A DERIVATIVE OF
ENCYCLOPEDIA OF OCEAN SCIENCES, 2ND EDITION

MARINE BIOLOGY

COMPILED BY JOHN H. STEELE

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MARINE BIOLOGY

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MARINE BIOLOGY: INTRODUCTION

This volume is a selection of articles from the second, electronic, edition of the *Encyclopedia of Ocean Science*. It is one of nine volumes that focus on particular aspects of marine studies. Marine Biology not only covers a great variety of plant and animal species but refers to diverse aspects of their physical, chemical and human environment.

The volume is divided into the traditional sub-disciplines: Plankton, Benthos, Fish, Marine Mammals and Seabirds. Within each category, there are articles on the main taxonomic groups, but also articles dealing with important processes such as primary production of phytoplankton, fish locomotion, feeding and foraging, marine mammal diving physiology and seabird conservation.

Marine organisms have an intimate relation with their fluid environment. Ocean currents play a large role in determining their migrations and vertical mixing and advection control the nutrient supply that regulates their food production. Longer term changes in these physical processes cause major stresses on populations and communities. This close coupling of ocean physics and biology is a theme of many articles, especially those concerned with the impact of climatic changes on plankton, marine mammals and seabirds.

There are others stresses on marine communities. The general topic of marine pollution is dealt with in a separate volume. The impact of fisheries not only on commercial stocks of fish but also on the remainder of their ecosystems, is considered at length in a companion volume to this one dealing broadly with ecological processes.

Each section of this volume opens with an "Overview" article written by the Section Editor responsible for this theme within the Encyclopedia. These Section Editors were also involved in the selection of authors for the individual topics. The Editors of the Encyclopedia are in their debt for their work in ensuring the quality and coverage of these articles.

Given the breadth of topics under the rubric of Marine Biology and their inter-relation with other aspects of ocean science, this one volume must be considered as a summary or introduction. For this reason each article has, not only a further reading list, but also references to articles in the Encyclopedia or in other volumes in this series.

The articles in this volume could not have been produced without the considerable help of the members of the Editorial Advisory Board of the Encyclopedia's second edition, from which these articles were chosen. The board provided advice and suggestions about the content and authorship of particular subject areas covered in the Encyclopedia. In addition to thanking the authors of the articles in this volume, the Editors wish to thank the members of the Editorial Board for the time they gave to identify and encourage authors, to read and comment on (and sometimes to suggest improvements to) the written articles, and to make this venture possible.

John H. Steele
Editor

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PLANKTON OVERVIEW

M. M. Mullin, Scripps Institution of Oceanography, La Jolla, California, USA

The category of marine life known as plankton represents the first step in the food web of the ocean (and of large bodies of fresh water), and components of the plankton are food for many of the fish harvested by humans and for the baleen whales. The plankton play a major role in cycling of chemical elements in the ocean, and thereby also affect the chemical composition of sea water and air (through exchange of gases between the sea and the overlying atmosphere). In the parts of the ocean where planktonic life is abundant, the mineral remains of members of the plankton are major contributors to deep-sea sediments, both affecting the chemistry of the sediments and providing a micropaleontological record of great value in reconstructing the earth's history.

'Plankton' refers to 'drifting', and describes organisms living in the water column (rather than on the bottom – the benthos) and too small and/or weak to move long distances independently of the ocean's currents. However, the distinction between plankton and nekton (powerfully swimming animals) can be difficult to make, and is often based more on the traditional method of sampling than on the organisms themselves.

Although horizontal movement of plankton at kilometer scales is passive, the metazoan zooplankton nearly all perform vertical migrations on scales of 10s to 100s of meters. This depth range can take them from the near surface lighted waters where the phytoplankton grow, to deeper, darker and usually colder environments. These migrations are generally diurnal, going deeper during the day, or seasonal, moving to deeper waters during the winter months to return to the surface around the time that phytoplankton production starts. The former pattern can serve various purposes: escaping visual predators and scanning the watercolumn for food. (It should be noted that predators such as pelagic fish also migrate diurnally.) Seasonal descent to greater depths is a common feature for several copepod species and may conserve energy at a time when food is scarce in the upper layers. However, vertical migration has another role. Because of differences in current strength and direction between surface and deeper layers in the ocean, time spent in deeper water acts as a transport mechanism relative to the near surface layers. On a daily basis this process can take plankton into different food concentrations. Seasonally, this effective 'migration' can complete a spatial life cycle.

The plankton can be subdivided along functional lines and in terms of size. The size category, picoplankton (0.2–2.0 μm), is approximately equivalent to the functional category, bacterioplankton; most phytoplankton (single-celled plants or colonies) and protozooplankton (single-celled animals) are nano- or microplankton (2.0–20 μm and 20–200 μm, respectively). The metazoan zooplankton (animals, the 'insects of the sea') includes large medusae and siphonophores several meters in length. Size is more important in oceanic than in terrestrial ecosystems because most of the plants are small (the floating seaweed, *Sargassum*, being the notable exception), predators generally ingest their prey whole (there is no hard surface on which to rest prey while dismembering it), and the early life stages of many types of zooplankton are approximately the same size as the larger types of phytoplankton. Therefore, while the dependence on light for photosynthesis is characteristic of the phytoplankton, the concepts of 'herbivore' and 'carnivore' can be ambiguous when applied to zooplankton, since potential plant and animal prey overlap in size and can be equivalent sources of food. Though rabbits do not eat baby foxes on land, analogous ontogenetic role-switching is very common in the plankton.

Among the animals, holoplanktonic species are those that spend their entire life in the plankton, whereas many benthic invertebrates have meroplanktonic larvae that are temporarily part of the plankton. Larval fish are also a temporary part of the plankton, becoming part of the nekton as they grow. There are also terms or prefixes indicating special habitats, such as 'neuston' to describe zooplanktonic species whose distribution is restricted to within a few centimeters of the sea's surface, or 'abyssoplankton' to describe animals living only in the deepest waters of the ocean. Groups of such species form communities (see below).

Since the phytoplankton depend on sunlight for photosynthesis, this category of plankton occurs almost entirely from the surface to 50–200 m of the ocean – the euphotic depth (where light intensity is 0.1–1% of full surface sunlight). Nutrients such as nitrate and phosphate are incorporated into protoplasm in company with photosynthesis, and returned to dissolved form by excretion or remineralization of dead organic matter (particulate detritus). Since much of the latter process occurs after sinking of the detritus, uptake of nutrients and their regeneration are partially separated vertically. Where and when photosynthesis is proceeding actively and vertical mixing is not excessive, a near-surface layer of low nutrient concentrations is separated from a layer of abundant nutrients, some distance below the euphotic depth, by a nutricline (a layer in which nutrient concentrations increase rapidly with depth). Therefore, the spatial and temporal relations between the euphotic depth (dependent on light intensity at the surface and the turbidity of the water), the nutricline, and the pycnocline (a layer in which density increases rapidly with depth) are important determinants of the abundance and productivity of phytoplankton.

Zooplankton is typically more concentrated within the euphotic zone than in deeper waters, but because of sinking of detritus and diel vertical migration of some species into and out of the euphotic zone, organic matter is supplied and various types of zooplankton (and bacterioplankton and nekton) can be found at all depths in the ocean. An exception is anoxic zones such as the deep waters of the Black Sea, although certainly types of bacterioplankton that use molecules other than oxygen for their metabolism are in fact concentrated there.

Even though the distributions of planktonic species are dependent on currents, species are not uniformly distributed throughout the ocean. Species tend to be confined to particular large water masses, because of physiological constraints and inimical interactions with other species. Groups of species, from small invertebrates to active tuna, seem to 'recognize' the same boundaries in the oceans, in the sense that their patterns of distribution are similar. Such groups are called 'assemblages' (when emphasizing their statistical reality, occurring together more than expected by chance) or 'communities' (when emphasizing the functional relations between the members in food webs), though terms such as 'biocoenoses' can be found in older literature. Thus, one can identify 'central water mass,' 'subantarctic,' 'equatorial,' and 'boreal' assemblages associated with water masses defined by temperature and salinity; 'neritic' (i.e. nearshore) versus 'oceanic' assemblages with respect to depth of water over which they occur, and 'neustonic' (i.e. air–sea interface), 'epipelagic,' 'mesopelagic,' 'bathypelagic,' and 'abyssopelagic' for assemblages distinguished by the depth at which they occur. Within many of these there may be seasonally distinguishable assemblages of organisms, especially those with life spans of less than one year.

Regions which are boundaries between assemblages are sometimes called ecotones or transition zones; they generally contain a mixture of species from both sides, and (as in the transition zone between subpolar and central water mass assemblages) may also have an assemblage of species that occur only in the transition region.

Despite the statistical association between assemblages and water masses or depth zones, it is far from clear that the factor that actually limits distribution is the temperature/salinity or depth that physically defines the water mass or zone. It is likely that a few important species have physiological limits confining them to a zone, and the other members of the assemblage are somehow linked to those species functionally, rather than being themselves physiologically constrained. Limits can be imposed on certain life stage, such as the epipelagic larvae of meso- or bathypelagic species, creating patterns that reflect the environment of the sensitive life stage rather than the adult. Conversely, meroplanktonic larvae, such as the phyllosome of spiny lobsters, can often be found far away from the shallow waters that are a suitable habitat for the adults.

See also

Bacterioplankton. Gelatinous Zooplankton. Protozoa, Planktonic Foraminifera.

Further Reading

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MARINE PLANKTON COMMUNITIES

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Introduction

By definition, a community is an interacting population of various kinds of individuals (species) in a common location (*Webster's Collegiate Dictionary*, 1977).

The objective of this article is to provide general information on the composition and functioning of various marine plankton communities, which is accompanied by some characteristic details on their dynamicism.

General Features of a Plankton Community

The expression 'plankton community' implies that such a community is located in a water column. It has a range of components (groups of organisms) that can be organized according to their size. They range in size from tiny single-celled organisms such as bacteria (0.4–1-μm diameter) to large predators like scyphomedusae of more than 1 m in diameter. A common method which has been in use for decades is to group according to size, which here is attributed to the organism's largest dimension; thus the organisms range from picoplankton to macroplankton (**Figure 1**). It is, however, the smallest dimension of an organism which usually determines whether it is retained by a mesh, since in a flow, elongated particles align themselves with the flow.

A plankton community is operating/functioning continuously, that is, physical, chemical, and biological variables are always at work. Interactions among its components occur all the time. As one well-known fluid dynamicist stated, "The surface of the ocean can be flat calm but below that surface there is always motion of the water at various scales." Many of the particles/organisms are moving or being moved most of the time: Those without flagella or appendages can do so due to processes within or due to external forcing, for example, from water motion due to internal waves; and those with flagella/cilia or appendages or muscles move or create motion of the water in order to exist. Oriented motion is usually in the vertical which often results in distinct layers of certain organisms. However, physical variables also, such as light or density differences of water masses, can result in layering of planktonic organisms. Such layers which are often horizontally extended are usually referred to as patches.

As stated in the definition, the components of a plankton community interact. It is usually the case that a larger organism will ingest a smaller one or a part of it (**Figure 1**). However, there are exceptions. The driving force for a planktonic community originates from sun energy, that is, primary productivity's (1) direct and (2) indirect products: (1) autotrophs (phytoplankton cells) which can range from near 2 to more than 300-μm width/diameter, or chemotrophs; and (2) dissolved organic matter, most of which is released by phytoplankton cells and protozoa as metabolic end products, and being taken up by bacteria and mixo- and heterotroph protozoa (**Figure 1**). These two components mainly set the microbial loop (ML; (*see* Bacterioplankton and Protozoa, Planktonic Foraminifera)) in motion; that is, unicellular organisms of different sizes and behaviors (auto-, mixo-, and heterotrophs) depend on each other – usually, but not always, the smaller being ingested by the larger. Most of nutrients and energy are recirculated within this subcommunity of unicellular organisms in all marine regions of our planet (*see* Bacterioplankton, Phytoplankton Size Structure, and Protozoa, Planktonic Foraminifera for more details, especially the ML)These processes of the ML dominate the transfer of energy in all plankton communities largely because the processes (rates of ingestion, growth, reproduction) of unicellular heterotrophs almost always outpace those of phytoplankton, and also of metazooplankton taxa at most times.

The main question actually could be: "What is the composition of plankton communities, and how do they function?" **Figure 1** reveals sizes and relationships within a plankton community including the ML. It shows the so-called 'bottom-up' and 'top-down' effects as well as indirect effects like the above-mentioned labile dissolved organic matter (labile DOM), released by auto- and also by heterotrophs, which not only drives bacterial growth but can also be taken up or used by other protozoa. There can also be reversals, called two-way processes. At times a predator eating an adult metazoan will be affected by the same metazoan which is able to eat the predator's early juveniles (e.g., well-grown ctenophores capturing adult omnivorous copepods which have the ability to capture and ingest very young ctenophores).

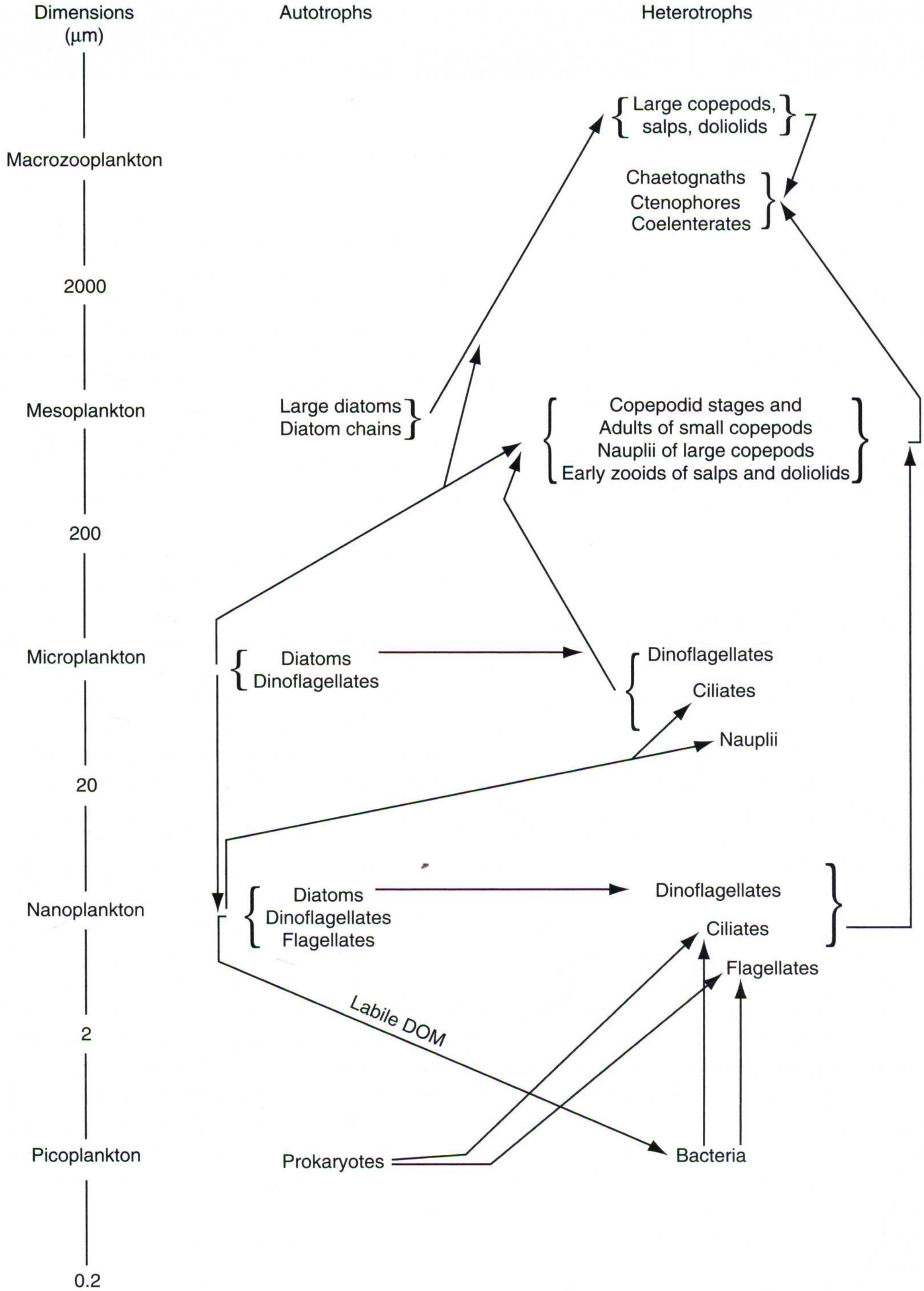

Figure 1 Interactions within a plankton community separated into size classes of auto- and heterotrophs, including the microbial loop; the arrows point to the respective grazer, or receiver of DOM; the figure is partly related to figure 9 from Landry MR and Kirchman DL (2002) Microbial community structure and variability in the tropical Pacific. *Deep-Sea Research II* 49: 2669–2693.

To comprehend the functioning of a plankton community requires a quantitative assessment of the abundances and activities of its components. First, almost all of our knowledge to date stems from *in situ* sampling, that is, making spot measurements of the abundance and distribution of organisms in the water column. The accurate determination of abundance and distribution requires using meshes or devices which quantitatively collect the respective organisms. Because of methodological difficulties and insufficient comprehension of organisms' sizes and activities, quantitative sampling/quantification of a community's main components has been often inadequate. The following serves as an example of this. Despite our knowledge that copepods consist of 11 juvenile stages aside of adults, the majority of studies of marine zooplankton hardly considered the juveniles' significance and this manifested itself in sampling with meshes which often collected merely the adults quantitatively. Second, much knowledge on rate processes comes from quantifying the respective organisms' activities under controlled conditions in the laboratory. Some *in situ* measurements (e.g., of temperature, salinity, chlorophyll concentrations, and acoustic recordings of zooplankton sizes) have been achieved 'continuously' over time, resulting in time series of increases and decreases of certain major community components. To date there are few, if any, direct *in situ* observations on the activity scales of the respective organisms, from bacteria to proto- and to metazooplankton, mainly because of methodological difficulties. In essence, our present understanding of processes within plankton communities is incomplete.

Specific Plankton Communities

We will provide several examples of plankton communities of our oceans. They will include information about the main variables affecting them, their main components, partly their functioning over time, including particular specifics characterizing each of those communities.

In this section, plankton communities are presented for three different types of marine environments: estuaries/inshore, continental shelves, and open ocean regions.

Estuaries

Estuaries and near-shore regions, being shallow, will rapidly take up and lose heat, that is, will be strongly affected by atmospheric changes in temperature, both short- and long-term, the latter showing in the seasonal extremes ranging from 2 to 32 °C in estuaries of North Carolina. Runoff of fresh water, providing continuous nutrient input for primary production, and tides contribute to rapid changes in salinity. This implies that resident planktonic taxa ought to be eurytherm as well as – therm. Only very few metazooplanktonic species are able to exist in such an environment (**Table 1**). In North Carolinian estuaries, representative of other estuaries, they are the copepod species *Acartia tonsa*, *Oithona oculata*, and *Parvocalanus crassirostris*. In estuaries of Rhode Island, two species of the genus *Acartia* occur. During colder temperatures *Acartia hudsonica* produces dormant eggs as temperatures increase and then is replaced by *A. tonsa*, which produces dormant eggs once temperatures again decrease later in the year. Such estuaries are known for high primary productivity, which is accompanied by high abundances of heterotroph protozoa preying on phytoplankton. Such high abundances of unicellular organisms imply that food is hardly limiting the growth of the above-mentioned copepods which can graze on auto- as well as heterotrophs. However, such estuaries are often nursery grounds for juvenile fish like menhaden which prey heavily on late juveniles and adults of such copepods, especially *Acartia*, which is not only the largest of those three dominant copepod species but also moves the most, and thus can be seen most easily by those visual predators. This has resulted in diurnal migrations mostly of their adults, remaining at the seafloor during the day where they hardly eat, thus avoiding predation by such visual predators, and only entering the water column during dark hours. That then is their period of pronounced feeding. The other two species which are not heavily preyed upon by juvenile fish, however, can be affected by the co-occurring *Acartia*, because from early copepodid stages on this genus can be strongly carnivorous, readily preying on the nauplii of its own and of those other species.

Nevertheless, the usually continuous abundance of food organisms for all stages of the three copepod species results in high concentrations of nauplii which in North Carolinian estuaries can reach $100\,l^{-1}$, as can their combined copepodid stages. The former is an underestimate, because sampling was done with a 75-μm mesh, which is passed through by most of those nauplii. By comparison, in an estuary on the west coast of Japan (Yellow Sea), dominated also by the genera *Acartia*, *Oithona*, and *Paracalanus* and sampling with 25-μm mesh, nauplius concentrations during summer surpassed $700\,l^{-1}$, mostly from the genus *Oithona*. And copepodid stages plus adults repeatedly exceeded $100\,l^{-1}$. Here sampling with such narrow mesh ensured that even the smallest copepods were collected quantitatively.

In essence, estuaries are known to attain among the highest concentrations of proto- and metazooplankton. The known copepod species occur during most of the year, and are observed year after year which implies persistence of those species beyond decades.

Table 1 Some characteristics of marine plankton communities

	Estuaries	*Shelves*	*Open ocean gyres*		
			Subarctic Pacific	*Boreal Atlantic*	*Epipelagic subtropical*
					Atlantic/Pacific
Physical variables	Wide range of temperature and salinity	Intermittent and seasonal atmospheric forcing	Steady salinity, seasonal temp. variability	Major seasonal variability of temperature	Steady temperature and salinity, continuous atmospheric forcing
Nutrient supply	Continuous	Episodic	Seasonal	Seasonal	Occasional
Phytoplankton abundance	High from spring to autumn	Intermittently high	Always low	Major spring bloom	Always low
Phytoplankton composition	Flagellates, diatoms	Flagellates, diatoms, dinoflagellates	Nanoflagellates	Spring: diatoms Other: mostly nanoplankton	Mostly prokaryotes, small nano- and dinoflagellates
Primary Productivity	High at most times	Intermittently high	Maximum in spring	Max. in spring and autumn	Always low
No. of metazoan species	≤ 5	~10–30	>10	>20	>100
Seasonal variability of metazoan abundance	High spring and summer, low winter	Highly variable	High	High	Low
Copepod Ranges	N[a] ~ 10–500 l^{-1}	<5–50 l^{-1}			3–10 l^{-1}
Abundance	Cop[b] ~ 5–100 l^{-1}	<3–30 l^{-1}	Up to 1000 m^{-3}	Up to 1000 m^{-3}	300–1000 m^{-3}
			Neocalanus	*C. finmarchicus*	
Dominant metazooplankton taxa	*Acartia* *Oithona* *Parvocalanus*	*Oithona* *Paracalanus* *Temora* *Doliolida*	*Neocalanus* *Oithona* *Metridia*	*Calanus* *Oithona* *Oncaea*	*Oithona* *Clausocalanus* *Oncaea*

[a]Nauplii.
[b]Copepodids and adult copepods.

Continental Shelves

By definition they extend to the 200-m isobath, and range from narrow (few kilometers) to wide (more than 100-km width). The latter are of interest because the former are affected almost continuously and entirely by the nearby open ocean. Shelves are affected by freshwater runoff and seasonally changing physical variables. Water masses on continental shelves are evaluated concerning their residence time, because atmospheric events sustained for more than 1 week can replace most of the water residing on a wide shelf with water offshore but less so from near shore. This implies that plankton communities on wide continental shelves, which are often near boundary currents, usually persist for limited periods of time, from weeks to months (**Table 1**). They include shelves like the Agulhas Bank, the Campeche Banks/Yucatan Shelf, the East China Sea Shelf, the East Australian Shelf, and the US southeastern continental shelf. There can be a continuous influx year-round of new water from adjacent boundary currents as seen for the Yucatan Peninsula and Cape Canaveral (Florida). The momentum of the boundary current (here the Yucatan Current and Florida Current) passing a protruding cape will partly displace water along downstream-positioned diverging isobaths while the majority will follow the current's general direction. This implies that upstream-produced plankton organisms can serve as seed populations toward developing a plankton community on such wide continental shelves.

Whereas estuarine plankton communities receive almost continuously nutrients for primary production from runoff and pronounced benthic-pelagic coupling, those on wide continental shelves infrequently receive new nutrients. Thus they are at most times a heterotroph community unless they obtain nutrients from the benthos due to storms, or receive episodically input of cool, nutrient-rich water from greater depths of the nearby boundary current as can be seen for the US SE shelf. Passing along the outer shelf at about weekly intervals are nutrient-rich cold-core Gulf Stream eddies which contain plankton organisms from the highly productive Gulf of Mexico. Surface winds, displacing shelf surface water offshore, lead to an advance of the deep cool water onto the shelf which can be flooded entirely by it. Pronounced irradiance and high-nutrient loads in such upwellings result in phytoplankton blooms which then serve as a food source for protozoo- and metazooplankton. Bacteria concentrations in such cool water masses increase within several days by 1 order of magnitude. Within 2–3 weeks most of the smaller phytoplankton (*c.* <20-μm width) has been greatly reduced, usually due to grazing by protozoa and relatively slow-growing assemblages of planktonic copepods of various genera such as *Temora*, *Oithona*, *Paracalanus*, *Eucalanus*, and *Oncaea*. However, quite frequently, the Florida Current which becomes the Gulf Stream carries small numbers of Thaliacea (Tunicata), which are known for intermittent and very fast asexual reproduction. Such salps and doliolids, due to their high reproductive and growth rate, can colonize large water masses, the latter increasing from $\sim$5 to $>$500 zooids per cubic meter within 2 weeks, and thus form huge patches, covering several thousands of square kilometers, as the cool bottom water is displaced over much of the shelf. The increased abundance of salps (usually in the warmer and particle-poor surface waters) and doliolids (mainly in the deeper, cooler, particle-rich waters, also observed on the outer East China shelf) can control phytoplankton growth once they achieve bloom concentrations. The development of such large and dense patches is partly due to the lack of predators.

Although the mixing processes between the initially quite cool intruding bottom (13–20 °C) and the warm, upper mixed layer water (27–28 °C) are limited, interactions across the thermocline occur, thus creating a plankton community throughout the water column of previously resident and newly arriving components. The warm upper mixed layer often has an extraordinary abundance of early copepodid stages of the poecilostomatoid copepod *Oncaea*, thanks to their ontogenetical migration after having been released by the adult females which occur exclusively in the cold intruding water. Also, early stages of the copepod *Temora turbinata* are abundant in the warm upper mixed layer; while *T. turbinata*'s late juvenile stages prefer the cool layer because of the abundance of large, readily available phytoplankton cells. As in estuaries, the copepod genus *Oithona* flourishes on warm, temperate, and polar continental shelves throughout most of the euphotic zone.

Such wide subtropical shelves will usually be well mixed during the cooler seasons, and then harbor, due to lower temperatures, fewer metazoplankton species which are often those tolerant of wider or lower temperature ranges. Such wide shelves are usually found in subtropical regions, which explains the rapidity of the development of their plankton communities. They, however, are also found in cooler climates, like the wide and productive Argentinian/Brazilian continental shelf about which our knowledge is limited. Other large shelves, like the southern North Sea, have a limited exchange of water with the open ocean but at the same time considerable influx