LARGE ZOOPLANKTON: ITS ROLE IN PELAGIC FOOD WEBS

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

Keywords: Metazoan zooplankton, pelagic food webs, carbon cycle, microphagy, macrophagy, biomass and metabolic requirements, climate effects, human exploitation

Contents

Summary

Zooplankton is the term used to describe a group of animals that live suspended in the water column at the mercy of currents and without any relation to the solid surfaces. As part of the community of organisms known as plankton, they play important roles in the transfer of matter and energy in pelagic food webs.

Their size spans from less than half a millimeter to tens of meters, and from a taxonomic point of view include representatives of almost all the animal *phyla*. Similarly diverse is their trophic position and the size-range of their potential food. While some groups spend all their life in the plankton (holoplankton), others (younger developmental stages of benthic animals and fishes) are only temporarily planktonic (meroplankton).

In the complex network of trophic relations of pelagic food webs, zooplankton organisms play a pivotal role in the transfer of the organic matter produced by microscopic autotrophs (phytoplankton) towards larger organisms exploitable by man. By overexploitation of natural marine resources, as well as dumping pollutants and all kind of waste products to the atmosphere and the oceans, man is severely threatening the structure and function of pelagic communities that have an important role in the control of the climatic equilibrium of the Earth.

1. Introduction

In seas and oceans, most of the biological activity is carried out by organisms that live suspended in the water column in a three dimensional domain, without contact with the sea floor or solid substrata.

It is known as the pelagic ecosystem, and is composed of organisms that cover an amazing range of sizes, from the smaller viruses, less than 0.02 µm in diameter (µm = micrometer, the thousand part of a millimeter, or 10^{-6} m) to the larger whales, more than 30 m long. Similarly diverse are their function in the ecosystem, from primary producers to top carnivores, including also herbivores, detritivores and parasites.

In pelagic food webs the primary producers are microscopic, unicellular plants, generally at a low density and of relatively low nutritious value, the phytoplankton.

Phytoplankton and the organic matter they release in dissolved form, are used by microscopic heterotrophs that utilize either the dissolved organic matter (osmotrophs, like bacteria and some heterotrophic flagellates), or directly the smaller phytoplankton forms (< 2 µm, picoplankton), forming the microbial side of pelagic food webs.

This fraction of pelagic food webs is considered to be responsible for the transfer of a high proportion of primary production.

Part of the larger phytoplankton (> 2 µm) and the larger components of the microbial food web are consumed by metazoans dimensionally scaled to efficiently exploit them—the zooplankton.

Taxonomically, zooplankton (Figure 1) include an almost complete set of all the animal phyla, their size span is about four orders of magnitude, and probably the only characteristic they share is that of being organisms that live suspended in the water column, with a limited capacity of swimming against water movements.

The lower size limit of what it is traditionally considered as true zooplankton is conventionally set according their catchability by 200 µm-mesh nets.

Zooplankton ranging from >200 µm to 2 cm is known as Mesozooplankton. Macrozooplankton span from 2 to 20 cm, and Megalozooplankton, from 20 cm to several meters.

Nevertheless, these size-groups are conventional divisions, some of them imposed by the pore size and mesh dimensions of the filters and nets used to catch or separate them for better study. Hereafter the organisms larger than 200 µm will be termed simply as zooplankton.

Some groups (Holoplankton) spend their whole life in the water column while others, usually juvenile developmental stages of benthic organisms and fishes, are only temporary members of plankton (Meroplankton).

Figure 1. Micrography of a mixed zooplankton sample in which copepods (the elongated semitransparent crustaceans) dominate. Photo: M. Alcaraz.

Zooplankton include both predator and prey organisms, although their respective roles are not clearly established, as the early developmental stages of some predators can be the prey of putative herbivores.

As a matter of fact, what usually matters is not the vegetal or animal origin of the food items, but the relationship between the size of organisms and that of their food, and except in the case of very particular groups it is almost impossible to attribute defined trophic roles.

Zooplanktonic organisms occupy, according to their size range and variety of feeding habits, a key position in pelagic food webs.

They exploit primary producers and the larger members of the microbial food webs like ciliates, large flagellates and small meroplankton. At the same time, zooplankton are the food source of small pelagic fishes, some of them sustaining the most productive fisheries in the world.

But aside from playing pivotal roles in the transfer of matter and energy towards larger organisms exploitable by man, directly linking primary producers with upper consumer levels and short-circuiting microbial food webs, zooplankton modulates the ultimate fate of marine biogenic carbon and the role of oceans as sources or sinks of greenhouse gases like CO_2.

2. Food Chains or Food Webs?

Pelagic ecosystems had been traditionally considered to be maintained by simple, direct matter and energy transfers of the type phytoplankton - zooplankton - fish—the so-called herbivorous metazoan, or classical food chain (Figure 2A). This was a short and relatively efficient chain, from the point of view of human exploitation.

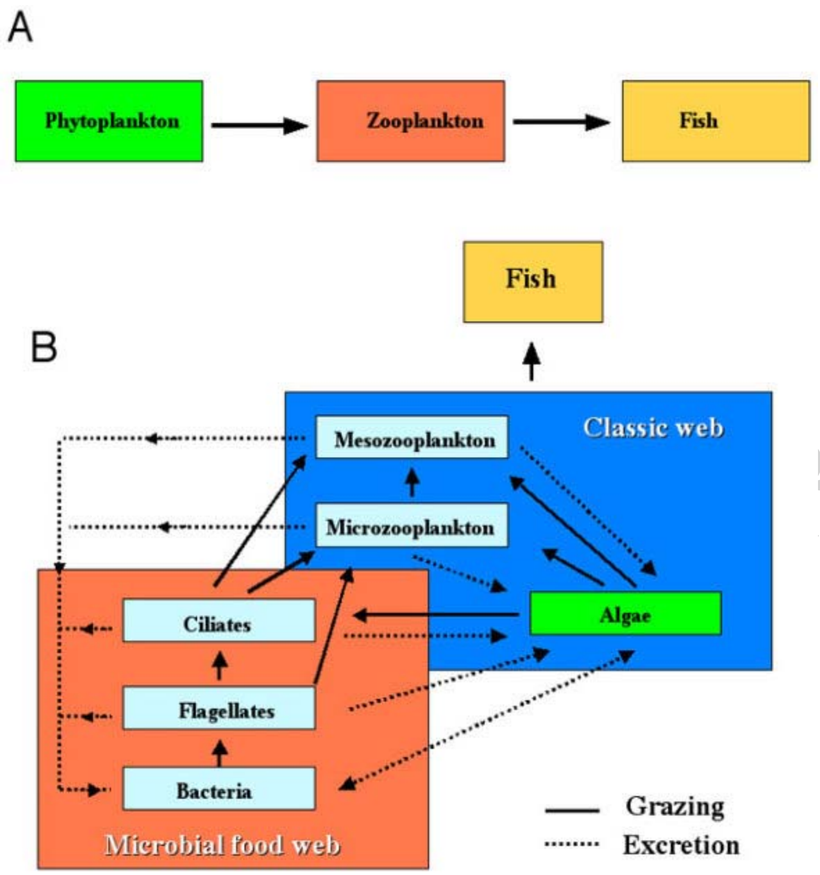

Figure 2. Schematic diagram of a typical marine food chain (A), and a food web (B). The microbial and metazoan sides of the food web are interconnected. The arrows indicate the direction of matter and energy transfers amongst the food levels or the nodes of the web. After A. Calbet, modified.

2.1. Properties of Food Webs: Relationships between Structure and Function

The assimilation efficiency along food transfers (i.e. the ratio between the growth of the organism and the amount of food ingested, either in terms of biomass or energy) is highly variable, depending on the nutritional value of the food item, but it has been accepted to be about 10% on average. Therefore, along its transfer across the different food levels, the matter and energy initially provided by the primary producers is successively reduced to about one tenth. For a primary production of 100, the production after two food transfers, that would correspond to a third trophic level (that of carnivores feeding on herbivores) would be around 1. For this reason, the production of consumers at a given trophic level is not only tightly controlled by the rate at which primary producers synthesize new organic matter, but by the number of knots traversed along the transfer pathways.

Some structural characteristics of food webs, like their complexity (i.e. the number of knots and food transfers) determine the functional properties of ecosystems, and in turn, food web complexity depends on this function. The complexity is equivalent to the species richness, estimated as specific diversity (not to be confounded with the concept of biodiversity), and is closely related to the flow of energy necessary to maintain a given amount of biomass (equivalent to the quotient between Primary Production/Total Biomass, or P/B). As far as food webs are more complex (diverse), their quotient P/B decrease, or in other words, a given rate of production can sustain higher biomass in complex systems than in simple ones. Similarly, the stability of the whole ecosystem increases as the complexity does. Although long, complex food webs including somewhat entangled microbial-metazoan links would mean a reduction in the production of top predators, there are clear advantages in terms of stability and sustained biomass. In complex pelagic food webs, the large size-span, trophic diversity, and plasticity of feeding habits of zooplankton permits switching feeding pressure towards almost any component of the plankton, short-circuiting the complex transfer pathways between both ends of pelagic food webs.

2.2. The Microbial and Metazoan Side of Pelagic Food Webs

About two decades ago, the development of new techniques (e.g. epifluorescence microscopy, new fluorescent DNA dyes, the use of radionuclides as tracers, molecular genetics, etc.) allowed understanding of the fundamental importance of trophic interactions at the microbial level. The smaller organisms (picoplankton, < 2 µm), are preyed upon by heterotrophic flagellates and small ciliates, and all of them can in turn be eaten by larger ciliates and dinoflagellates (up to 10^2 µm length). With viruses (of a size around 0.02 µm), able to infect any plankton taxon, all these groups integrate the so-called microbial pelagic food web or microbial loop. Aside from the unicellular components of microbial food webs, metazoans like young developmental stages of true planktonic or benthic organisms that have a size lower than 200 µm, technically must be included into the microzooplankton, and thus are part of the microbial food webs.
The circulation of matter and energy through the microbial side of pelagic food webs is important in all the environments. However, it is in impoverished marine systems like the center of tropical oceans, where the solar warming of the surface water layers create stable conditions that limit adequate nutrient supply for primary production in well illuminated layers, where the food transfer through the microbial side is essential. To the complex pathways across the microbial side, and to the already low food production by autotrophs in these oligotrophic areas, a long transfer of food across many steps must be added, so the proportion of primary production that reaches the upper, exploitable trophic levels, or that is exported towards the ocean floor, is very low in these areas.

Zooplankton is linked to the microbial side of pelagic food webs through large flagellates, ciliates and small metazoans. Most of the zooplanktonic species are omnivores, and rather than the vegetal, animal or detritic nature of food items, what really matters from a trophic point of view is the size of food particles. The direct transfer from primary producers across the metazoan side of food webs is proportionally more important in zones of enhanced fertility where zooplankton can directly exploit phytoplankton, and these conditions are found in upwelling areas or during the spring phytoplankton blooms in mid and high latitudes. However, the proportion of the primary production addressed towards either the microplankton or the zooplankton (metazoan) side of food webs strongly depends on match-mismatch mechanisms between the somewhat intermittent episodic bursts of primary production, and the relative abundance and development rate of micro- and zooplankton communities.

In any case, the division into microbial and herbivorous food transfers is artificial, pelagic food webs being a complex network of feeding relations including both the microbial and metazoan webs, without a real segregation amongst them.

3. Zooplankton Feeding Habits: Microphagy *versus* Macrophagy

The zooplanktonic animals that feed predominantly on small food particles (relative to their size) are defined as microphages. The food items that are part of their diet can be living organisms like phytoplankton or small protists, or dead particles or detritic material.

Some can combine mechanical filter-feeding habits with selective preying on food, and in general they can be described as highly selective but adaptable feeders (Figure 3).

Most of the zooplankton that feeds on small food particles is included in two large animal groups: Crustaceans and Prochordates, with few exceptions (e.g. pelagic mollusks, Pteropods).

Crustacean zooplankton are shrimp-like invertebrates, and amongst them three taxons frequently account for more than 80% of the zooplankton abundance and biomass in all seasons and environments: Cladocerans, Copepods and Euphausiids.

The second microphagous group in importance are Prochordates, primitive relatives of vertebrates, although nothing in their aspect would suggest such a relation. Part of them (the Tunicates) look like gelatinous sacs, barrel-like tubes with muscle bands, whereas others, the Appendicularians, are small tadpole-like organisms that excrete temporary, gelatinous “houses” where the animal lives.

The houses have a relatively complex structure and are in fact highly efficient filtering systems for gathering food in the lower range of particle sizes.

Finally Pteropods, (“winged” planktonic mollusks), although generally less abundant, are also active microphages.

Macrophagy (usually linked to carnivory) refers to zooplankton that feed upon prey of relatively large size. Although, as already mentioned, carnivory is not always a strict feeding option for zooplankton, some groups are adapted to a strict carnivorous diet. Copepods, for example, are mainly omnivorous, being able to switch from a microphagous diet when feeding on phytoplankton, to a carnivorous one, preying on relatively large animal items, like early developmental stages of other copepod species or even their own. Some groups, however, are less opportunistic and can be considered as strict macrophages and carnivores. Ctenophores (comb jellies), a variety of jellyfish, and Chaetognaths (arrow worms) are amongst the most important. Minor groups like Amphipods (crustaceans) and Pteropods also have representatives that feed on larger zooplankton prey, and similarly occur with some meroplanktonic groups.

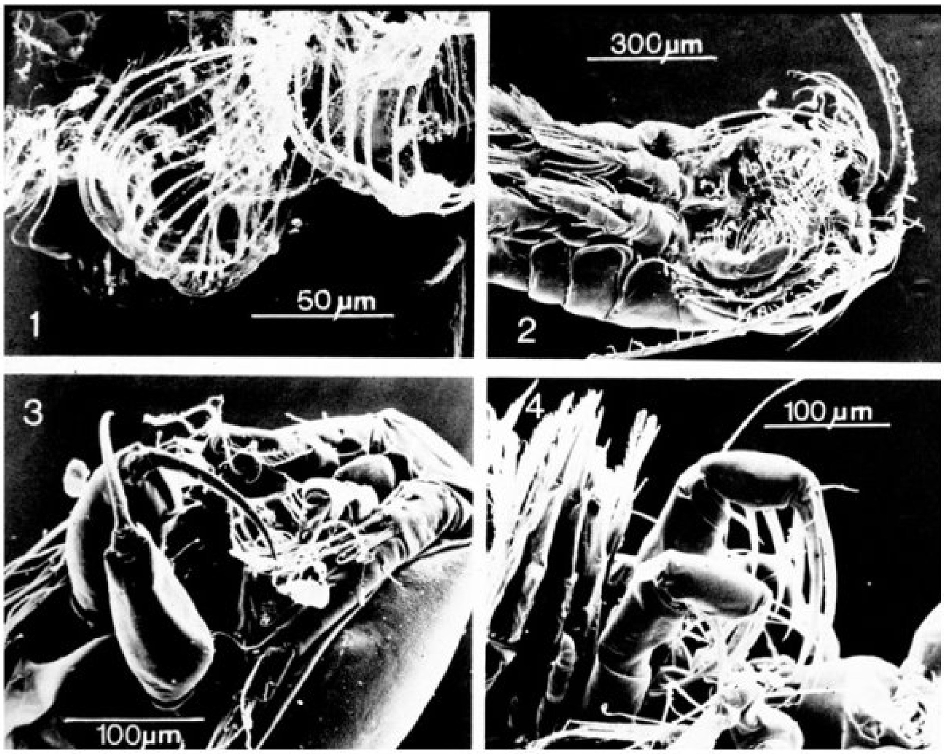

Figure 3. Scanning electron image of the feeding appendages of planktonic crustaceans. 1) Microphage (Cladoceran, *Penila avirrostris*). 2) Microphage copepod, *Temora stylifera*. 3) Macrophage copepod (*Oncaea sp*. 4) Macrophage copepod, *Candacia sp*. Photo: M. Alcaraz.

-
-
-

Bibliography

Boyd P.W. and Doney S.C. (2003). The impact of climate change and feedback processes on the Ocean carbon cycle. In Ocean Biogeochemistry (Ed. Fasham M.J.R.). Springer. New York. pp 157-193. Paris. [A very comprehensive assay of global change effects on planktonic populations]

Calbet A. and Saiz E. (2005). The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38: 157-165. [A review of the present data on the relevance of ciliates on the diet of copepods]

Barange M., and Harris R. (2003). Marine Ecosystems and Global Change. IGBP Science no. 5 [A brief, comprehensive description of prevailing changes in and future challenges for marine ecosystems]

Hernandezl L.S. and Ikeda, T. (2005). A global assessment of zooplankton respiration in the sea. Journal of Plankton Research 27: 153-158. [A recent compilation of the metabolic carbon requirements of zooplankton at global scale]

Omori M. (1978). Zooplankton fisheries of the world: A review. Marine Biology 48: 199-205. [The first evaluation of zooplankton as an exploitable marine resource)

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]

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]

Biographical Sketches

Miquel Alcaraz was born in Barcelona, Spain, in July 1945. 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). Research Professor at the Institut de Ciències del Mar of Barcelona (CSIC) since 1987, he is member of the Doctorate Commission in Marine Sciences of the University of Barcelona and the Polytechnic University, and professor of the Doctorate in Oceanography of the University of Las Palmas de Gran Canaria-CSIC. He is currently participating in evaluation panels for national and international research projects, and is also part of the editorial board of several international scientific journals related to marine sciences.

During the last 10 years he has participated in ten national and international research projects and a similar number of oceanographic cruises, in some of them as a coordinator, and has assisted in 18 international congress and symposia, in some of them by invitation, or as chairman of sessions. Since 1996 he has published about 30 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 multiple scales.

Albert Calbet was born in Barcelona, Spain, in December 1968. Degree in Biology from the University of Barcelona (1992). Ph.D. in Marine Sciences at the Institut de Ciències del Mar (CSIC) in 1997. 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, where he has now a tenured position. He is professor of the Doctorate in Marine Sciences of the University of Barcelona and the Polytechnic University, and of the Doctorate in Oceanography of the University of Las Palmas de Gran Canaria-CSIC.

He is advisor and reviewer of several national and international agencies, and journals, currently being a member of the editorial board of the Journal of Plankton Research. He has participated in 19 national and international research projects and 22 scientific cruises. His work has led to 50 presentations to international meetings or workshops, and also nearly 50 peer reviewed papers published in first rate international journals on marine ecology. His research topics include the ecology of marine zooplankton, planktonic food web dynamics, and the interaction between physical characteristics and biological phenomena, among others.