is also a measure of the carbon flow when the growth efficiency is known. As a crude generalization a phagotrophic plankton organism incorporates about 40%, excretes about 30% (in the form of dissolved or particulate organic material), and mineralizes another 30% of what it eats (this applies to carbon as well as to nitrogen or phosphorus). Direct measurements of nitrogen excretion e.g. by phagotrophic protozoa (28, 36) largely support this generalization. The considerations also suggest that the microbial loop, which includes at least two trophic levels in addition to bacteria, may be responsible for the bulk of the mineralization (20, 28).

Bacteria are more complicated in this context because the content of essential elements in their organic substrates may vary. If the concentration of nitrogen e.g. is sufficiently low, bacteria may show a net uptake of mineral

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nutrients from the water and so compete with photosynthetic organisms. This phenomenon is well known from soils and detrital sediments, but its importance in plankton is not well understood; at least sometimes bacteria seem to show a net excretion of mineral nutrients (see below).

The in situ cycling of nitrogen has been studied by incubating water samples with N-15 labelled ammonia (nitrate or urea), and then following the concentration of these compounds as well as their isotope ratios over time. This yields information on both uptake and excretion rates. Size fractionation of the plankton samples before the incubation gives additional information on the relative importance of different constituents of the plankton. Such studies in all cases suggest that organisms smaller than 200 μm are responsible for the largest fraction of nitrogen (and by implication, carbon and phosphorus) mineralization. In most cases (34, 39) the bacterial fraction alone, or sometimes the nanoplankters, is responsible for considerably more than half of the nitrogen mineralization. Only in the productive Oslofjord did the microplankton fraction (heterotrophic dinoflagellates, ciliates, rotifers) yield the largest contribution to the ammonia production (63). Here only 28% of the nitrogen uptake could be met by in situ regeneration; the rest was supplied as new nutrients. In other cases (34) regeneration and uptake of ammonia were nearly balanced.

While there are some methodological difficulties with the N-15 technique, the general results probably hold. The discrepancies between different investigations are probably also real and reflect differences between oceanic and coastal waters. Most likely temporal variation occurs paralleling population oscillations and seasonal differences, but so far data to show this are not available.

Microscale Patchiness

Spatial and temporal heterogeneity on different scales is an important aspect of community ecology. Regarding marine plankton, attention was previously directed at large-scale patchiness, that is, differences between different ocean currents or vertically zoned water masses and phenomena like local algal blooms. Turbulent mixing and the motility of organisms probably exclude plankton patchiness at a fine scale. Most recently, however, there has been a considerable interest in the role of microscale patchiness in plankton communities. One important reason is that the existence of some sort of aggregates consisting of different physiological types of plankters (photosynthetic cells, heterotrophic bacteria, and phagotrophs) and with more or less self-contained mineral cycling and energy flow would make it easier to understand the relatively high turnover of carbon and mineral nutrients observed in oligotrophic oceanic waters.

Thus, it has recently been suggested that heterotrophic bacteria are capable

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of congregating around photosynthetic cells, and so they enjoy an increased concentration of dissolved organic material (5). Many bacteria are motile, and chemosensory behavior which allows them to move along chemical gradients has been experimentally established. However, direct observation of this phenomenon under conditions approximating those of oligotrophic seawater would seem very difficult and has not been attempted. Instead various theoretical approaches have been made. Mitchell et al (62) found, based on scaling arguments, that bacteria would have difficulty in keeping up with the sinking velocity of algal cells. However, they concluded that in vertically stratified waters where algal cells may be trapped (e.g. at the thermocline), attraction by bacteria to a microzone around the cells could play a role. However, most of the phytoflagellates are motile and have swimming speeds which exceed that of bacteria, so under all circumstances it may be difficult to understand how chemokinetic behavior of bacteria can be effective in this situation. Jackson (44, 45) made simulation models of chemosensory behavior of bacteria in the vicinity of algal cells. Some other possibilities for microscale patchiness (such as phytoplankton cells using pulses of mineral nutrients excreted from copepods) were also considered. In most cases various physical constraints suggest that such phenomena do not occur or are unimportant.

Seawater always contains smaller or larger amounts of suspended detrital particles. Such particles originate from dissolved organics through bacterial activity (8, 69) or from dead phytoplankton cells including diatom frustules, larvacean houses, or other remains of zooplankters, fecal pellets, and especially in coastal areas, debris of macroalgae or seagrasses or mineral grains. Often several such particles occur in small aggregates believed to be held together by microbial mucus excretions (1, 9, 19).

The surfaces of such particles usually harbor concentrations of microorganisms that far exceed those of the surrounding waters, and in particular, bacteria and protozoa are important (16, 73). Among the protozoa, many are not typical planktonic forms but are adapted to live on surfaces (e.g. hypotrich ciliates). Many planktonic heterotrophic flagellates have the ability to attach temporarily to solid surfaces (and often do so in cultures). They occur on suspended particles together with flagellates particularly adapted to life on surfaces, such as bodonids and euglenoids. Some forms may exploit attached bacteria, but others are filter feeders which must depend on the surrounding suspended bacteria. From a hydrodynamic view point, it is usually advantageous for filter feeders to be attached to solid surfaces (27). The attached bacteria may be favored by absorption of dissolved organics to surfaces, or they may utilize the detrital material through the excretion of hydrolytic enzymes. Dead phytoplankton cells incubated in seawater develop a characteristic succession of microbial communities and are relatively rapidly

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decomposed (9, 10). It is reasonable to consider suspended solids as having a special planktonic microbiota.

It has been argued that such microaggregates play a great role in the sea and that they are perhaps responsible for the largest part of microbial activity (35). Direct counting of plankton samples does not, in general, support this neither for oceanic or for coastal waters (25, 41). Although the concentration of microorganisms on such particles is high, by far the largest number of bacteria and protozoa are not associated with particles but occur as freely suspended cells. It is, however, possible that the standard method for enumerating planktonic bacteria and protozoa (fixing and filtering the sample on membrane filters) tends to disintegrate such microbial communities, thus giving a biased picture.

Symbiosis and Mutualism

Any discussion on planktonic food chains would be incomplete without a mention of symbiosis and mutualism. In a sense it could be discussed in the context of microscale spatial heterogeneity, since the adaptive significance is often that assumed for bacteria concentrating around algal cells. But in the case of symbiosis the phenomenon certainly exists. As in other ecological systems, a vast number of symbiotic relationships have been described, and in many cases the functional significance is not yet understood (82).

I concentrate on the mutualistic relationship between photosynthetic and heterotrophic organisms. From the viewpoint of the former component, the adaptive significance is the increased access to mineral nutrients (the motile behavior of the host may also be of significance). The heterotrophic component receives organic compounds either by digesting the symbiont cells or through organic excretions from the phototrophs. In some cases the consortium is totally self-contained in that the heterotrophic component is independent of or even incapable of phagocytosis.

The large planktonic protozoa of oceanic waters (foraminifera, radiolaria, and achantharia) seem all to harbor intracellular and sometimes also extracellular photosynthetic symbionts belonging to different taxonomic groups (82). These mutualistic consortia represent at least in part a self-contained mineral cycling and are possibly responsible for a significant fraction of the primary production. Among planktonic ciliates harboring endosymbiotic photosynthetic organisms, *Mesodinium* has been most thoroughly studied (59). It seems incapable of phagocytosis and is totally dependent on its (presumably cryptomonad) symbiont. *Mesodinium* occurs in high densities in coastal waters and sometimes forms (innocuous) red tides; it may be responsible for a large fraction of the photosynthetic activity.

Recently it has been shown that a phenomenon, "chloroplast symbiosis," previously known from some marine slugs and from benthic foraminifera

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occurs in many nontintinnid oligotrich ciliates (46, 57, 79). These ciliates do not digest the chloroplasts of their algal or flagellate flood but retain them in a functional state in their cytoplasm for several days. Incubating the ciliates with C-14 labelled bicarbonate shows that the chloroplasts can provide these phagotrophs with a measurable fraction of their metabolic needs. Of course, chloroplast symbiosis is not real symbiosis at all, but only an unusual way for a predator to use parts of its prey.

The "Sink or Link" Problem

The discovery of the microbial loop has led to the question of whether it represents a "link" or a "sink" in planktonic food chains; that is, will the organic carbon channelled through the heterotrophic and the photosynthetic picoplankton be mineralized entirely by microbes or will it, via an protozoan link, be used by zooplankton (20, 21). As phrased, the question may seem nonsensical: ecosystems are always a "sink" in that virtually all the reduced carbon deriving from photosynthesis is eventually mineralized. The question is really the extent to which the existence of the microbial loop affects the production of organisms harvested by humans.

No compelling evidence suggests that the nutritive value of living food particles for consumer species depends on anything else than size. Since the phagotrophic planktonic organisms taken together represent a continuum with respect to food particle size preference, everything can be eaten. The question therefore would seem simple to answer. If a phagotrophic food chain is initiated by heterotrophic bacteria utilizing algal exudates, or by photosynthetic picoplankton, there will be two or three more trophic levels between these organisms and, e.g., a cod fish than there would be if the classical food chain initiated by copepods eating diatoms were dominant. Assuming an ecological efficiency of 30% (although, in fact, the excreted organic material will be recycled to bacteria) the increased number of trophic levels will mean that the fraction of the primary production which ends up in larger animals will be only 3–9% of that in the case of the classical plankton food chain. In this sense, of course, the microbial loop does represent a sink. The considerations also show that knowledge of the rate of primary production is not sufficient to predict the production of fish. This would also require an understanding of the circumstances that influence the structure of the planktonic food web.

Sedimentation and the Supply of Food for Benthic Organisms

The sedimentation of particulate organic material from the surface waters represents another sink for planktonic production. The role in removing limiting mineral nutrients from the photic layers has already been mentioned. It is also clear that except for very shallow or landlocked seas, the basis for all benthic life is the sedimentation of particulate organic carbon from the surface

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layers of the water column. This has been recognized for a long time, but the phenomenon attracted only little attention among planktologists. In part, this may have been because plankton modellers already had "too little food" to explain secondary production in the plankton. Maybe it was also considered a trivial and uninteresting problem.

Recently it has been found that sedimentation from the plankton is a more complex and interesting phenomenon than just a continuous rain of plankton debris. In temperate waters the bulk of the sedimentation takes place in early spring towards the end of the diatom bloom, and a later less impressive peak in sedimentation follows the late summer bloom of dinoflagellates. Very little sedimentation takes place during the rest of the year (18, 75). For reasons not quite understood, only part of the spring diatom bloom is consumed by copepods. One explanation may be that the spring bloom takes place in cold water, in some places even under ice, and so it is possible that the numerical response of copepod populations is not sufficiently rapid. Consequently the diatom population eventually declines, in part due to grazing but also due to nutrient depletion.

The sinking diatoms are presumably mainly senescent or dead cells. However, Smetacek (76) has argued that a change in buoyancy of nutrient starved diatoms is an adaptive response and that the sinking cells represent a resting stage which survives in the sediments to recruit the bloom of the following year. This explanation may well be correct even though the bulk of the sedimented diatoms are consumed by benthic invertebrates. It has been demonstrated that the life cycles of some of the benthic consumers are adapted to this periodical input of food to the benthos (50, 75).

CURRENT AND FUTURE PROBLEMS

In terms of carbon flow in the water column, the discovery of the microbial loop, combined with realistic estimates of the sedimentation of organic carbon, suggests a pertinent question: Is there enough food? That is, are current estimates of photosynthesis sufficiently high to explain secondary production. Steele's (78) analysis of the North Sea, which did not take the microbial loop into consideration, and which also considered sedimentation to be neglible, found it difficult to account for the magnitude of secondary production. Probably several factors at least in part explain the discrepancy. First of all previous estimates of primary production using the C-14 method may represent underestimates. Excreted material is lost, pico- and nanoplankton cells may either pass through or lyse on filters, and carbon turnover due to heterotrophic activity during the incubation period may be significant. Secondly, previous estimates of the gross growth efficiency of phagotrophic organisms were too low (10%). Figures around 30% are now considered

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more realistic. In addition excreted organic material will be recycled by bacteria. Therefore, while it is quite possible that the secondary production of planktonic systems can be accounted for, an attempt to repeat Steele's approach including the newly discovered aspects of the pelagial ecosystem is desirable.

Another fundamental approach is to integrate physical oceanography into our picture of planktonic chains; that is, how stratification, upwelling, fronts, and hydrographic factors affect the structure of the food web. An attempt to use simulation models to describe such problems is discussed in (83). Further progress towards a full understanding of the structure and diversity of plankton communities will, however, also depend on an increased knowledge about the individual species including aspects such as adaptations to temporal heterogeneity and life cycles, food capture and food selectivity, and motile behavior.

Literature Cited

1. Alldredge, A. L., Cole, J. J., Caron, D. A. 1986. Production of heterotrophic bacteria inhabiting macroscopic organic aggregates (marine snow) from surface waters. *Limnol. Oceanogr.* 31:68–78
2. Andersen, A., Lee, C., Azam, F., Hagström, Å. 1985. Release of amino acids by heterotrophic marine microflagellates. *Mar. Ecol. Prog. Ser.* 23:99–106
3. Andersen, P., Fenchel, T. 1985. Bacterivory by microheterotrophic flagellates in seawater samples. *Limnol. Oceanogr.* 30:198–202
4. Andersen, P., Sørensen, H. M. 1986. Population dynamics and trophic coupling in pelagic microorganisms in eutrophic coastal waters. *Mar. Ecol. Prog. Ser.* 33:99–109
5. Azam, F., Cho, B. C. 1987. Bacterial utilization of organic matter in the sea. See Ref. 30a, pp. 261–81
6. Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A., Thingstad, F. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10:257–63
7. Beers, J. R., Stewart, G. L. 1969. Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. *Mar. Biol.* 4:182–89
8. Biddanda, B. A. 1985. Microbial synthesis of macroparticulate matter. *Mar. Ecol. Prog. Ser.* 20:241–51
9. Biddanda, B. A., Pomeroy, L. R. 1988. Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. I. Microbial succession. *Mar. Ecol. Prog. Ser.* 42:79–88
10. Biddanda, B. A., Pomeroy, L. R. 1988. Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. II. Microbial metabolism. *Mar. Ecol. Prog. Ser.* 42:89–95
11. Bjørnsen, P. K. 1988. Phytoplankton release of organic matter: why do healthy cells do it? *Limnol. Oceanogr.* 33:151–54
12. Burkill, P. H. 1982. Ciliates and other microplankton components of a nearshore food-web: standing stocks and production processes. *Ann. Inst. océanogr., Paris* 58:335–50
13. Calow, P. 1977. Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52:385–409
14. Capriulo, G. M., Carpenter, E. J. 1980. Grazing by 35 to 202 μm microzooplankton in Long Island Sound. *Mar. Biol.* 56:319–26
15. Caron, D. A. 1983. Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. *Appl. Environ. Microbiol.* 46:491–98
16. Caron, D. A., Davis, P. G., Madin, L. P., Sieburth, J. McN. 1982. Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. *Science* 218:795–97
17. Caron, D. A., Goldman, J. C., Andersen, O. K. Dennett, M. R. 1985. Nutrient cycling in a microflagellate food chain: II. Population dynamics and

This content downloaded on Fri, 1 Feb 2013 03:44:13 AM
All use subject to JSTOR Terms and Conditions

carbon cycling. *Mar. Ecol. Prog. Ser.* 24:243–54
18. Christensen, H., Kanneworff, E. 1986. Sedimentation of phytoplankton during a spring bloom in the Øresund. *Ophelia.* 26:109–22
19. Davoll, P. J., Silver, M. W. 1986. Marine snow aggregates: life history sequence and microbial community of abandoned larvacean houses from Monterey Bay, California. *Mar. Ecol. Prog. Ser.* 33:111–20
20. Ducklow, H. W. 1983. Production and fate of bacteria in the oceans. *BioScience* 33:494–501
21. Ducklow, H. W., Purdie, D. A., Williams, P. J. leB., Davies, J. M. 1986. Bacterioplankton: A sink for carbon in a coastal marine plankton. *Science* 232:865–67
22. Dugdale, R. C., Goering, J. J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* 12:196–206
23. Estep, K. W., Davis, P. G., Keller, M. D., Sieburth, J. McN. 1986. How important are algal nanoflagellates in bacterivory? *Limnol. Oceanogr.* 31:646–50
24. Fenchel, T. 1982. Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. *Mar. Ecol. Prog. Ser.* 8:225–31
25. Fenchel, T. 1982. Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as consumers of bacteria. *Mar. Ecol. Prog. Ser.* 9:35–42
26. Fenchel, T. 1984. Suspended marine bacteria as a food source. In *Flows of Energy and Materials in Marine Ecosystems,* ed. M. J. R. Fasham, pp. 301–15. New York & London: Plenum
27. Fenchel, T. 1986. The ecology of heterotrophic flagellates. *Adv. Microb. Ecol.* 9:57–97
28. Fenchel, T. 1988. Microfauna in pelagic food chains. In *Nitrogen Cycling in Coastal Marine Environments,* ed. T. H. Blackburn, J. Sørensen, pp. 59–65. London: John Wiley & Sons
29. Fenchel, T., Finlay, B. J. 1983. Respiration rates in heterotrophic, free-living protozoa. *Microb. Ecol.* 9:99–122
30. Ferguson, R. L., Rublee, P. 1976. Contribution of bacteria to the standing crop of coastal bacteria. *Limnol. Oceanogr.* 21:141–45
30a. Fletcher, M., Gray, T. R. G., Jones, J. G. 1987. *Ecology of Microbial Communities.* Cambridge: Cambridge Univ. Press
31. Flood, P. R. 1978. Filter characteristics of appendicularian food catching nets. *Experientia* 34:173–75
32. Fogg, G. E., Nalewajko, C., Watt, W. D. 1965. Extracellular products of phytoplankton photosynthesis. *Proc. Roy. Soc. London B* 162:517–34
33. Fuhrman, J. A., Azam, F. 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in surface waters: evaluation and field results. *Mar. Biol.* 62:1–12
34. Glibert, P. M. 1982. Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. *Mar. Biol.* 70:209–22
35. Goldman, J. C. 1984. Conceptual role for microaggregates in pelagic waters. *Bull. Mar. Sci.* 35:462–76
36. Goldman, J. C., Caron, D. A., Andersen, O. K., Dennett, M. R. 1985. Nutrient cycling in a microflagellate food chain: I. Nitrogen dynamics. *Mar. Ecol. Prog. Ser.* 24:231–42
37. Haas, L. W. 1982. Improved epifluorescence microscopy for observing planktonic microorganisms. *Ann. Inst. océanogr., Paris* 58:261–66
38. Hagström, Å., Larsson, U., Hörstedt, P., Normark, S. 1979. Frequency of dividing cells, a new approach to the determination of bacterial growth rates in aquatic environments. *Appl. Environ. Microbiol.* 37:805–12
39. Harrison, W. G. 1978. Experimental measurements of nitrogen mineralization in coastal waters. *Limnol. Oceanogr.* 23:684–94
40. Hobbie, J. E., Daley, R. J., Jasper, S. 1977. Use of Nucleopore filters for counting bacteria by fluorescence microscopy. *Appl. Environ. Microbiol.* 33:1225–28
41. Hobbie, J. E., Holm-Hansen, O., Packard, T. T., Pomeroy, L. R., Sheldon, R. W., Thomas, J. P., Wiebe, W. J. 1972. A study of the distribution of activity of microorganisms in ocean water. *Limnol. Oceanogr.* 17:544–55
42. Holligan, P. M., Williams, P. J. leB., Purdie, D., Harris, R. P. 1984. Photosynthesis, respiration, and nitrogen supply of plankton populations in stratified, frontal and tidally mixed shelf waters. *Mar. Ecol. Prog. Ser.* 17:201–13
43. Itturiaga, R., Mitchell, B. G. 1986. Chroococcoid cyanobacteria: a significant component in the food web dynamics of the open ocean. *Mar. Ecol. Prog. Ser.* 28:291–97
44. Jackson, G. A. 1987. Physical and chemical properties of aquatic environments. See Ref. 30a, pp. 213–33
45. Jackson, G. A. 1987. Simulating che-

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All use subject to JSTOR Terms and Conditions

mosensory responses of marine microorganisms. *Limnol. Oceanogr.* 32:1253–66
46. Jonsson, P. R. 1987. Photosynthetic assimilation of inorganic carbon in marine oligotrich ciliates (Ciliophora, Oligotrichina). *Mar. Microb. Food Webs* 2:55–68
47. Johnson, P. W., Sieburth, J. McN. 1979. Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. *Limnol. Oceanogr.* 24:928–35
48. Johnson, P. W., Xu, H.-S., Sieburth, J. McN. 1982. The utilization of chroococcoid cyanobacteria by marine protozooplankton but not by calanoid copepods. *Ann. Inst. océanogr., Paris* 58:297–308
49. Joint, I. R., Owens, N. J. P., Pomroy, A. J. 1986. The seasonal production of picoplankton and nanoplankton in the Celtic Sea. *Mar. Ecol. Prog. Ser.* 28:251–58
50. Kanneworff, E., Christensen, H. 1986. Benthic community respiration in relation to sedimentation of phytoplankton in the Øresund. *Ophelia* 26:269–84
51. Kerr, S. R. 1974. Theory of size distribution in ecological communities. *J. Fish. Res. Board Can.* 31:1859–62
52. King, K. R., Hollobaugh, J. T., Azam, F. 1980. Predator-prey interactions between the larvacean *Oikopleura dioica* and bacterioplankton in enclosed water columns. *Mar. Biol.* 56:49–57
53. Koch, A. L. 1971. The adaptive responses of *Escherichia coli* to a feast and famine existence. *Adv. Microb. Physiol.* 6:147–217
54. Lancelot, C. 1979. Gross excretion rates of natural marine phytoplankton and heterotrophic uptake of excreted products in the southern North Sea as determined by short-term kinetics. *Mar. Ecol. Prog. Ser.* 1:179–86
55. Lancelot, C., Billen, G. 1984. Activity of heterotrophic bacteria and its coupling to primary production during the spring phytoplankton bloom in the southern bight of the North Sea. *Limnol. Oceanogr.* 29:721–30
56. Larsson, U., Hagström, Å. 1982. Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. *Mar. Biol.* 67:57–70
57. Laval-Peuto, M., Febvre, M. 1986. On plastid symbiosis in *Tontonia appendiculariformis* (Ciliophora, Oligotrichina). *BioSystems* 19:137–58
58. Lessard, E. J., Swift, E. 1985. Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. *Mar. Biol.* 87:289–96
59. Lindholm, T. 1985. *Mesodinium rubra*—a unique photosynthetic ciliate. *Adv. Aquat. Microbiol.* 3:1–48
60. Lohmann, H. 1911. Über das Nannoplankton und die Zentrifugierung kleinster Wasserproben zur Gewinnung desselben in lebenden Zustande. *Int. Rev. Ges. Hydrobiol. Hydrogr.* 4:1–38
61. Mills, E. L. 1982. Saint-Simon and the oceanographers: Patterns of change in the study of plankton dynamics 1897–1946. In *Selected Works of Gordon A. Riley,* ed. J. S. Wroblewski, pp. 3–18. Halifax: Dalhousie Univ.
62. Mitchell, J. G., Okubo, A., Fuhrman, J. A. 1985. Microzones surrounding phytoplankton form the basis for a stratified marine microbial ecosystem. *Nature* 316:58–59
63. Paasche, E., Kristiansen, S. 1982. Ammonium regeneration by microzooplankton in the Oslofjord. *Mar. Biol.* 69:55–63
64. Platt, T., Denman, K. 1977. Organisation in the pelagic ecosystem. *Helgoländer wiss. Meeresunters* 30:575–81
65. Platt, T., Li, W. K. W., eds. 1987. *Photosynthetic Picoplankton. Canadian Bull. Fish. Aquat. Sci. 214* Ottawa: Dep. Fisheries & Oceans
66. Platt, T., Subba Rao, D. U., Irwin, B. 1983. Photosynthesis of picoplankton in the oligotrophic sea. *Nature* 301: 702–4
67. Pomeroy, L. R., Johannes, R. E. 1968. Occurrence and respiration of ultraplankton in the upper 500 meters of the ocean. *Deep-Sea Res.* 15:381–91
68. Rassoulzadegan, F., Sheldon, R. W. 1986. Predator-prey interactions of nanozooplankton and bacteria in an oligotrophic marine environment. *Limnol. Oceanogr.* 31:1010–21
69. Robertson, M. L., Mills, A. L., Zieman, J. C. 1982. Microbial synthesis of detritus-like particles from dissolved organic carbon released by tropical seagrass. *Mar. Ecol. Prog. Ser.* 7:279–85
70. Sheldon, R. W., Prakash, A., Sutcliffe, W. H. Jr. 1972. The size distribution of particles in the ocean. *Limnol. Oceanogr.* 17:327–40
71. Sheldon, R. W., Rassoulzadegan, F. 1987. A method for measuring plankton production by particle counting. *Mar. Microbial. Food Webs.* 2:29–44
72. Sieburth, J. McN. 1979. *Sea Microbes.* New York: Oxford Univ. Press. 491 pp.
73. Silver, M. W., Gowing, M. M., Brownlee, D. C., Corliss, J. O. 1984. Ciliated

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protozoa associated with oceanic sinking detritus. *Nature* 309:246–48
74. Smetacek, V. 1981. The annual cycle of protozooplankton in Kiel Bight. *Mar. Biol.* 63:1–11
75. Smetacek, V. 1984. The supply of food to the benthos. In *Flows of Energy and Materials in Marine Ecosystems,* ed. M. J. R. Fasham, pp. 517–47. New York: Plenum
76. Smetacek, V. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.* 84:239–51
77. Sorokin, Yu. I. 1977. The heterotrophic phase of plankton succession in the Japan Sea. *Mar. Biol.* 41:107–17
78. Steele, J. H. 1974. *The Structure of Marine Ecosystems*. Cambridge, Mass: Harvard Univ. Press. 128 pp.
79. Stoecker, D. K., Michaels, A. E., Davis, L. H. 1987. A large proportion of marine planktonic ciliates contain functional chloroplasts. *Nature* 326:790–2
80. Stockner, J. G., Antia, N. J. 1986. Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. *Can. J. Fish. Aquat. Sci.* 43:2472–2503
81. Takahashi, M., Bienfang, P. K. 1983. Size structure of phytoplankton biomass and photosynthesis in subtropical Hawaiian waters. *Mar. Biol.* 76:203–11
82. Taylor, F. J. R. 1982. Symbiosis in marine microplankton. *Ann. Inst. océanogr., Paris* 58:61–90
83. Tett, P. 1987. Modelling the growth and distribution of marine microplankton. See Ref. 30a, pp. 387–424
84. Williams, P. J. leB. 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforsch., Sonderh.* 5:1–28

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