Pelagic Ecology

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Pelagic ecology

"The pelagic," as a noun or as an adjective, refers to the open oceans beyond the continental shelves (from Greek, the sea). However, "the pelagic" is understood by freshwater ecologists to distinguish "the open water" of large lakes and reservoirs from the shallow (littoral) margins. In either instance, the notion of a liquid environment, remote from the shores and bottom of the containing basin, is explicit. In extent, the marine pelagic is, by far, the greatest of the world's major ecosystems, covering some $361 \times 10^6\,\mathrm{km}^2$ (or 71% of the planet's surface) and accommodating an estimated volume of $1.35 \times 10^9\,\mathrm{km}^3$. It is subdivisible vertically by its energetics. The upper, *epipelagic* layer, reaching to a depth of no more than 250 m beneath the surface [1], absorbs most of the incoming solar radiation. Thus, only the upper ocean is warmed directly and only the upper 30 m or so (occasionally more, up to 100 m, in the clearest waters, but often much less, owing to the turbidity of fine particulate material in suspension) receives sufficient light to support net photosynthetic primary production. Heating is greatest in low latitudes, whence poleward convection of some $1.4 \times 10^{15}\,\mathrm{W}$ drives the major oceanic circulations, with deep compensating counterflows and localized upwellings. These *bathypelagic* water masses, extending from 200 to 6000 m beneath the ocean surface, are relatively cold and habitually dark. The deep-water trenches, reaching to almost 11 000 m, comprise the *hadal* zone; here the water is similarly cold and dark, and exerts extreme pressures (up to 100 MPa). By comparison, the aggregate volume of the world's lakes and rivers is a relatively modest $225 \times 10^3\,\mathrm{km}^3$, covering some $2.8 \times 10^6\,\mathrm{km}^2$. With a few noted exceptions, most of the 8.5×10^6 inland waters are small and <200 m in depth [2], and well within the oceanographer's understanding of "epipelagic."

Self-evidently, the quantifiable inter-relationships struck among the autotrophs and heterotrophs of open water, and with the environmental constraints, are the concern of *pelagic ecology*.

Pelagic Adaptations

As in other ecosystems, pelagic communities comprise plantlike primary producers (the *phytoplankton*), a miscellany of protist and animal consumers (the *zooplankton*), and the great variety of microbial decomposers (the *bacterioplankton*). However, the properties of water pose important constraints on the adaptive traits and selection of aquatic organisms: the adaptations of pelagic organisms, from bacteria to cetaceans, cannot be appreciated fully without a basic understanding of the physical behavior of large pelagic water masses. Although the high density of water offers Archimedean buoyancy and mechanical support, and its high specific heat buffers against sharp changes in temperature, the undoubted benefits of these features to organisms living in water are countered by several severe drawbacks. Water has a high viscosity, which exerts powerful drag forces on larger animals swimming through the medium, necessitating powerful musculature and mechanisms for overcoming friction. High viscosity (attributable to the mutual attraction of water molecules) resists motion and tends to overwhelm the introduced energy of convection and wind. Mechanical forcing is rapidly dissipated through a series of recoiling turbulent eddies of diminishing size and velocity, until they collapse into viscous forces. Against the most violent natural forcing (storms, torrential streamflow, estuarine mixing), the smallest eddy size can be as little as 0.4–0.5 mm [3]. Yet this dimension defines a microscale viscous world wherein microscopic organisms experience no direct turbulence, save that they remain liable to be transported throughout the vertical and horizontal extent of the turbulent motion.

Being generally smaller than 0.2 mm, and often considerably so, the majority of pelagic primary producers and decomposers is passively dispersed through the medium. The phytoplankton comprises many species of algae and cyanobacteria whose small size and modest sinking rates are adapted to maximize pelagic suspension [4]: some are unicellular, some form simple colonies. Individuals do range in size, over four orders of magnitude, between $\sim 0.2\,\mu\mathrm{m}$ and ~ 2 mm. The ability to live consistently at the viscous scale, in effective suspension and supported by the water, is arguably the most efficient way of maintaining a photosynthetic surface in a turbulent liquid environment [5]. This way of life has

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been adopted, probably quite independently, within each of the dozen photosynthetic phyla represented in the pelagic; in contrast, the macrophytic, arboreal, or subarboreal habit characterizing terrestrial plants has arisen and survived (albeit, probably more than once) exclusively within the chlorophyte phylum ("green algae") [6].

Nevertheless, there is a wide variation in size and density among the phytoplankton, which affects their persistence, their dynamic behavior, and, ultimately, their ecology. While the smallest species of the picoplankton (cells $< 2\,\mu\mathrm{m}$) are almost perfectly entrained, increasingly larger species of the nanoplankton ($2-20\,\mu\mathrm{m}$) and microplankton ($20-200\,\mu\mathrm{m}$) are likely have higher indigenous sinking rates (in accordance with Stokes' Law governing settlement of particles through fluids) and to be liable to escape from turbulent eddies [4]. Mechanisms to reduce passive sinking (including by distortion from the spherical form [7, 8] or production of swathing mucilage to lower average unit density [9]) are well understood. Several marine species are able to adjust solute content [10] while most planktonic cyanobacteria are able to regulate the buoyancy imparted by intracellular gas vesicles [11]. In many instances, species are flagellate but for them to effect beneficial vertical migrations (for instance, to avoid strong light) or even simply to compensate the tendency to sink, the larger microplanktonic size is essential [4].

The free-living eubacteria are mostly picoplanktonic, typically measuring $0.2-1\,\mu\mathrm{m}$ in length. Most are aerobic decomposers of (presumably) particular classes of organic compounds, according to genomically determined capabilities. Certain chemolithotrophic genera (such as the sulfide-oxidizing *Thiobacillus*) are primary producers and another group of photolithoautotrophs (including the photosynthetic sulfur bacteria, *Chromatium* and *Chlorobium*) inhabits anaerobic water. Interestingly, the pelagic herbivores include nanoplanktonic and microplanktonic protists (flagellates, rhizopods, and ciliates) living at the viscous scale [12]. There are more robust, millimeter-scale, mesoplanktonic feeders that exploit the viscous–turbulent boundary in foraging for small food particles (including phytoplankton and bacterioplankton). In freshwaters, most of these belong to the Rotifers and to the Crustacean orders of Copepods and Cladocera [13]. Some crustacean genera (*Cyclops, Leptodora*) are carnivorous, predating on rotifers and small cladocerans. Marine zooplankton is much more diverse in phylogeny, but many of its components are the dispersive larvae of (inter alia) molluscs and echinoderms, as well as the more sedentary crustaceans (barnacles, crabs, etc.). For most of their lives, larger vertebrates (especially pelagic fish) rely on being able to gain access to and to strain the large volumes of pelagic water that are needed to yield their immediate food requirements. Most of these need to be highly mobile and capable of controlling their speed and direction of swimming in the pursuit of suitable pelagic foods. Thus, many species of macroscopic nektonic organisms minimize turbulent drag in order to fulfill their food requirements from defined ranges. The sleek, streamlined body forms they have adopted attest to the evolutionary convergence of traits adapted for life in the pelagic [14].

Many other kinds of organism are represented in the plankton. Fungi and actinomycetes are known, some saprophytic, some parasitic, and very high concentrations of free-living viruses are apparently ubiquitous. However, the extent of their role in pelagic communities is only now becoming clear [15].

Ecological Organization of Pelagic Communities

Pelagic ecosystems essentially resemble those of other major habitats in being functionally organized around the processing flow of carbon and other resources (*see* **Nutrient cycling**). The small size of most phytoplankton determines that, individually, they do little to structure the environment, although their presence and activities contribute to the generation of gradients of light energy and residual nutrients. On the other hand, the relatively small size of the primary producers confers the property of potentially rapid reproduction. It is a peculiarity of pelagic ecosystems that body size generally increases up the food chain: the main primary producers are generally eaten intact. In consequence, structure and function in pelagic communities is influenced strongly by the comparative dynamics of recruitment and removal of producer biomass.

Oceanic photosynthesis continues to be seen, correctly, as a major engine in the planetary fixation of carbon and the generation of oxygen: net marine primary production is generally estimated to be 45–50 Pg C annually (compared to

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55–60 Pg C generated by terrestrial domains [16]). This equates to $<150\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ though remote-sensed disparities [17] reveal localized "hot-spots" ($>800\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$) among shallow shelf waters and upwellings Over much of the open oceans, primary production is consistently in the range $30–90\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$. Yet, in the well-illuminated, near-surface layers of the sea, the yield of light energy and its investment in high-energy bonds, about $15\,\mathrm{kJ\,g^{-1}}$ carbon or $180\,\mathrm{kJ\,(mol\,C)^{-1}}$, is about the same as is observed among terrestrial higher plants: photoautotrophic performance is highly conserved [18]. Chlorophyll-specific photosynthesis is similarly subject to analogous physiological limits: carbon fixation is a function of the photon flux density, the efficiency of photon interception, and the rate of electron transfer. Saturation of the plastoquinone pool of electrons, the overspill of electrons driving in vivo fluorescence, and the initial reduction of CO_2 (carboxylation, as mediated through the action of the enzyme, RUBISCO), each contribute to the regulation of biomass-specific photosynthetic output of phytoplankton [19].

Frequently described as being "unproductive," the net photosynthetic yield to biomass ratio in pelagic phytoplankton can be high, up to $1.2\,\mathrm{mg\,C\,(mg\ cell\ C)^{-1}\,day^{-1}}$ in the epipelagic [4]. The productive poverty of the open ocean owes most to the low-standing biomass supported (often $<1\,\mathrm{g\ cell\ C\,m^{-2}}$ through the upper 200 m). Such is the absorbance of downwelling light energy, even by clear water, that net photosynthetic carbon fixation rapidly becomes depth dependent, falling below the rate of respiration at the base of the *euphotic* layer. This is rarely >35 m beneath the water surface [20]. Suspended particulate matter (tripton) and, where relevant, greater concentration of chlorophyll, only increase the coefficient of vertical light extinction and diminish the depth of the euphotic layer. When convective mixing of the water column, driven by winds, tides, and hemispheric flows entrains phytoplankton beyond the euphotic depth, shortening the photoperiod it experiences, the photosynthetic production in the entire mixed layer is proportionately reduced [21]. The capacity of deep-mixed layers to support photosynthetic populations is predictably lowered [4, 22].

The main reason for low oceanic biomass is the poverty of certain key nutrients. Pelagic biomass consists, broadly, of the same blend of 20 or so elements encountered elsewhere and in similar proportions. Six of them – C, O, H, N, P, and S – are major nutrients, each contributing $>0.5\%$ of the fresh mass of healthy protoplasm [23]; diatoms have a generic requirement for skeletal silicon; the so-called micronutrients (Fe, Mn, Cu, Co, Mo, Ba, and Va) are required only in trace quantities; yet others are abundant, relative to biomass requirements (Ca, Mg, Na, K, Cl). The elements whose supply is likely to be prejudicial to (or "to limit") the assembly of pelagic biomass include nitrogen (in assimilable combinations – typically ammonium and nitrate – but, except to specialized dinitrogen-reducing cyanobacteria, not gas [23]). In lakes, especially larger ones with mountainous catchments; phosphorus (as orthophosphate) more likely to limit biomass production [24]. In much of the open ocean, owing to remoteness from terrestrial sources of bioavailable sources of iron, concentrations may be severely and persistently limiting (often $< 10^{-9}$ M Fe): memorably verified by the first fertilization experiments in the Southern Ocean (IRONEX [25]): iron levels are just too low to support any greater biomass than they do.

Besides providing the fuel for aquatic ecosystems, carbon is also the principal constituent of biomass and, thus, is properly regarded as a vital nutrient. The proximal source of inorganic carbon in aquatic systems has, for long been assumed to be carbon dioxide dissolved in the medium. A satisfying similarity between the magnitude of net areal production in the open ocean with the verifiable rates of invasion of carbon dioxide from the atmosphere [26] notwithstanding, higher concentrations of inorganic carbon and faster rates of biomass assembly are achieved in, for example, low-latitude shelf waters and in shallow lakes, generally without obvious symptoms of carbon limitation (high pH, carbonate precipitation) in most instances. Large fluxes of dissolved carbon dioxide, as with substantial amounts of other nutrients, are delivered in the fluvial run-off, emanating from terrestrial sources [27]. Organic sources of carbon are also prominent in the function of aquatic ecosystems. The sustained and substantial presence of a supposedly recalcitrant base of dissolved organic carbon (DOC) in the sea, of around $1\,\mathrm{g\ C\ m^{-3}}$, is now well established [28]; its supposed derivation from terrestrially produced humic matter has been confirmed circumstantially but its low residual energy content is released less by microorganismic respiration than by near-surface

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photooxidation [29]. Carbon dioxide is released to the pelagic pool of dissolved inorganic carbon (DIC). The humic content of inland waters lakes was already known to be concentrated, (especially among the brown waters draining swamps and peatlands [30]). Because dissolved humic matter may be shown frequently to account for some 50–90% of all the organic carbon present in lakes and rivers, including live organisms [31], the transport of DOC from land to water is far from being ecologically insignificant. Individual rivers also transport considerable loads of particulate organic carbon (POC) in the form of debris and detrital remains of once-living biota. The flux is seaward, though a large proportion may be buried in lakes and offshore.

Current estimates of the scale of global fluxes of organic carbon to the ocean place them more than an order of magnitude smaller than primary production ([32]: 0.9 Pg C year^{-1}, or about 2.5 g C $\text{m}^{-2}\,\text{year}^{-1}$). It is interesting that this total is net of reoxidation to CO_2 in freshwaters (approximated to be ≥ 0.8 Pg C year^{-1}) and the burial of organic carbon in lakes (~ 0.2 Pg C year^{-1}); thus, not less than ~ 1.9 Pg organic carbon is shed annually from terrrestrial habitats to inland waters, at a mean rate equivalent to $\sim 670\,\text{g C m}^{-2}\,\text{year}^{-1}$.

Carbon and Energy Flow in Pelagic Food Webs

Despite the general poverty of pelagic biomass, its productivity can be impressively high. The theoretical stoichiometry of photosynthesis supposes that the energy of 8 mol photons is required to fix 1 mol carbon, that is, the yield of photosynthesis should be 0.125 mol carbon $(\text{mol photon absorbed})^{-1}$. Measured yields (0.07–0.09 mol carbon $(\text{mol photon absorbed})^{-1}$) do not achieve quite this level of efficiency. However, on the basis that a flux density of $250\,\mu$ mol photons $\text{m}^{-2}\text{s}^{-1}$ is adequate to saturate the light-harvesting capacity of 0.1 g chlorophyll m^{-2}, when it is generating some $20\,\mu$ mol carbon $\text{m}^{-2}\text{s}^{-1}$, the yield of photosynthate is $\sim 200\,\mu$ mol carbon (g chlorophyll) s^{-1}. Given that the typical cell complement of chlorophyll to be in the order of 1/50 of its carbon content, the carbon-specific yield is $\sim 4\,\mu$ mol C fixed (g cell carbon) $\text{s}^{-1}\text{m}^{-2}$, or about $50\,\mu$g carbon $(\text{g cell C})^{-1}\text{s}^{-1}$. Were this rate of fixation to be maintained, the cell would accumulate sufficient carbon (i.e., a further gram of carbon per gram of cell carbon) to sustain a precise doubling of the population within 13 863 s, or a little under 4 h.

Such rates of cell growth are attainable in the laboratory, under saturating light, at temperatures in excess of 30°C and with a full supply of nutrients [4]. Mostly, natural rates of sustained cell growth are rather slower, because the water is colder, the light is poorer or intermittent, or one or more key nutrients is in short supply. Often the fastest rates of natural growth are observed following a period when growth has been energy limited and nutrients have accumulated in the water. Then, lengthening days, surface warming, and a weakening of turbulent mixing provide the opportunity for a more sustained increase. These are the classic conditions in temperate waters for the onset of the "spring bloom," when the active population may double its mass every two or three days, until it begins to shade itself, or it runs out of nutrients, or increased vertical mixing deprives it of energy.

It is generally the case that chronic deficiencies in the supply of nutrient regulate the accumulation of autotrophic production at far below the productive potential. Low biomass in turn restricts the concentrations of high-quality food resources that are ostensibly available to zooplankton, subject to encounter and ingestibility, being too dilute and difficult to harvest for substantial periods of the year. Filter-feeding rotifers and, especially, cladocerans, like the freshwater *Daphnia,* are the most efficient planktonic converters of algal carbon to animal biomass. Within a single generation time (perhaps 14 days or so under good conditions) and supposing the individual algae are suitably small (food size is scaled to the size of the consumer, though in general $< 50\,\mu$ m) and palatable, *Daphnia* can increase in biomass 10- to 20-fold. Within two generations, *Daphnia* populations can be removing algae faster than they can be replaced through growth. There is a threshold food concentration (~ 0.1 g C m^{-3}), below which filter feeding cannot be sustained [33]. When food concentration is depleted by active filter feeding below this threshold, consumers soon become liable to starvation and death. In those waters where a lack of nutrients normally keeps the food concentration well beneath this threshold, the zooplankton is likely to be dominated by calanoid copepods. These are selective feeders which "cherry pick" planktonic algae and protists. The latter may be sustained mainly by bacterioplankton, which itself draws primarily upon the supply of fixed carbon excreted as photosynthetic intermediates by nutrient-limited algae, as well as from some forms of DOC delivered from external (terrestrial) sources. However, in such cases, the bacteria are also subject to nutrient limitation and, like the algae, are demonstrably dependent upon the nutrients reactivated by zooplankton excretion. The steady, low-productivity system that is attainable by this sequence of carbon transfer through picoplankton and microzooplanktonic consumers is known as the "*microbial loop*" [34].

At concentrations of ingestible foods adequate to satisfy the growth and reproductive demands of the consumer (in the case of cladocera, between 0.5 and $0.7\,\mathrm{g\,C\,m^{-3}}$ [13, 33]), filter-feeding is able to saturate consumptive needs in a shorter period of time; the rate of feeding may slow, until such food is depleted to levels that fail to satisfy individual consumers. *Daphnia* biomass may, in theory, go on increasing for as long as phytoplankton sustains the carbon requirement of the consumers. Eventually, however, populations of *Daphnia,* the product of whose numbers and individual sizes is sufficiently large, remove food organisms from the water faster than phytoplankton growth can recoup by growth. The filtration capacity achieved by *Daphnia* populations equivalent to $0.1-0.2\ \mathrm{g\ C\ m^{-3}}$ (say, 20 000 individuals $\mathrm{m^{-3}}$, depending on species, and at water temperatures of about of $\sim 20\,^{\circ}\mathrm{C}$), may well be sufficient to clear the water of all edible particles. In this way, "boom" moves swiftly toward the "bust" of severe starvation and mass mortality.

The important deduction is that, far from representing the main productive pathway to supporting larger pelagic animals (especially fish), zooplankton represents only a modest nutritional resource. Against the energetic food requirements of salmonid fish [35, 36], it is calculable [37] that, were they to feed exclusively on maximal densities of *Daphnia*, they would *each* need to crop *each* day *all* the crustaceans present in > 0.3 (small fish) to 4 $\mathrm{m^3}$ of water (a 250-g fish); to permit continued recruitment of *Daphnia*, a volume of fish-free water at least 5 times greater is demanded. Were the slower-breeding calanoids to sustain the food requirements of the fish, a proportionately greater volume of water would have to be available to each individual.

In reality, at concentrations substantially $<0.1\,\mathrm{g\,C\,m^{-3}}$, zooplankton represents an unattractive resource to a majority of non-planktivorous adult fish; consumption of zooplankton is opportunistic and significant when present in the range, $0.1-1\ \mathrm{g\ C\ m^{-3}}$, but episodes of such abundance are too brief and stochastic to offer a sustainable feeding niche [38]. It is evident that planktivory alone is quite inadequate to support the production of the populations of adult fish observable in many lakes or even coastal areas of the sea. In the true pelagic (of large lakes and especially the sea), however, planktivory is the main feeding pathway that is open to fish suitably adapted to the straining and concentrating of food from the large volumes of water that are passed over the gill rakers as they swim. Even so, plankton-based food webs are typically unproductive and oligotrophic in function. The more prolific and more readily exploitable fish production in small-to-medium lakes and in the inshore regions of shallow seas is substantially supported instead through adults feeding on larger macroinvertebrate prey, foraged from the accessible benthos of the littoral fringes or slightly deeper offshore sublittoral regions [39]. Structurally and functionally, the benthos and the shallow margins of lakes are rather more complex than the open pelagic, providing a greater variety of microhabitats and feeding opportunities to consumers. Frequently, the productive intensity of shallow areas is considerably greater than the pelagic (*see also* **Benthic ecology**).

It is to be emphasised that planktivory does fulfill an important role in the overall cycle of production of many species of fish, as their eggs are hatched in or are rapidly recruited into the pelagic zone (as the "young-of-the-year"), where their early growth exploits the seasonal abundance of crustacean zooplankton [40]). Initially, while they are scarcely much larger than their zooplanktonic prey, young fish feed and grow until, within a few weeks or months, they begin to migrate to the shallow margins of the water body, to forage for more larger, macroinvertebrate inhabiting the littoral and benthic areas. These (mainly) horizontal relocations do not just couple the biology of the pelagic zone to the containing margins but, owing to the motility and subsequent electivity of potential feeding opportunities, their activities tend to overlap and, ultimately, integrate the dynamics of the benthos with those of the pelagic. Except in very large and deep water-bodies, the energy flow in the pelagic is strongly influenced by the productive dynamics of the shallow margins [41].

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(*See also* **Aquatic toxicology**; **Benthic ecology**; **Community food webs**; **Ecosystem element cycling**)

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