Plankton Ecology: The Past Two Decades of Progress

Ulrich Sommer

Institut für Meereskunde der Universität,
D-24105 Kiel, Germany

This is a selected account of recent developments in plankton ecology. The examples have been chosen for their degree of innovation during the past two decades and for their general ecological importance. They range from plankton autecology over interactions between populations to community ecology. The autecology of plankton is represented by the hydromechanics of plankton (the problem of life in a viscous environment) and by the nutritional ecology of phyto- and zooplankton. Population level studies are represented by competition, herbivory (grazing), and zooplankton responses to predation. Community ecology is represented by the debate about bottom-up vs. top-down control of community organization, by the PEG model of seasonal plankton succession, and by the recent discovery of the microbial food web.

P lankton are those organisms which live suspended in the water of seas, lakes, ponds, and rivers, and which are not able to swim against the currents of water. This latter feature distinguishes plankton from nekton, the community of actively swimming organisms like fish, larger cephalopods, and aquatic mammals. Plankton range in size from ca. 0.2 µm to several meters (large jellyfish), but only the small ones have been the objects of intensive research, the Antarctic krill being the only well-studied plankton organism of >5 mm. Plankton comprise bacteria (bacterioplankton), plants (phytoplankton, including cyanobacteria), animals (zooplankton), and fungi (mycoplankton). Plankton form complex biotic communities which are functionally as diverse and show the same richness of interaction as terrestrial communities.

Because of the central role of plankton in the functioning open-water foodwebs and ecosystems, plankton ecology has always been a core discipline of limnology and biological oceanography. Beyond their importance for aquatic systems, plankton are most suitable model organisms for classic topics of general ecology, such as competition, predator-prey relationships, food-web structure, succession, transfer of matter, and energy. Small size, rapid population growth (doubling times <1 day for bacteria and small phytoplankton to several days or weeks for zooplankton), high abundances (millions per ml for bacteria, millions per l for phytoplankton), and a relatively homogeneous distribution in their environment facilitate field and experimental studies. Processes which take years to centuries in terrestrial systems, like competitive exclusion and succession, take only weeks in plankton.

Plankton ecology of the past two decades has fully used its potentials to pick up the major themes of theoretical ecology. On the other hand, terrestrial ecology of this period was about to abandon the hope

that the theoretical models of interaction between populations would ever be tested conclusively. Today, an entire curriculum of ecology without too many gaps can be build from the experimental achievements of the past 20 years of plankton ecology. Here, I will focus on some highlights, where new theory has been developed, where long-lasting discussions have been settled, or where new paradigms have emerged. Only the first section (hydromechanics of plankton) covers a topic which is exclusive to plankton, the other sections (nutritional ecology, interactions between populations, organization of communities) being of general ecological importance. For the sake of brevity, I will not include the important contribution of plankton research to the understanding of local and global biogeochemical cycles, which would merit a review of its own.

The Planktonic Life Form:
Life in Suspension

The Reynolds Number

The movement of small plankton organisms in water cannot be viewed as a downscaled version of the swimming of fish. Plankton perceive their medium in a completely different way [1–3]. This difference is best expressed by the Reynolds number, a dimensionless quotient between inertial and viscous forces working upon a particle moving in a liquid. The Reynolds number increases linearly with size and velocity. Reynolds numbers of swimming fish range from 10^4 to 10^7. At the other end of the spectrum of aquatic organisms, Reynolds numbers of flagellated bacteria are in the order of 10^{-4}, and of swimming or sinking phytoplankton usually $< 10^{-2}$ [4]. This means that their movements in water are almost entirely governed by viscous and not inertial forces. The swimming of bacterio- and phytoplankton is comparable to slow (cm min^{-1}) swimming of fish through honey:

– there is practically no inertia,
– the swimming body is surrounded by laminar, not turbulent flow,
– the swimming particle carries most of the surrounding liquid along instead of being permanently washed by fresh medium. Therefore, earlier assumptions are not tenable that flagellar movements or sinking would substantially improve the flux of dissolved nutrients to phytoplankton cells.

The Sinking of Phytoplankton

Most phytoplankton species are heavier than water (densities 1.02 to 1.30 g cm^{-3}; see [4]). Therefore, they are ultimately bound to sink unless they can swim by themselves like flagellates. The most notable exceptions are cyanobacteria with gas vesicles; these can regulate their density and become both heavier (by ballast carbohydrates) and lighter (by gas vesicles) than water [5].

Sinking velocities of small particles (Reynolds number $< 10^{-1}$) in stagnant water can be described by Stokes' law [2]. The sinking velocity increases quadratically with the size of the sinking particle and linearly with the density difference between the sinking particle and the water. Sinking velocities of nonspherical particles have to be corrected for "form resistance", the factor by which a body sinks more slowly than a sphere of equivalent volume and density. Measured sinking velocities ([2, 4] and references therein) conform quite well to calculated ones if realistic values are inserted into Stokes' equation. The feature most important for phytoplankton sinking velocities is the size, because of the quadratic dependence and because of the large size range of phytoplankton (cells and colonies from < 1 μm to several mm). The density difference is also quite important: in fresh water, a diatom with a density of 1.26 g cm^{-3} would sink about ten times as fast as a green alga with 1.026 g cm^{-3}. Form resistance is relatively unimportant because it does not exceed 4 for most of the common shapes. The restricted importance of form resistance contradicts the view of early planktologists who interpreted bristles, spines, and complicated shapes as adaptations to minimize sinking velocities.

Large diatoms sink fastest (up to several m per day), because of their heavy silica cell walls. Small diatoms and large immotile algae without silicification sink at velocities of several cm or dm per day. Smaller phytoplankton sink much more slowly. At the end of phytoplankton blooms, sinking velocities sometimes exceed the values calculated for individual cells or colonies [6]. The mechanism of this acceleration is not yet completely understood, but formation of larger aggregates (marine snow [7]) by flocculation of senescent phytoplankton cells and detritus seems the most plausible explanation.

Sinking has a twofold impact:

1. It is a loss factor for phytoplankton populations dependent on the light in the upper water layers. The impact of sinking losses depends on the ratio between the sinking velocity and the thickness of the mixed surface layer [2, 4]. In practice, only rapidly sinking algae (e.g., large diatoms) under small mixing depths (several

m) will suffer from significant sinking losses.

2. Sinking supplies the dark deep-water zones and the bottom of seas and lakes with food and energy for their organisms. In lakes, 10 to 50% of the annual primary production of organic matter is exported by sedimentation to the deep-water zone [8]. The exported fraction decreases with increasing primary productivity. In marine habitats, 10 to 25% is exported via sedimentation, the fractional value increases with primary production [9].

The Problem of Filtration
by Herbivorous Zooplankton

Many well-studied zooplankton species have comb- or sieve-like structures for collecting suspended food particles from the water. Initially, the process of food collection was interpreted as filtration or sieving. The distance between the finest bristles (setulae) was interpreted as the mesh size of a sieve and, hence, as the lower size limit of edible particles. The intersetular distances of typical herbivorous zooplankton species range from 0.2 to several µm [10], thus giving Reynolds numbers in the order of 10^{-3} for the transport of water through the presumed filter. Filtration of water at the zooplankton scale becomes a problem, like the filtration of honey at the macroscopic scale. The boundary layers of laminar and extremely retarded flow at the margin of the setulae overlap and leave no pores for free flow. Therefore, the sieving hypothesis was challenged and the comb-like structures were interpreted as paddles producing a water flow towards the mouth. Particle capture was explained by electrostatic or chemical attraction between the feeding animal and the food particles [11]. However, the surface-attraction hypothesis could not explain the good agreement between expected (from intersetular distances) and observed minimum sizes of food particles in the well-studied freshwater zooplankton *Daphnia* spp. [12].

Meanwhile, the debate is settled. In *Daphnia* spp. and some other cladocerancans, filter combs move in a closed chamber, giving the water no chance to flow around the filter. The pressure needed to squeeze the water through the filter has been calculated to be <0.5 mbar, the power consumption for filtration amounts to less than 5% of the total metabolic demand [13]. Both values are within easy reach for *Daphnia* spp. On the other hand, the comb-like structures of copepods move in open water instead of a closed chamber and, therefore, seem to act like paddles.

The Nutrition of Plankton

The Enigma of Phytoplankton Nutrient Limitation

There is no doubt that the potential of biomass production is limited by mineral nutrients in the majority of freshwater and marine habitats. For temperate lakes, there is a well-established, almost linear relationship between total phosphorus concentrations and annual mean or maximal values of phytoplankton biomass [14]. Marine ecologists usually consider nitrogen rather than phosphorus to be limiting, but the close correlation between N and P concentrations and the almost constant N:P ratio near the physiological optimum (16:1 by atoms) in most marine habitats make a decision difficult [15].

Until 1979, nutrient limitation of phytoplankton growth rates was as well accepted as nutrient limitation of biomass. It was usually described by a saturation curve where the growth rate was an increasing function of the dissolved nutrient concentration in the medium (Monod model). Phytoplankton ecologists and physiologists were aware that this equation is valid only at constant nutrient concentrations. At variable nutrient concentrations, storage during nutrient pulses can support growth rates higher than expected during subsequent low-nutrient periods. Under variable nutrient concentration, a more reliable prediction of growth rates can be based on the intracellular nutrient pool (cell quota; Droop model [16]).

For average phytoplankton species, saturating N and P quotas and thus the absence of N and P limitation are indicated by a cellular stoichiometry of C:N:P = 106:16:1 (Redfield ratio). A review of particulate organic matter composition in the oceans [17] showed mostly values near the Redfield ratio, especially for the most oligotrophic oceanic habitats, where ambient nutrient concentrations would have suggested severe nutrient limitation. The apparent absence of nutrient limitation was explained by microscale spatial and temporal nutrient patchiness and storage of nutrients if phytoplankton cells come into contact with nutrient micropatches. Excretion by zooplankton and local enrichment in marine snow particles are the main source of micropatchiness.

Goldman's [17] hypothesis of nutrient sufficiency contained a challenging paradox: how can biomass be nutrient-limited while growth, the process through which biomass is attained, seems to be nutrient-saturated. The scientific community accepted the challenge and refined the methods of assessing nutrient limitation [18, 19]: separation techniques to measure cell quotas of individual species instead of
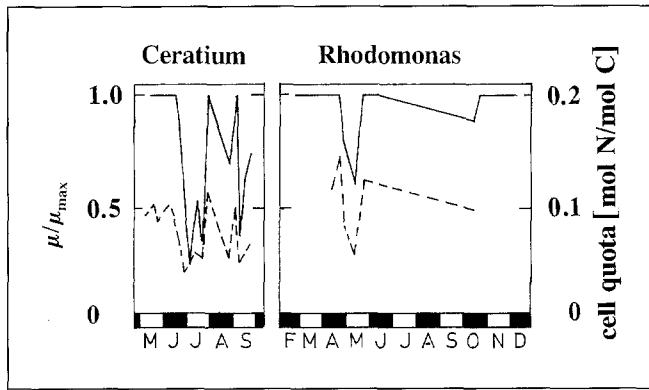
Fig. 1. Nitrogen limitation of *Ceratium hirundinella* and *Rhodomonas minuta* in Plußsee. *Full line:* quotient between nutrient-saturated (μ_{max}) and nutrient-limited growth rates (μ); *broken line:* cell quota of nitrogen (Fig. 6.10 in [4])

bulk organic matter, physiological assays for growth limitation, and elaborate enrichment bioassays were employed. The conclusions of these detailed studies (summarized in [4, 20]) were:

– Severe Si limitation of diatom growth is common and can be described by the Monod model.
– P and N limitation can be described reliably by the Droop model; the Monod model works only sometimes.
– P and N limitation are episodic in time and usually weak (Fig. 1).
– P and N limitation tend to be more severe in eutrophic than in oligotrophic waters.

The latter finding is surprising at first sight but plausible from an evolutionary point of view. In oligotrophic waters, nutrient concentrations are always low, and species without adaptations to a low-nutrient regime will be eliminated by natural selection. In eutrophic waters, dissolved nutrient concentrations are much more variable. There are frequent episodes of high concentrations during which species with high demands can thrive.

Zooplankton Nutritional Ecology

The past two decades have been a golden age of zooplankton nutritional ecology. Especially the research on *Daphnia* spp., the pet animal of freshwater zooplanktologists, became very fruitful, as demonstrated by the Lampert school of ecophysiology ([21] and refs. herein). The functional response of *Daphnia's* ingestion (food consumption) rates to food concentrations was found to follow Holling's type I: below a threshold value (called incipient limiting level,

ILL) there is a linear increase of ingestion rates with food concentrations; above the ILL, ingestion rates remain constant. On the other hand, filtration rates, i.e., the rate at which water is cleared during the filtration process, are constant below the ILL and decline with food concentrations above the ILL. ILL values for adult medium and large-sized *Daphnia* spp. are around 0.25 mg food carbon l^{-1} [22].

Being a true filter feeder, *Daphnia* spp. select their food particles on the basis of size. Depending on species and body size, there is an upper size limit between 20 and 50 μm and a lower size limit of 0.5 to 2 μm [10]. Gelatinous algae of appropriate size are ingested but may pass through the guts without being digested. High concentrations of large, filamentous algae mechanically impede the filtration process and, thereby, also reduce grazing rates upon the edible food items [23]. Herbivorous copepods behave quite differently [24]: they select individual food particles based on chemical qualities (taste), being able even to discriminate between live and freshly killed diatoms of the same species.

Until recently, food limitation of zooplankton was considered to be a function of food quantity, measured as energy or organic carbon. The importance of chemical food quality was discovered when it was shown that strongly N- or P-limited algae with a low cell quota where inadequate for growth and reproduction of *Daphnia galeata* [25, 26], even when energy and carbon supply were sufficient (Fig. 2). Thus, nutrient limitation of the primary producers can be propagated upward through the trophic chain to herbivores. The effect of algal nutrient limitation might be a direct or an indirect one: the direct effect is inadequacy of food stoichiometry for the production of
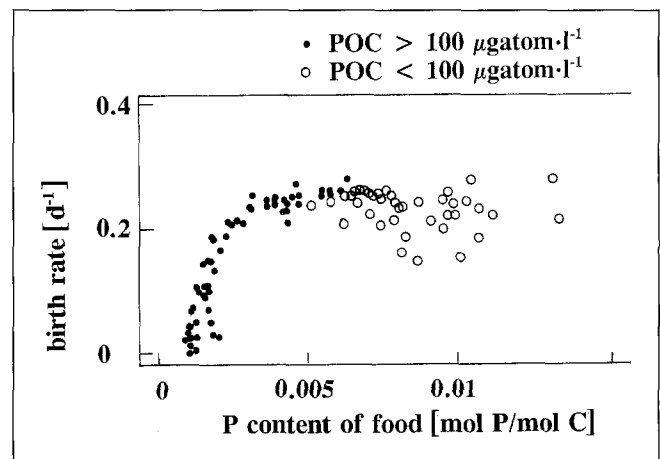

Fig. 2. Birth rates of *Daphnia galeata* in dependence on the P content of the food alga *Scenedesmus acutus* (Fig. 6.19 in [4])

animal tissue; one of the indirect effects is decrease in polyunsaturated fatty acids in nutrient-limited algae [27]. In the green alga *Scenedesmus acutus*, the content of the 20:5ω3-fatty acid decreases strongly with P shortage; in the diatom *Cyclotella meneghiniana*, it decreases only weakly. Severely P-limited *Scenedesmus* is a completely inadequate food for *Daphnia*, while severely P-limited *Cyclotella* has an only slightly reduced nutritional value. Contrary to *Daphnia*, the rotifer *Brachionus rubens* reacts only to the P content of the food [28].

Interactions Between Populations

Phytoplankton Resource Competition

Initiated by Tilman's experiments with the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* [29], phytoplankton became the predominant model community for the experimental test of the modern theory of resource competition [30]. The equilibrium outcome of interspecific competition for limiting nutrients can be predicted from the kinetics of nutrient-limited growth of the competing species using simple graphical models. More complicated models are needed for light competition within the vertical light gradient [31]. Meanwhile, a rich and contradiction-free body of experimental evidence has confirmed Tilman's theory ([32] and refs. herein). The most important findings of phytoplankton competition research are:

- If several species compete for the same nutrient, the one with the lowest nutrient requirement for a growth rate in balance with the mortality rate will become dominant and exclude the other species.
- Under equilibrium conditions, only as many species can coexist as there are different limiting resources (e.g., a Si-limited diatom could coexist with a P-limited green alga).
- If two resources are potentially limiting, the taxonomic outcome of competition is governed by the ratio of these resources, not by the absolute concentrations.
- In freshwaters, diatoms tend to be the winners of competition at high Si:P ratios [33] and blue green algae at low N:P ratios.
- In marine waters (Fig. 3), diatoms tend to dominate at high Si:N ratios [34].
- Heterotrophic bacteria and algae compete for dissolved phosphorus. A homogeneous supply of P tends to favor bacteria, a patchy supply tends to favor algae [35].
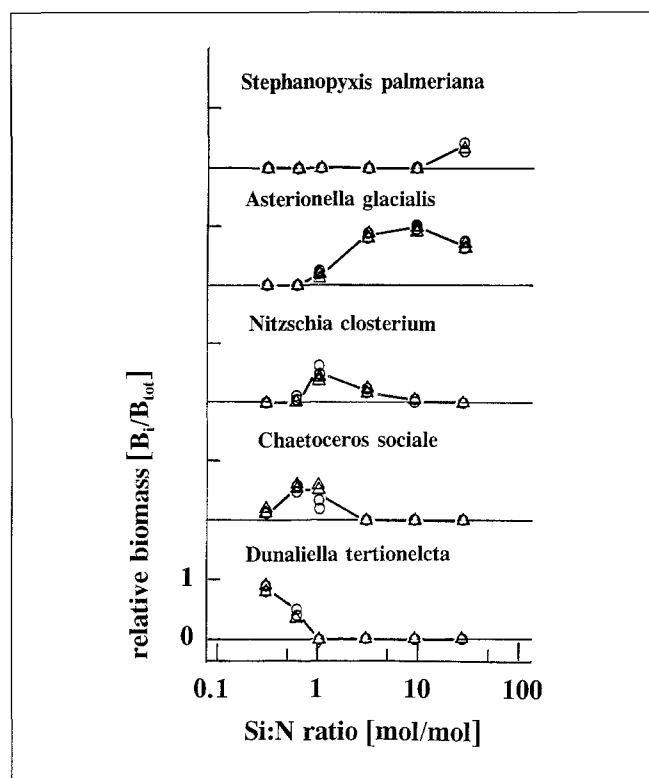

Fig. 3. Relative contribution of North Sea phytoplankton species to the final equilibrium biomass in competition experiments at various Si:N ratios. *Circles:* nitrate as N source; *triangles:* ammonium as N source (from a lecture given at the 1995 ICES meeting, Aalborg, Denmark)

The apparent contradiction between the exclusion of inferior competitors and the observed species richness of natural phytoplankton (Hutchinson's paradox of the plankton) was resolved by experimentally applying the intermediate disturbance hypothesis, originally developed for rainforests and coral reefs [36], to phytoplankton [37]. External disturbances (e.g., dilution of cultures, episodic mixing events in natural habitats) of intermediate frequency and intensity interrupt the process of competitive exclusion and maintain a high level of species richness.

Grazing

Prior to Lampert's [38] pioneering analysis of the clear-water phase, the ups and downs of phytoplankton population densities were ascribed exclusively to favorable and adverse conditions for growth and reproduction. This view could not explain the spring/early summer clear-water phase, a widespread phenomenon in meso- and eutrophic lakes and seas. The clear-water phase is a minimum of phytoplankton biomass immediately following the spring bloom. The

drastic drop in phytoplankton biomass occurs in spite of favorable light and nutrient conditions. At the same time, zooplankton density reaches its annual maximum. Grazing rates upon phytoplankton are higher than their growth rates, thus causing a decline in phytoplankton biomass. Such combinations of temporarily low prey and high predator densities had been anticipated by classic predator-prey models already half a century ago, but still it took about a decade until Lambert's explanation became generally accepted.

During the summer period, grazing pressure in meso- and eutrophic waters is not strong enough to prevent high levels of phytoplankton biomass. It does, however, exert a selective pressure in favor of inedible or poorly edible algal species, most of which are usually large [39]. Twenty years ago, this explanation of a predominance of large phytoplankton species met considerable resistance; today it is widely accepted.

Indirect Effects of Grazing

Grazing does not only inflict differential rates of mortality on phytoplankton populations, but also influences the supply of nutrients. Zooplankton excrete parts of the P and of the N content of their food as dissolved phosphate and ammonium, thus fertilizing planktonic algae [40]. Poorly edible phytoplankton species might thus gain a growth advantage which overcompensates the losses by grazing. If food algae are severely nutrient-starved (low cell quota), zooplankton reduce excretion rates of the limiting nutrient because they need the entire nutrient content of their food for the production of their own tissue [41]. This is a positive feedback loop reinforcing nutrient limitation. Contrary to P and N, Si from diatom cell walls is not excreted in dissolved form but as particulate detritus which rapidly sinks out of the surface layer. Therefore, Si : P and Si : N ratios decline and the competitive advantage of diatoms is reduced when recycling by zooplankton excretion is the dominant form of nutrient supply [42].

Zooplankton Response to Predation

Vertical Migration

The evolutionary explanation of diurnal vertical migration has been one of the longest-lasting debates in plankton ecology. Many zooplankton species spend the night near the surface and the daytime in deeper, dark, and cold water layers where there is a reduced abundance of food. The metabolic-advantage hypoth-
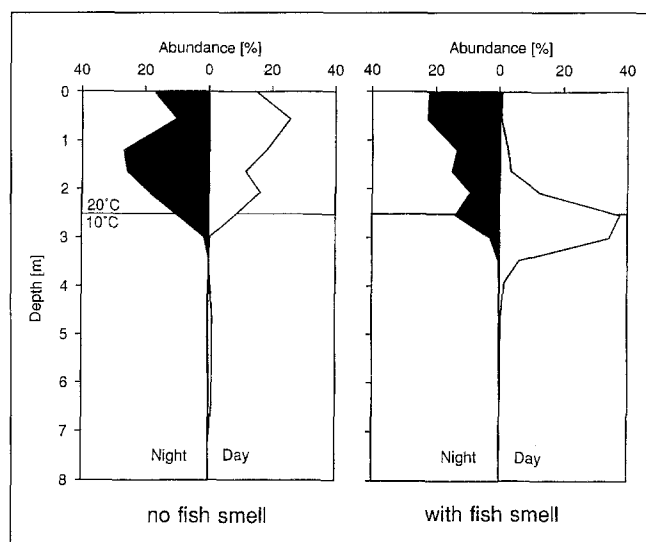

Fig. 4. Day- and night-time vertical distribution of *Daphnia* in plankton towers exposed to water in contact with fish and without (Fig. 9 in [44])

esis assumed that reduced respiratory rates in the cold water would outweigh the disadvantage of reduced food availability. The predator-avoidance hypothesis assumed that losses to optically oriented predators (mainly fish) could be minimized by spending the light period in the darker, deep-water layers. Recent research has revealed a number of facts supporting the predator-avoidance hypothesis, while no support for the competing hypothesis was found.

A survey of mountain lakes which had been artificially stocked with fish in historic time showed larger diurnal migration amplitudes of the copepod *Cyclops abyssorum* in lakes with older fish stocks and no vertical migration in fishless lakes [43]. In laboratory mesocosms (plankton towers) vertical migration of *Daphnia hyalina×galeata* could be induced by water that had been in contact with fish [44] and must have contained a substance excreted by fish (kairomone). In the absence of such water, no migration took place (Fig. 4).

Cyclomorphosis

Similar conclusions have been reached for seasonal morphological shifts in a number of herbivorous zooplankton species. Earlier speculations about hydromechanic reasons (e.g., temperature-dependent changes of the viscosity of water) were not supported by experimental evidence. On the other hand, morphological changes and changes of life-history traits of *Daphnia* spp. are induced by a kairomone released by the predatory planktonic larva of the midge *Chaoborus* sp. [45].

The Organization of Plankton Communities

Bottom-Up or Top-Down Control?

The rapidly increasing evidence for the importance of predator-prey relationships in plankton ecology gave rise to a debate as to whether the structure and dynamics of plankton communities are mainly controlled by physical conditions and nutrients (bottom-up) or by predators (top-down). The traditional bottom-up view assumes a positive correlation between the biomass of different trophic levels, because more prey can support more predators: more plant nutrients support more algae, more algae support more herbivorous zooplankton, more zooplankton support more planktivorous fish, and more planktivorous fish support more piscivorous fish, respectively. The top-down view assumes negative correlations between adjacent trophic levels, because more predators leave less prey, thus leading to a trophic cascade [46]: More piscivorous fish leave less planktivorous fish alive. This releases zooplankton from predation pressure, leading to higher zooplankton densities. Higher densities of hervivorous zooplankton cause reduced phytoplankton densities.

The concept of the trophic cascade has also been applied to the management of eutrophicated lakes (biomanipulation). Most of the deleterious consequences of lake eutrophication are directly or indirectly connected to excessive phytoplankton growth. Therefore, it was attempted to reduce algal biomass by artificial removal of fish and, hence, increased grazing pressure [47]. Biomanipulation sometimes worked and sometimes failed, the reasons for failure and success still being under debate [48].

The second half of the 1980s saw a rapid proliferation of pro- and contra examples in the debate about bottom-up vs. top-down control, until it turned out that much of the heated debate was based on an insufficient appreciation of the problem of scale [3, 4]. Large-scale comparisons of systems with very different nutrient levels support the bottom-up hypothesis. The biomass and production of all trophic levels are positively correlated with nutrient richness and primary productivity. Comparisons on a smaller scale tend to support the top-down hypothesis: if systems of similar nutrient status are compared, there are indeed negative correlations between phytoplankton and zooplankton and between zooplankton and planktivorous fish.

Seasonal Succession

The causal explanation of the well-known seasonal cycles of plankton species (called succession by planktologists) has strongly profited from the study of biotic interactions. Prior to the late 1970s, plankton seasonality has been mainly explained by the physical factors light, temperature, and stratification. Some allowance was also made for the nutrient depletion of surface waters during the summer stratified period. Margalef's [49] minority view of a truly autogenic, i.e., biologically controlled succession was more based on life-form analogies with terrestrial vegetation succession than support by in-depth studies of the mechanisms of species replacements within plankton. Floristic and life-form studies at that time [50, 51] began to support this view without providing firm mechanistic evidence. The major breakthrough was arrived through multidisciplinary field studies supported by experimental research [52], field experiments in mesocosms [53], and the experimental progress in the study of biotic interactions.

The new paradigm of plankton succession finally became condensed in the PEG model [54] of plankton succession (Fig. 5). This assumes a physically controlled minimum of phytoplankton (lack of light) and zooplankton (lack of food) in winter. The spring in-
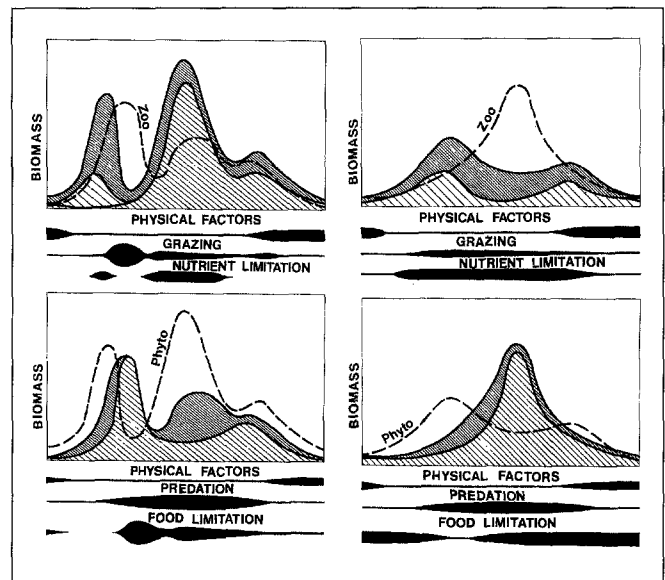

Fig. 5. The seasonal development of phytoplankton (*top*) and zooplankton (*bottom*) in an idealized eutrophic (*left*) and oligotrophic (*right*) water. *Top panel:* small algae (*fine hatching*), large algae (*medium shading*), diatoms (*coarse hatching*), zooplankton biomass (*broken line*). *Bottom panel:* small herbivores (*fine hatching*), large herbivores (*medium hatching*), phytoplankton biomass (*broken line*). The black horizontal diagrams indicate the seasonal change in the importance of major environmental constraints (Fig. 6 in [54])

crease of light and high nutrient concentrations gives rise to the spring bloom of phytoplankton, dominated by small and fast-growing species. These are well edible for grazers and, therefore, give rise to the spring bloom of zooplankton. Zooplankton increase until grazing rates exceed the growth rate of phytoplankton, thus leading to the clear-water phase in late spring. Subsequently, zooplankton decline as well, partly because of fish predation, partly because of food shortage.

In early summer, successional pathways diverge between oligotrophic and eutrophic systems. In eutrophic systems, nutrient recycling during the clear-water phase permits a regrowth of phytoplankton. The summer bloom of phytoplankton develops under a two-fold selection pressure. Selective grazing on small algae leads to a dominance by large phytoplankton species, and competition for nutrients leads to taxonomic shifts within the size structure imposed by grazing. Within zooplankton, fish predation and interference by poorly edible algae favor the species. In oligotrophic systems, the nutrient increase during the clear-water phase is insufficient to permit the summer bloom of large, inedible algae. Algal biomass remains low throughout the entire summer. In autumn, decreased light, sinking temperatures, and the end of summer stratification terminate autogenic succession and lead to a predominance of physical control.

The Microbial Food Web

Until recently, plankton community ecology (including the PEG model) has concentrated on multicellular zooplankton and phytoplankton of >2 μm size. Aquatic microbiology concentrated on the biochemistry, physiology, autecology, and the search for methods of production measurements of bacteria. The role of heterotrophic bacteria within the planktonic system was seen as decomposing dead organic matter. A widened appreciation of the role of planktonic bacteria emerged when Azam introduced the concept of the microbial loop [55]. This loop comprises the energy and carbon flow starting from excretion of organic matter by "classic" plankton and subsequent uptake by bacteria. The bacteria are then grazed by protozoa which are subsequently grazed by filter-feeding classic zooplankton.

The introduction of fluorescence microscopy [56] led to the discovery of much higher numbers of planktonic bacteria (10^6 to 10^7 cells ml^{-1}) than were found by classic plate-count techniques. In spite of the high potential growth rates of bacteria, the numbers are much more constant through time than those of phytoplankton and zooplankton. This constancy was ex-

plained by the rapid growth response of bacterivorous protozoa to increases in their food level and, thus, a top-down control by bacteria almost without delay [57]. Heterotrophic flagellates turned out to be the most important grazers of bacteria. The flagellates themselves are fed upon by larger protozoa and multicellular zooplankton. It was discovered that hitherto neglected picoplanktonic algae (<2 μm) contributed substantially to phytoplankton primary production, especially in oligotrophic systems [58]. Inclusion of picoplankton algae, bacteria, and protozoa into production measurements led to an increase in the estimates of planktonic primary and secondary productivity. The traditional estimate of an "ecological efficiency" (the quotient between the production rates of successive trophic levels) of ca. 10% as a mean and 20% as a maximum has to be replaced by a range extending to 35% [59].

At the present time a shift from energy- and matter-flow studies to studies of community organization within the microbial food web is taking place. Topics are similar to studies of biotic interactions in classic plankton: resource competition, predator-prey dynamics, selectivity of predation, resource regeneration by predators, etc. Special emphasis is given to the integration of processes within the classic planktonic food web and processes within the microbial food web [28].

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