BIOLOGICAL OCEANOGRAPHY

Legendre, Louis and **Rassoulzadegan, Fereidoun**
Laboratoire d'Océanographie de Villefranche, France.

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Contents

Summary

The paper reviews the central topics of modern biological oceanography. After examining the wide variety of marine living organisms, the review focuses on dissolved and particulate organic matter in the sea, and the origin and fate of the latter. Next, comes a review of different ecological groupings of marine organisms, and the

description of functional groups of pelagic organisms. The initial sections are followed by the systematic examination of a large number of processes in which marine organisms are involved directly or indirectly: main effects of ocean physics and light, effects of inorganic and organic substances on marine organisms, effects of marine organisms on inorganic and organic substances, interactions among groups of marine organisms. The information from the previous Sections is put together in the context of marine pelagic food webs, followed by conclusions and perspectives.

A large proportion of the facts reported in the review were unknown as recently as two or three decades ago. It follows that very large components of marine autotrophic and heterotrophic production and degradation of organic matter in oceans were totally unknown until recently. Our knowledge of biological oceanographic processes is still progressing fast. Even without new discoveries, regional and global changes to the marine environment caused by human activities (e.g., pollution of coastal waters, destruction of marine environments, overfishing, climate change) would force deep revisions of biological oceanographic models in the coming decades. The combination of continuing discoveries with the rapidly changing marine environment is a major challenge for the biological oceanographic community. The present review is therefore a chapter in a rapidly evolving story.

Biological oceanography has traditionally focused on the water column. As a consequence, organisms and processes in the water column are generally studied independently from those on the bottom. Hence, there is presently little information on functional relationships between the two environments. This situation is reflected in the present review, of which the scope is limited by the lack of detailed knowledge on the interactions between water-column and bottom organisms. Two articles (see *Littoral Zone* and *Deep Sea Benthos, Contrasting Ecosystems*) provide complementary, up-to-date information, on bottom life in shallow and deep waters, respectively.

1. Introduction

1.1 The Marine Living Organisms

All living organisms, except viruses, are made up of cells. Viruses are small particles about 20 to 200 nm long, whereas cellular organisms range in size from 0.2 µm (bacteria) to about 30 m (baleen whales). The cellular organisms belong to either procaryotes or eukaryotes (cells without or with a well-defined nucleus, respectively). The eucaryotes may be unicellular or pluricellular (single cells or cells organized in tissues, respectively). The former are called protists, and the latter belong to either plants or metazoa. There are several intermediates between single-celled and pluricellular organisms, e.g., chain of cells, thallus (plant with no differentiation into leaves, roots, etc., e.g., seaweeds) and animal with cells that are all similar (i.e., not differentiated into organs, such as in sponges).

The organisms that synthesize their organic matter from inorganic substrates are called autotrophs. The energy they use to synthesize organic compounds is either that of light (photoautotorphs, e.g., photosynthetic algae), or inorganic chemicals (chemoautotrophs, e.g., chemosynthetic bacteria). The organisms that feed on external organic matter are called heterotrophs. There are various mixotrophic intermediates between autotrophic and heterotrophic organisms, which take advantage of both photosynthesis and heterotrophy.

Marine organisms are found on or close to the bottom, and in the water column. The former belong to the benthos, and the latter to either the plankton (organisms with no or little capacity to move horizontally against currents) or nekton (organisms with swimming ability strong enough for moving across currents and small-scale water mass circulation). Most planktonic organisms are small (from bacteria <1 µm, to small crustaceans a few 10s cm long), but some have a diameter >1 m (jellyfish). The smallest nektonic organisms are small fish (a few cm long), and the largest include large sharks and whales. Concerning the benthos, see *Deep sea benthos, contrasting ecosystems* and Littoral Zone.

Some planktonic organisms spend their whole lives in the water column (holoplankton), whereas others are present in the plankton during the larval stage only and spend their adult lives in either the nekton or benthos (meroplankton). Both procaryotic and eucaryotic organisms are found in the plankton.

Free viruses in the water column are collectively called virioplankton. These viruses are phages of bacterioplankton or phytoplankton (defined in the following paragraphs).

The planktonic autotrophs (also called phytoplankton or primary producers) include both procaryotic and eucaryotic organisms that contain photosynthetic pigments (chiefly chlorophyll). There are three main categories of autotrophic plankton: cyanobacteria (photosynthetic bacteria ≤1 µm, mostly represented in oceans by the genera *Synechococcus* and *Prochlorococcus*), naked flagellates (ranging in size from 1.2 to about 20 µm and planktonic algae (often dominated by diatoms, dinoflagellates or coccolithophores). According to the objectives or methodology of studies, phytoplankton may include, or not, all organisms with photosynthetic pigments, i.e., in addition to the above photoautotrophs, the auxotrophs (autotrophs which have a physiological growth requirement for some vitamins) and mixotrophs.

The planktonic heterotrophs are organisms that acquire external organic matter by osmosis (osmotrophic) or ingestion (phagotrophic). There are several categories of heterotrophic plankton: bacterioplankton (heterotrophic bacteria), mycoplankton (fungi: zoosporic phycomycetes and yeasts) and zooplankton, the latter including both protozoa (protozooplankton; flagellates and ciliates) and metazoa (metazooplankton, e.g., small crustaceans, pelagic mollusks and various larvae). The microorganisms in heterotrophic plankton are said to be colorless because they do not contain photosynthetic pigments. The main consumers of dissolved organic matter (DOM) are bacterioplankton, but flagellates can also consume DOM since they are all more or less osmotrophic (it is doubtful, however, that most flagellates can compete with bacterioplankton for the concentrations of DOM in the sea).

Planktonic organisms that use both photosynthesis and heterotrophic feeding are called mixotrophs. They include cells with chloroplasts that take up organic particles (phagocytosis), such as phytoflagellates, and taxa without chloroplasts that acquire and exploit either whole algal cells (symbiosis) or isolated chloroplasts (pseudosymbiosis). Mixotrophic taxa are found among foraminifers, flagellates and ciliates.

Planktonic organisms are often divided on the basis of size. The growth and various metabolic rates of living organisms are largely size-dependent. In addition, trophic relationships depend very much on size, because the latter determines the limit between osmotrophy and phagotrophy and, for most phagotrophs, the size ranges of their food particles. The matter will be further discussed in Section 3. Table 1 shows the generally used size-based classification of plankton and nekton.

Size class	Size range	Types of organisms
Femtoplan cton	0.02 to 0.2 µm	Bacteriophage and phytophage viruses
Picoplankt on	0.2 to 2.0 µm	Autotrophic and heterotrophic bacteria, and smallest algae and eucaryotic flagellates
Nanoplankt on	2.0 to 20 µm	Mycoplankton, phytoplankton and protozooplankton
Microplank ton	20 to 200 µm	Phytoplankton and protozooplankton, and smallest metazooplankton (e.g. crustacean nauplii stages)
Mesoplank ton	0.2 to 20 mm	Largest protozooplankton, and metazooplankton
Macroplan kton Centimetre nekton	2 to 20 cm 2 to 20 cm	Metazooplankton Krill, small fish, etc.
Megaplank ton Decimetre nekton	20 to 200 cm 20 to 200 cm	Largest metazooplankton Cephalopods, fish, etc
Metre nekton	>2 m	Cephalopods, fish and marine mammals

Table 1. Size-based classification of plankton and nekton.

2. Organic Matter in the Sea

2.1. Dissolved and Particulate Organic Matter

Organic matter in the sea ranges in size from monomers less than 1000 daltons (1 dalton =1/16 of the mass of one oxygen atom = 1.65 10^{-24} g) to 30 m long baleen whales. The size continuum of organic matter is divided, for methodological convenience, between DOM and particulate organic matter (POM). It must be noted that the actual threshold between DOM and POM depends on the type of filter used for separating the two size fractions, i.e., 0.1, 0.22 or 0.7 µm. The dynamics of organic matter, and more generally life in the oceans, is largely determined by the interactions between DOM and POM.

Figure 1 shows the relative abundances in marine waters of dissolved organic carbon

(DOC) and the two components of particulate organic carbon (POC), i.e., organic detritus and pelagic organisms. The striking feature of the Figure is that only about 10% of organic carbon in oceans is particulate, and that only about one quarter of that 10% belong to living organisms. Given the very low overall abundance of living organisms in the ocean, it is legitimate to wonder if these play a significant role in the dynamics of organic matter. The short answer is "yes", because the very large pool of DOC and the large pool of detrital particles are both managed by living organisms. This will be discussed below.

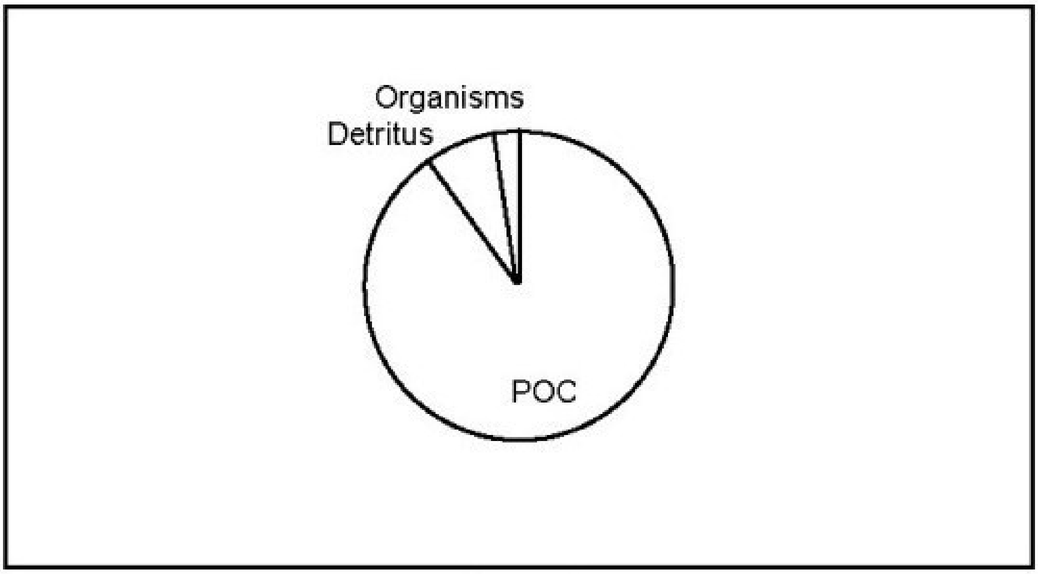

Figure 1 - Relative abundances in marine waters of dissolved organic carbon (DOC) and the two components of particulate organic carbon (POC), i.e. organic *detritus* and pelagic organisms.

The DOM consists mostly of non-living compounds (monomers, dimers and polymers), but it also includes living viruses. The non-living compounds come from the progressive dissolution of POM by the bacterial release in seawater of hydrolytic enzymes (exoenzymes). The heterotrophic bacteria involved in the process are either free-living small coccoid cells in the water column, or large cells attached to sinking or sedimented detrital particles.

The POM occurs both on the bottom (living organisms: benthos; non-living detrital particles: deposited and buried detritus, or organic sediments) and in the water column. The latter component is divided into nekton (actively swimming organisms, see above) and seston (suspended particles), of which the living component is called plankton (see above) and the non-living consists of suspended detritus.

The fact that POM represents only 10% of DOM is paradoxical, because all DOM is necessarily derived from POM, which itself ultimately comes from the autotrophs. One explanation is that the time of DOM degradation ranges from minutes to centuries, which would result in the accumulation of the slowly degrading components. In oceans, the autotrophs mostly belong to phytoplankton. Heterotrophic bacteria dissolve detrital POM and hydrolyze DOM down to monomers, and they use some of the resulting monomers for building up their body masses. Hence, heterotrophic bacteria degrade both POM and DOM into progressively smaller compounds, and they re-inject the ingested DOM into the pool of living POM. Because the complex interactions between DOM and POM are a fundamental characteristic of aquatic ecosystems, it is useful to first examine the origin and the fate of DOM in oceans.

2.2. Origin and Fate of Dissolved Organic Matter

The following paragraphs briefly review the main sources of DOM in the oceans. Some sources of DOM are from outside ocean basins (allochthonous), but most of them are internal to the marine environment (autochthonous).

Allochthonous DOM comes from land. It may be transported to oceans by water or the atmosphere. The flows from land include rivers and groundwater, which may be significant in coastal and estuarine areas. There is also significant atmospheric transport of continental DOM into the ocean. It follows that marine regions downstream or downwind from areas of high human population or industrial activity are especially influenced by allochthonous DOM, which contributes to coastal eutrophication and possibly the increasing occurrence of harmful algal blooms (HABs). In semi-enclosed basins with strong freshwater input (e.g., the Arctic Ocean), a large part of the DOM on shelves is allochthonous.

The autochthonous sources of DOM include bacterial solubilization of POM, exudation by phytoplankton, excretion by heterotrophs, sloppy feeding, leakage from fecal pellets, and viral cell lysis. Each of these sources is briefly described in the following paragraphs.

As explained above, free-living bacteria use diversified hydrolythic exoenzymes to progressively break particles down to polymers, and to depolymerize the latter to dimers and monomers. This process is called bacterial solubilization of POM. The resulting monomers are readily usable by bacteria, which take them up to build their body masses.

Phytoplankton spontaneously release DOM to surrounding waters under various circumstances, including when essential nutrients are scarce (oligotrophy). In oligotrophic waters (>80% of the World Ocean), the extremely low supply of some inorganic macronutrients (that contain N, P and/or Si), and/or inorganic micronutrients (e.g., Fe) or/and chelators (organic substances needed for using inorganic substances) do not allow phytoplankton cells to grow fast. However, the photosynthetic fixation of carbon goes on, so that there is an "overflow" of polysaccharides (or sugars), hence their exudation. This process has a significant effect on the interaction between bacteria and phytoplankton, because it leads to a mutualism between the two groups of organisms, i.e., phytoplankton cells attract bacteria into the sugar gradient around them, and then bacteria release inorganic nutrients in the vicinity of phytoplankton and attract their predators (protists), which in turn massively excrete nutrients (ammonia and orthophosphates) in the phytoplankton environment.

Proto- and metazooplankton can release as DOM up to 30 and 20%, respectively, of the organic matter from the ingested prey (excretion). This means that, (1) in large areas of the open ocean where all phytoplankton production is grazed by protozoa, up to one third of the former is transformed to DOM by the latter (in addition, protozoa release DOM when eating bacteria), and (2) in coastal areas where metazooplankton often consume a large fraction of phytoplankton production, significant amounts of DOM may be released by zooplankton.

Another important mechanism of DOM production is leakage of DOM from fecal pellets during their sinking through the water column. The mechanisms involved include diffusion, mechanical breakage (several organisms feed on the sinking pellets) and hydrolysis by bacterial exoenzymes. Pellets that sink relatively slowly (e.g., copepods, <100 m day^{-1}) release more DOM in the upper water column than those that sink fast (e.g., salps, >1000 m day^{-1}).

Several grazers (e.g., crustaceans and copepods) break up the spines and other fragile parts of their algal food. As a consequence, protoplasm of algal cells is liberated in the water, leading sometimes to high concentrations of DOM in areas where intense grazing occurs. This phenomenon is known as sloppy feeding.

Finally, the lysis of bacterial and phytoplankton cells following viral lytic infection (defined in Subsection 3.2) causes the release of DOM into the environment. Some viruses specifically infect bacteria (bacterial viruses), and others algae (algal viruses).

It was explained above that monomers are readily usable by bacteria. It is therefore expected that, when organic compounds can be depolymerized down to monomers, DOM will be easily used by bacteria (labile DOM). However, the labile or recalcitrant nature of DOM in marine waters is presently highly controversial. Among other problems is the unknown fate of the high molecular weight DOM in the sea (up to 90% of total DOC): some studies have shown that these compounds can be used rapidly, and even preferentially by bacteria, whereas others conclude a long-term accumulation of DOM. Hence, the fate of global DOM in oceans (i.e., dynamic steady-state, or long-term accumulation) is presently under debate.

3. Functional Groups of Marine Pelagic Organisms

3.1. Ecological Groupings of Marine Organisms

The article *Marine Biodiversity* discusses the biodiversity of marine organisms in terms of taxa, genetics and ecology. The present section focuses on marine pelagic organisms, for which functional groups of taxa are defined. These functional groups are used in the remainder of the present paper.

Ecologists use the following terms to describe different groupings of living organisms. A population is a group of individuals belonging to the same species, which are found in a given area. An assemblage is the general term for a group of species belonging to a supraspecific taxon (e.g., fish assemblage), or an ecological group (e.g., phytoplankton assemblage). A community is a group of interacting populations. An ecosystem is a group of interacting communities and the environment in which these communities thrive. In all ecosystems, there is a complex flux of organic matter from autotrophic to heterotrophic organisms; the various pathways of this flux are known as food webs.

Organisms can also be grouped on the basis of shared ecological or behavioral characteristics, as already described in the previous Section. In aquatic ecology, the most usual groups of this type are the plankton, nekton and benthos, but others are sometimes recognized, e.g., the pleuston (sea-surface organisms with bodies that project partly into the air) or neuston (organisms that inhabit the uppermost few to tens of millimeters of the water column).

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Bibliography

Cushing, D. (1996). *Towards a science of recruitment in fish populations*. Oldendorf/Luhe, Institute of Ecology [Keystone book in the emerging discipline of fisheries oceanography].

Falkowski P.G. and Raven J.A. (1997). *Aquatic photosynthesis*. Malden, Mass., Blackwell Science [Comprehensive text on aquatic photosynthesis, from molecular to global scales, and from fractions of seconds to billions of years].

Kirchman, D. Ed. (2000). *Microbial ecology of the oceans*. New York, Wiley-Liss [Latest advances in the ecology of marine microbes, including viruses, bacteria and their grazers].

Lalli C.M. and Parsons T.R. (1997). *Biological oceanography: an introduction*. 2nd ed., Pergamon Press [Introductory textbook to biological oceanography].

Legendre L. and Rassoulzadegan F. (1995). Plankton and nutrient dynamics in marine waters. *Ophelia* **41**, 153-172 [Description of the generalized planktonic food web discussed above].

Mann K.H. (2000). *Ecology of coastal waters*. 2nd ed., Malden, Mass., Blackwell Science [Textbook on the structure and functioning of the various types of coastal ecosystems].

Mann K.H. and Lazier J.R.N. (1996). *Dynamics of marine ecosystems*. 2nd ed., Cambridge, Mass., Blackwell Science [Comprehensive text on biological-physical interactions in the oceans].

Margalef R. (1997) *Our biosphere*. Oldendorf/Luhe, Institute of Ecology [A personal, integrative view of the biosphere, by a foremost ecologist].

Biographical Sketches

Louis Legendre was born in Montréal, Canada, in 1945. He obtained a B.Sc. in Biology-Zoology from the University of Montréal in 1967, and a Ph.D. in Biological Oceanography from Dalhousie University (Halifax) in 1971. After a 2-year NATO postdoctoral fellowship at the Station Zoologique de Villefranche-sur-Mer, he became Assistant Professor at the Department of Biology, Laval University (Québec City, Canada), in 1973, Associate Professor in 1977 and Full Professor in 1981. He was elected Fellow of the Royal Society of Canada (Academy of Science) in 1988. He holds a permanent research position of the Centre National de la Recherche Scientifique (CNRS, France) at the Villefranche-sur-Mer Oceanology Observatory since 2000. He has been Director of the Villefranche Oceanography Laboratory since 2001.

Prof. Legendre works on the hydrodynamic control of primary production and export of biogenic carbon in oceans. Within this conceptual framework, he studied the photosynthetic/hydrodynamic coupling and physiological ecology of microscopic algae, pelagic and sea-ice ecosystems and oceanographic theory. He conducted research in the Estuary and Gulf of St. Lawrence and in polar waters of the Canadian Arctic; he also worked in a variety of other ecosystems that include the Greenland Sea, Okhotsk Sea, Arctic polynyas, Gulf of Maine, Equatorial Atlantic, and lagoons of Polynesian coral reefs and atolls. By comparing these various environments, he could propose general mechanisms to explain the control that hydrodynamics exert on biological production and its export. In addition, he pioneered the development of numerical ecology, i.e., the theory and practice of the numerical analysis of ecological data sets. He is the author of about 200 primary publications, and he published 14 books and chapters.

Fereidoun Rassoulzadegan was born in Maragheh, Iran, in 1944. He obtained a B.Sc. in Biology from Tehran University in 1966. After heading the Department of Sturgeon Hatching and Alvin Feeding at the Iran Fishery Institute (Shilat), he turned to the ecology of planktonic protozoa. He obtained a Diplôme d'Etudes Approfondies (DEA, University of Paris VI) in 1972, a Ph.D. in Biological Oceanography (University of Paris VI) in 1975 and a D.Sc. (Doctorat d'Etat, Sciences, University Pierre and Marie Curie, Paris) in 1982. He holds a permanent research position of the Centre National de la Recherche Scientifique (CNRS, France) at the Station Zoologique de Villefranche-sur-Mer (now Villefranche Oceanology Observatory) since 1977. He was Director of the Marine Plankton Ecology Laboratory in 1996, and of the Biological Oceanography Laboratory, Villefranche-sur-Mer from 1997 to 2000. He is presently a Senior Scientist in the research team on Diversity, Biogeochemistry and Microbial Ecology of the Villefranche Oceanography Laboratory. He was Deputy Editor and Executive Editor of *Marine Microbial Food Webs* from 1985 to 1994, and he has been editing its successor, *Aquatic Microbial Ecology*, since 1995.

Dr. Rassoulzadegan has devoted his career to marine microbial ecology. He pioneered the development of paradigms on the functioning of the microbial food web: trophic roles of marine protozoa, control of bacterial production, microbial production of DOM, microheterotrophy in coral reefs, microbial recycling of NH_4 and PO_4, nutrient limitation of microbial activity and diversity of food web structure. He is the author of about 100 primary publications.