ZOOPLANKTON ECOLOGY

Miguel Alcaraz and **Albert Calbet**
Institut de Ciències del Mar, CSIC, Barcelona, Catalonia, Spain.

Keywords: plankton, zooplankton, spatial distribution, temporal changes, biomass, variability scales, food webs, taxonomic composition, food and feeding, production, trophic levels, autotrophs, heterotrophs, protists, metazoans, pelagic, neritic.

Contents

Summary

Zooplankton is a term applied to the community of animals that live adrift in the water, with a limited capacity to counteract the movements of water by swimming. The complexity of taxonomic composition, morphological structure, size range, and trophic role of zooplankton are probably unique in the marine world. The lack of rigid relations (i.e. space occupation) between these organisms living suspended in water is probably one of the main sources of zooplankton diversity. Taxonomically, zooplankton ranges from the most primitive unicellular organisms (protists) to vertebrates (fish larvae). While some species spend their entire life suspended in water, without any contact with solid surfaces (holoplankton), most bottom-living marine invertebrates and fishes, have also a transitory planktonic life, usually the first larval stages, and are known as meroplankton.

Despite their quite limited swimming capacity, they perform night-day rhythmic vertical displacements of hundreds of meters, most of them to feed at night in surface waters. Their main food source is phytoplankton, microscopic plants that provide most of the matter and energy in marine systems, although their trophic mode is by no means rigid.

Some are strict carnivores, but in general they can switch from vegetal to animal or even detritus food sources. This article briefly describes the role of zooplankton in the marine environment, its important feeding links, as well as the potential socio-economic consequences of shifts in its spatial distribution and time changes.

1. Introduction

Life consists basically in a series of synthesis and decomposition processes fueled by the energy provided by the highly energetic chemical bonds contained in organic matter. In marine systems, organic matter is mainly produced by microscopic, unicellular plants that are part of the plankton, a term applied to the organisms free-floating in the water column and almost unable to counteract their transport by water movements. The word originates from the Greek *planktos*, that means “something that floats passively”, and was first applied by Victor Hensen in 1887 to the tiny plants and animals obtained after gently sieving marine water through a conical net of thin muslin towed by a boat.

Due to the extreme dilution, small size and relatively low energetic value of planktonic primary producers (the above mentioned unicellular plants, the phytoplankton), their usefulness as a food source could be somewhat conditioned. Marine herbivores must have a size scaled to that of their food to exploit it efficiently, and have mechanisms to detect, capture and ingest (or reject) particles with as low energetic expenditure as possible. Most of the marine herbivores able to exploit phytoplankton are included in the animal fraction of plankton, the zooplankton. This is a heterogeneous group of organisms, which includes almost all the animal phyla, from single-celled protozoa to chordates. Probably, the only characteristic most of them share is to have a transparent body, a clear advantage to avoid capture by visual predators.

As broad as the taxonomic composition of zooplankton, is their size range. Although they are usually very small, so most of their components are only visible through a microscope or a magnifying glass (usually they are under one millimeter in length), some gelatinous forms (jellyfish and related organisms) are in the range size from centimeters to meters. From the point of view of their feeding habit and behavior, they are also very variable. Not only does zooplankton include herbivores, carnivores, omnivores and detritivores, but also parasites of other planktonic animals, and their methods to obtain food range from pumping water and filtering it through special structures and retaining the food particles (filter-feeding), to the active capture of motile prey.

2. Zooplankton in the context of marine life

Zooplankton is considered the most important link between planktonic primary producers and large carnivores, amongst them fish species subject to human exploitation. The reason is that the organic matter produced by phytoplankton circulates through marine ecosystems following two main pathways, as schematically represented in Figure 1. When nutrients are scarce (oligotrophic conditions), or when phytoplankton outbursts are too ephemeral to allow the development of zooplankton populations, very small phytoplankton species and planktonic bacteria develop. As they are too small to be ingested by zooplankton, the organic matter must be transferred through several trophic levels before reaching fish stocks, resulting in relatively long and inefficient multilevel food webs (microbial food webs). Nutrient-rich conditions, on the other hand, favor the development of relatively large phytoplankton that can be preyed upon by large herbivorous zooplankton, and finally these by fish. These shorter, more efficient food webs are known as classical or herbivorous food webs. The way through which zooplankton transfers matter and energy towards higher trophic levels will therefore determine not only the potential yield of fisheries, but their stability and sustainability.

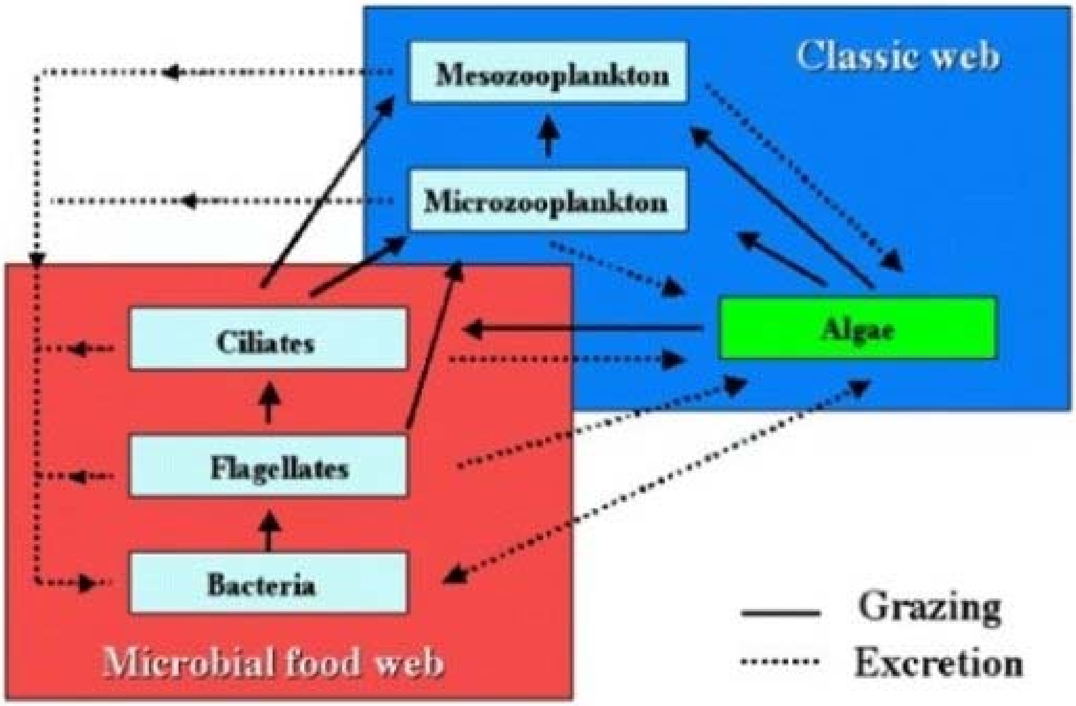

Figure 1. Schematic diagram of the links among the different components of the planktonic food webs. Red: Microbial food web. Blue: Classical food web. In green, the primary producers, the phytoplankton. (Source: A. Calbet)

Apart from influencing community structure and function, and therefore fisheries production, zooplankton can contribute the role of marine systems as sources or sinks of CO_2 and other greenhouse gasses. When feeding, zooplankton compacts small, slowly settling particles into larger ones (fecal pellets) that can reach the bottom before being recycled, so that biogenic carbon can be sequestered in the sediment, thus enlarging the time for CO_2 to return to the atmosphere.

2.1 Size and taxonomic composition: holoplankton and meroplankton

Plankton is frequently divided into size classes, to which functional categories are traditionally attributed. The whole range of plankton size extends across eight orders of magnitude, and is usually divided into quite arbitrary size classes, partially derived from the pore size of the filters and nets used to sample the different components (see Figure 2). However, there is a clear superposition in size between very different functional categories, so that autotrophs and diverse categories of heterotrophs (osmo- and phagotrophic groups, herbivores and carnivores) overlap across a size range of three orders of magnitude (from 20 micrometers to 20 000 micrometers).

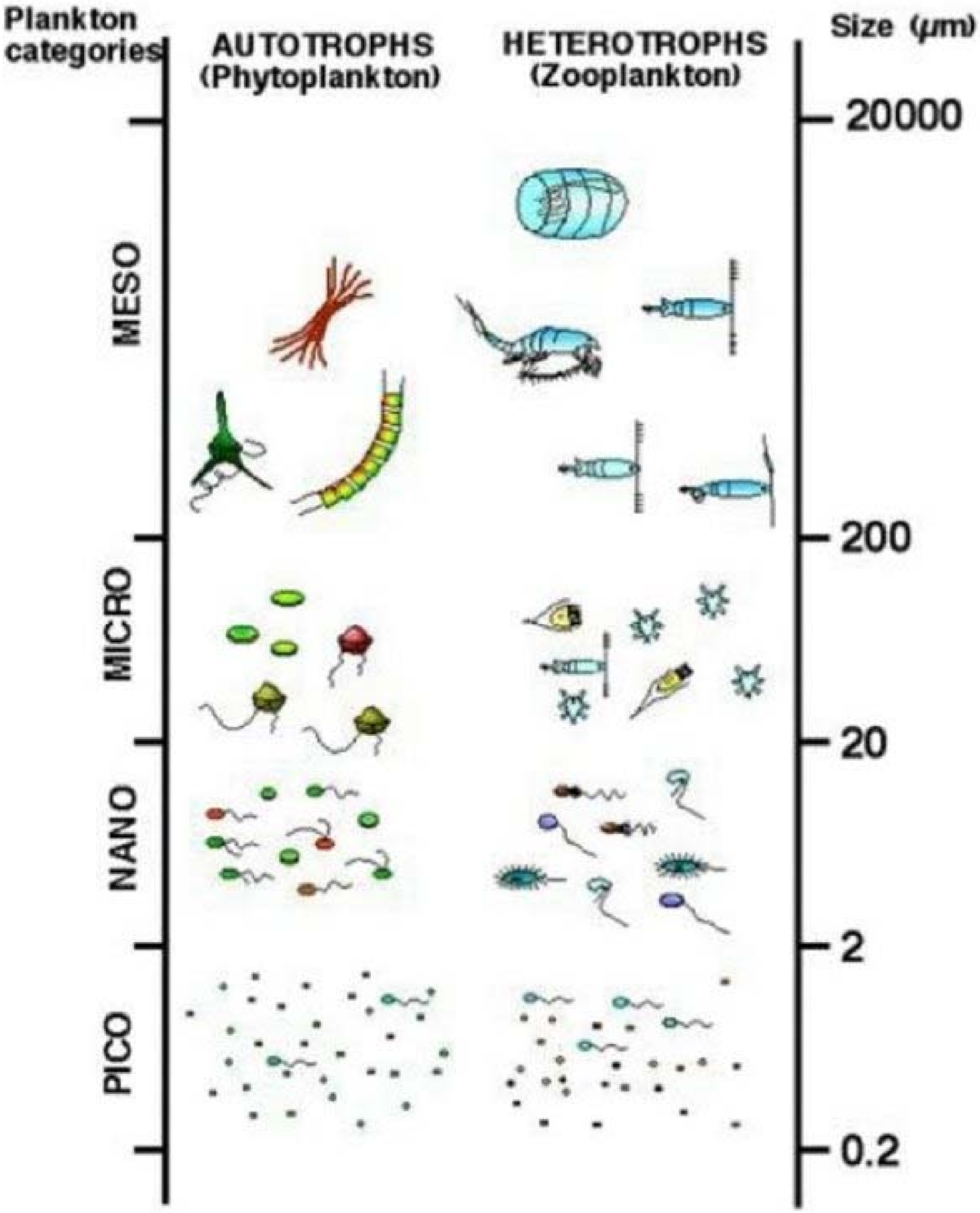

Figure 2. The division of plankton into size-classes, functional groups, and major plankton organisms. (Source: A. Calbet)

As zooplankton size extends from less than 2 micrometers (nanoplankton, unicellular heterotrophs) to several meters (megaplankton, large gelatinous forms), a complete representation of all its components in a single sample is difficult to obtain. Classically, the sampling methods for zooplankton studies have been based on its capture by concentration by filtering different volumes of water, depending on the relative abundance of the group under study. Modern methods include the use of "in situ" identification, counting and measuring devices like submersible video cameras and electronic or optical counters. Whatever the method used, the size range and the inverse relation between organismal size and abundance, impose severe restrictions for its study. The capture methods have not changed basically since the first studies made by Charles Darwin and Victor Hensen—essentially a conical net of fine gauze, ending in a cod-end or bucket to retain the organisms, which is towed either horizontally, vertically or obliquely (see Figure 3). Modern improvements on these methods consist of sophisticated devices that allow the collection of multiple samples in a single tow, automatically recording environmental conditions (depth, temperature, salinity, chlorophyll or particle abundance), as well as the volume of water filtered by the net. Another possibility consists of pumping water from the required depth and retaining the organisms in adequate filters, with the same array of sensors for automatic control of the environmental conditions. In both cases, depending on the mesh-size, there is a catching selectivity; the organisms retained representing only a size fraction of the whole community. Other limitations of zooplankton hauls are the mixing and integration across the space, so the fine details of distribution patterns and trends are lost. Submersible video cameras and optical particle counters allow better estimates of zooplankton distribution, abundance and size spectrum, at the expense of losses in taxonomic resolution.

Figure 3. A modern plankton net (LHPR), being deployed from an oceanographic vessel. This net allows the collection of separate samples for different depths, simultaneously recording environmental conditions like temperature, salinity, phytoplankton (chlorophyll) concentration, etc. (Photo courtesy of the UTM, Institut de Ciències del Mar, CSIC)

According to the duration of the planktonic life, two large zooplankton groups can be differentiated: While some organisms spend their entire life in the plankton (Holoplankton), others (Meroplankton) have a transitory planktonic life, usually as eggs or larval stages of non-planktonic animals. As the life cycles of most bottom marine invertebrates and fish include planktonic developmental stages, meroplankton is more frequent in the vicinity of the coast, where rich communities of bottom living invertebrates develop, and fish concentrate to lay eggs. Sponges, gastropod and bivalve mollusks, sea urchins, sea stars, etc., most of the sessile fauna, have planktonic larval stages, some of them named as new species by the first planktologists when their relation with adults was unknown. These names are used today to describe different morphological types of planktonic larva (i.e., *Tornaria*, *Nauplius*, *Zoea*, *Bipinnaria*, etc.).

A brief account of the taxonomic composition of holoplankton must start with its most primitive components, the Protists. They include the smallest zooplankters, their size ranging from less than 0.01 millimeter to a few millimeters. Among them, the Foraminifera secrete a skeleton, typically of calcium carbonate, consisting of one or more perforated chambers that enclose the cytoplasm. The skeletons of dead foraminiferans fall to the oceanic floor, accumulating into the “foraminifera mud” or *Globigerina* ooze (from the most frequent genus of foraminifera). Similar planktonic protists are the Acantarians and Radiolarians, solitary or forming colonies, and some forms including symbiotic algae known as Zooxanthellae. The Acantarians secrete skeletons of calcium sulfate, while Radiolarians have a silica skeleton, sometimes a combination of spines and spheres that can form intricate lace-like patterns that accumulate in the oceanic sediments, like in the case of Foraminiferans. Ciliates and flagellates are in general less spectacular than the two previous groups, but have a crucial role in microbial food webs. While most ciliates are naked forms, there is a group, the Tintinnids, that secrete a chitinous shell, the lorica (see Figure 4). From a trophic point of view, the group includes auto- and heterotrophic forms, although some can shift from one to another trophic role (mesotrophs)

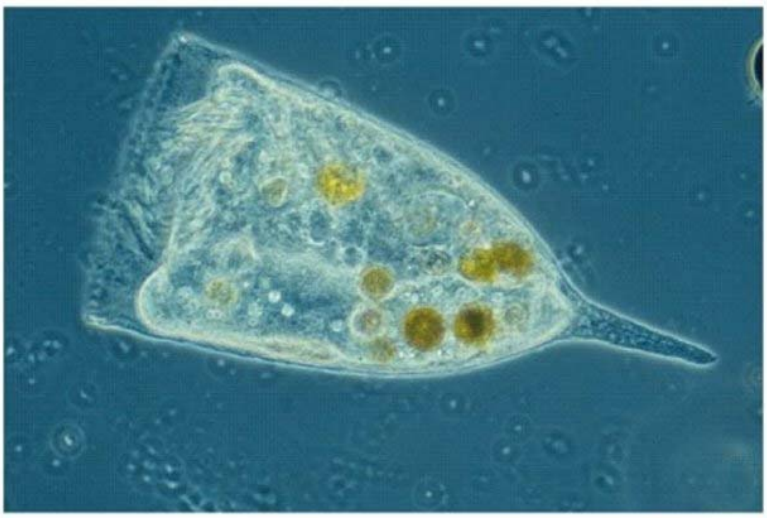

Figure 4. A planktonic protist. The tintinnid (loricate ciliate) *Favella sp*. (Source: A. Calbet)

Among the Metazoans, the Coelenterata include some of the largest zooplankters (jellyfish, Ctenophora or comb jellies, Siphonophora, etc., that can be more than one meter long). Their body contains more than 90% water and they are transparent and gelatinous. Almost exclusively carnivores, these groups can be important predators of other zooplankton. They catch their prey using long tentacles provided with nematocysts, which are sometimes extremely toxic. In the case of *Physalia*, known as 'Portuguese Man-of-War', and some species of Cubomedusae, they can be fatal even for adult persons.

The Mollusca are represented by a group related to snails, the Pteropoda, with the foot modified and expanded to swim. Some of them have shells either chitinous and transparent like glass (sometimes found stranded in the shore, the "Venus shoes"), or incrusted with calcium carbonate that fall to the ocean floor, forming the pteropoda ooze. Other minor groups are the Polychaeta, which are multi-segmented and worm-like, with a few species adapted to planktonic life, like *Tomopteris*. The crystal or arrow worms (Chaetognatha) are voracious carnivores and, as their name suggests; transparent, long, narrow, and ending in fins like arrow feathers.

But the most important zooplankton group by their abundance and significant role in planktonic food webs are Crustaceans, a group of invertebrates which includes the shrimps. Among them, Copepods have attained an extraordinary success in the aquatic domain, and are considered the most abundant metazoans in our planet (Figure 5).

Figure 5. The planktonic copepod *Calanus minor,* a member of the ubiquitous genus *Calanus*. (Source: A. Calbet)

In all seasons and marine environments they can be found in the plankton, generally forming the bulk of holoplankton communities both in biomass and in number of individuals. They are quite small, from few tenths of a millimeter to less than 1 cm., and among them, the Calanoida (named according the best studied of all copepods, *Calanus finmarchicus*) are the most frequent. The word Copepoda also derives from Greek, from *koipe*, that means oar, and *podos*, which means feet.

Generally elongated, the body has two distinct parts, the anterior or *cephalothorax* and the posterior, which is thin and ending in a two branches *furca*, the abdomen or *urosome*. In the cephalothorax two filiform appendices are laterally widespread, the *antennae*.

These are sometimes modified into a sexually modified grasping organ in the males. Following the antennae, there are several feeding appendages, plus four to five double-branched swimming feet. Females can lay eggs free in the water, or carry them in egg sacs. There is not a clear separation between feeding habits, the size of food items being usually more important than their possible animal or vegetal origin.

Next to copepods in importance are the Euphausiacea. They are shrimp-like creatures from one to a few centimeters long that form enormous swarms in high latitude seas, known as *krill*. They are a crucial link between primary producers and carnivores of high latitude (both arctic and antarctic) food webs, and the main food source of food for baleen whales, penguins, seals, etc..

The marine Cladocera, with only seven species, are much less diverse than those of freshwater environments. However, in surface waters near the coast they can attain large concentrations, mainly during summer months. Finally, the Ostracoda have the body covered by a bivalve shell (*ostracon* means shell in Greek). They are widespread, but not very abundant, and more common in deep water layers.

Other planktonic crustaceans are the Mysidacea, very much like the Eupahusiacea, the Amphipoda, the Isopoda, and the Cumacea.

Close relatives of the vertebrates, among the Chordata there are the Tunicates, with four interesting planktonic groups. Doliolids and Salps are transparent, barrel-like organisms, with muscular bands very much like hoops. They move gently by inhaling water at one end of the body (the *pharinx*) and exhaling it at the other (the *atrium*), at the same time retaining small food particles by filtration. Similar are the Pyrosomes (from *pyros*, fire and *soma*, body), bioluminiscent and colonial organisms that can reach more than one meter long.

Finally, the Appendicularians are very common in all marine environments. They are small (few millimeters), tadpole-like, with a small body that contains all the organs, and a swimming tail. They secrete and live within a gelatinous “house”, a complex and extraordinary functional filtering structure that allows them to efficiently feed on the smallest particles, smaller than one micron.

-
-
-

Bibliography

Bougis P. (1974). *Écologie du plancton marin. II, Le zooplancton* Masson, Paris. [This book presents essential aspects of zooplankton ecology in a comprehensive way]

Levinton J.S. (1982). *Marine Ecology* Prentice Hall, N.J. [This text contains introductory aspects to marine ecology]

Margalef R. (1974). *Ecologia*, Omega, Spain. [This book is one of the most rigorous and complete approaches to general ecology. Mostly used as a high-level textbook]

Omori M., and Ikeda T. (1976). *Methods in marine zooplankton ecology*. John Wiley and Sons [This is a complete guide of the common methodology used to study marine zooplankton]

Raymont J.E.G. (1983). *Plankton and productivity in the oceans. Volume 2 zooplankton*. Pergamon Press, Oxford. [This book is the re-edition of a classical compendium of the biology and ecology of marine phyto-and zooplankton]

Tregouboff M. and Rose M (1957). *Manuel de planctonologie méditerranéenne. 2 vol.* Centre Nartional de la Recherche Scientifique, Paris. [Classical zooplankton manual, describing most of the phyto- and zooplankton forms]

Wimpenny R.S. (1966). *The plankton of the sea*. Faber and Faber, London. [A classic introductory book to knowledge of marine plankton]

Biographical Sketches

Miquel Alcaraz was born in Barcelona, Spain, in July 1945. He has a degree in Biology from the University of Barcelona (1969). His Ph.D. Thesis on Biology obtained the Excellence Doctorate Award of the University of Barcelona (1977). He has been Research Professor at the Institut de Ciències del Mar of Barcelona (CSIC) since 1987. He is a member of the Doctorate Commission in Marine Sciences of the University of Barcelona and the Polytechnic University. Currently participating in evaluation panels for national and international research projects, he is also part of the editorial board of several international scientific journals related to marine sciences. A member of the Advisory Council of the Spanish Oceanographic Institute.
During the last ten years Professor Alcaraz has participated in 12 national and international research projects and a similar number of oceanographic cruises, in some of them as a coordinator, and has assisted at 12 international congresses and symposia, in some of them by invitation, or as chairman of sessions. Since 1991 he has published about 25 scientific papers in first-rate international journals and several book chapters. His research expertise includes plankton ecology, zooplankton systematics and community structure, phyto-zooplankton coupling, zooplankton physiology, control of rate-processes in micro- and meso-zooplankton, and interaction between physical variability and biological phenomena at multiscale.

Albert Calbet was born in December 1968, in Barcelona, Spain. He has a degree in Biology from the University of Barcelona (1992), and a Ph.D. in Marine Sciences at the Institut de Ciències del Mar (CSIC) (1997). He was awarded a postdoctoral fellowship from the Ministry of Education and Culture (Spain) to work at the University of Hawaii (USA) from march 1997 to March 1999. In May 1999 he was contracted by the University of Hawaii as postdoctoral scientist under the HOT (Hawaiian Ocean Time-series, JGOFS) program. In September 1999 he returned to Barcelona to work at the Institut de Ciències del Mar (CSIC) under a research contract by the Ministry of Education and Culture. He has participated in ten national and international research projects and 21 scientific cruises. His work has lead to 15 presentations to international meetings or workshops, and more than 20 peer reviewed papers published in first rate international journals on marine ecology. His research topics include the ecology of marine zooplankton, planktonic food webs and dynamics, and the interaction between physical characteristics and biological phenomena.