ADAPTATIONS TO LIFE IN THE OCEANS. PELAGIC MACROFAUNA

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Contents

Summary

A perspective of the adaptations of the pelagic macrofauna in marine systems is presented. The term pelagic macrofauna overlaps with the commonly established size-categories of the meso and the macroplankton. Crustacea (decapods and euphausiids) and Coelenterata are the most important invertebrate taxa of pelagic macrofauna in terms of biomass and diversity, while fishes are usually beyond the upper limit of the macrofaunal size. Pelagic macrofauna are worlwide distributed along the different zones of the water column from the surface to the deepest abyssal and hadal oceanic depths. In all the world oceans, an exponential decrease of plankton biomass with increasing depth has been reported as a

general rule. However, there is a secondary increase of plankton biomass around 50-100 meters above the bottom in the Benthic Boundary Layer (BBL).

Often with a daily periodicity, vertical migrations of the zooplankton probably constitute the most important adaptive feature of this fauna. Vertical movements are performed towards the photic zone, where phytoplankton production takes place, both by phytophagous and carnivorous zooplankton apparently to feed in more productive levels. Further than the photic zone, the BBL also plays a crucial role in the dynamics of trophic webs in deep waters.

The downward extension of pelagic species make them directly available to predation particularly by demersal fish living on the bottom. Chemoreception, mechanoreception and vision are the main forms of communication in the pelagic domain, serving for feeding behavior (to locate food and potential predators) or for reproduction. Even below depths where light does not reach useful levels for vision (800-1300 m) this sense is important for species communication thanks to the phenomena of bioluminescence.

Bioluminescence is involved in a large variety of intra and interespecific events (e.g. prey attraction, warding off predators, formation of shoals, reproductive behavior, etc). A decline in metabolic rates in pelagic fishes and crustaceans with an increase in the minimum depth of occurrence of species has been documented. The life strategy adopted by these species seems to have also similar adaptative trends as a function of depth. The adaptative basis of all these trends in pelagic fauna remains to be well understood, though both abiotic (e.g. temperature, pressure, or minima in O_2 concentrations), and biotic (animal activity, food availability) factors have been discussed as possible explanatory variables.

1. Introduction

1.1. Definition of pelagic macrofauna

Marine pelagic fauna include those organisms inhabiting the water column of the sea. Marine fauna is usually classified based on size categories, and the deduced size compartments have been influenced by the gear used to collect fauna. The term macrofauna is mainly employed for benthos to define those organisms sieved through 0.3 to 1 mm mesh size. By contrast, the pelagic fauna is mainly classified using the terms plankton and nekton.

The term macrofauna applied to organisms of the pelagic domain may, at least partially, overlap with the size-categories of mesoplankton (organisms of size between 0.2-20 mm) and macroplankton and also with the term micronekton (see Figure 1). Thus, and depending on the classifications of various authors, it can be considered that the term pelagic macrofauna may include those organisms of between 1 and 200 mm in size (usually collected with plankton nets of mesh size between 0.75 to 4 mm). The size and the quantity of animals captured also depends on the speed of towing, the size of the net opening, and the mobility of species. One of the most frequently gears used to catch macroplankton, the Isaacs-Kidd midwater trawl, captures animals usually not exceeding 20 to 100 mm.
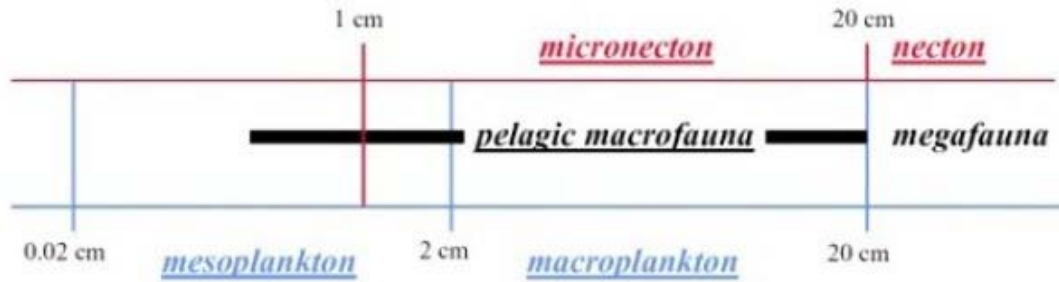
Figure 1. The size of the pelagic macrofauna in relation to the size compartments
of the zooplankton and nekton.

In order to avoid duplication of contents treated in other chapters (see *Zooplankton Ecology*; *Ecology, Behavior* and *Productivity of Marine Fish*), in this chapter pelagic macrofauna comprises those organisms of the macroplankton-micronekton, often excluding both mesoplanktonic (e.g. copepods), and large nektonic (megafauna: size > 200 mm) organisms.

1.2. Taxonomic composition

Crustacea are the most diversified invertebrate group of pelagic macrofauna (see Table 1) with no less than 2300 pelagic species (copepods included). Coelenterata (included within the jellyfish or gelatinous plankton) and Mollusca (Cephalopoda included) are also highly diversified taxa, while other minor groups are Ctenophora, Polychaeta, Thaliacea and Chaetognatha. In terms of biomass, Crustacea are also the dominant taxa. In the case of pelagic shrimps (Decapoda) biomass values usually range between 0.04 to 0.62 g DW (dry weight)/1000 m^3.

Fish are also a diversified taxa of pelagic macrofauna, comprising entire families of relatively small (usually < 20-30 cm) meso and bathypelagic species (e.g. the Gonostomatidae or the lanternfish family of the Myctophidae). However, the size of groups such as (adult) fish, and cephalopods is beyond the upper limit of the macroplankton and they must be considered as nekton or pelagic megafauna. Only the larvae or juvenile stages of these nektonic species can be considered as pertaining to the pelagic macrofauna.

Phylum	Taxa	Number of species (n)	Observations
Coelenterata	Medusae*	900	
	O. Siphonophora	150	
Ctenophora		80	
Annelida	Cl. Polychaeta	50	
Crustacea	SCl. Copepoda		
	O. Calanoidea	1725	
	SCl. Eucarida		
	O. Decapada	213	
	O. Euphausiacea	85	
	SCl. Peracarida		
	O. Mysidacea [2]	30	500 benthopelagic species
	O. Amphipoda		

	SO. Gammaridea[2]	21	216 benthopelagic species
	SO. Hyperiidea	250	
	O. Isopoda[2]	unknown	2800 marine species
	O. Cumacea[2]	unknown	800 marine species
Mollusca	Cl Gastropoda**	50	mainly Pteropods
	Cl. Cephalopoda [1]	410	
Chaetognatha		60	
Chordata	Cl. Appendicularia	58	
	Cl. Thaliacea		
	Fam. Doliolidae**	8	
	Fam. Salpidae**	23	
	Fam. Pyrosomatidae	8	
	Cl. Osteichthyes [1][3]	414	

* included in the Cl Scyphozoa and Cl. Hydrozoa
** only European species
(3) Only including the small size taxa of Gonostomatidae, Sternoptychidae, Photichthydae, Chauliodontidae, Stomiidae, Myctophidae, Evermannellidae, and Paralepididae.

Table 1. A list of the main taxa of pelagic macrofauna with the approximate number of species when available. Taxa included are those mainly considered as nektonic by size and species mainly considered as hyperbenthos (suprabenthos). The Table does not include species whose larval stages are part of the pelagic macrofauna.

Among crustaceans, the most diversified groups of pelagic macrofauna (copepods excluded) are within the Orders Decapoda, Euphausiacea, Mysidacea and Amphipoda (Hyperiidea and to a lesser extend Gammaridea). Euphausiacea are probably the most exclusive crustacean taxa of pelagic macrofauna, containing 85 species exclusively distributed throughout the oceans of the world, living the major part in the oceanic epipelagic and mesopelagic environments.

2. The distribution of pelagic macrofauna

2.1. Pelagic domains

Animals included in the size-spectra of the pelagic macrofauna are usually distributed worlwide throughout the water column. An exponential decrease of plankton biomass with increasing depth has been reported as a general rule in all the world oceans. However, close to the sea floor (usually 50 to 100 meters above the bottom in deep waters) there is a secondary increase of plankton biomass. This increase has widely been documented for bathyal and abyssal domains and also for meso and macroplankton organisms. This interface level is the called Benthic (or Benthopelagic) Boundary Layer (BBL).

As a basic function of the depth and the distance from the shore, a number of ecological or faunistic zones have been defined and worldwide recognized as distinct water masses of the pelagic system. As indicated in Figure 2 the main pelagic zones are: (i) the epipelagic zone (comprising the 0 to 150 m depth of the water column), the lowest limit of which coincides with the shelf-slope break; (ii) the mesopelagic zone between 150 and 1000 m; (iii) the bathypelagic zone, the limits of which are situated between 1000 and 3000 m; (iv) the abyssopelagic zone, the lower limit of which is *ca*. 6000 m; and (v) the hadalopelagic (or ultra abyssal) zone below 6000 m depth. The meso and bathypelaic zones are situated

on the continental slope, a level charachterized by a sloping sea-floor. The abyssopelagic domain is above the rise and the abyssal plain, these last comprising the large areas of almost flat bottoms which cover most of the deep sea floor, whereas the hadalopelagic zone is restricted to the deepest oceanic trenches. Animal life in these zones is respectively known as epipelagic, mesopelagic, bathypelagic, abyssopelagic, and hadalopelagic fauna. In addition, the benthopelagic domain is an important ecological boundary zone close to the sea floor, inhabited by the benthopelagic organisms of the BBL.

2.2. Vertical migrations

Organic matter penetrates into the sea depths following two basic routes: (i) sinking passively down as dead organic matter from surface production; and (ii) by the active downward migration of zooplankton. The vertical migration of zooplankton is the most important migratory movement in the globe. Within this important phenomenon, we can distinguish between: (i) the movements effected towards the photic zone, where phytoplankton production takes place, by phytophagous epipelagic mesoplankton; and (ii) the migration of mesopelagic carnivorous macroplankton (pelagic macrofauna), from the meso and bathypelagic levels upwards to feed.

Although copepods (treated in *Plankton*) are the main component of phytophagous mesoplankton, some small-macroplankton euphausiids and mysids from meso and bathypelagic depths may form part of this component. These basic migratory patterns are really very complex because they vary as a function of latitude, season and age.
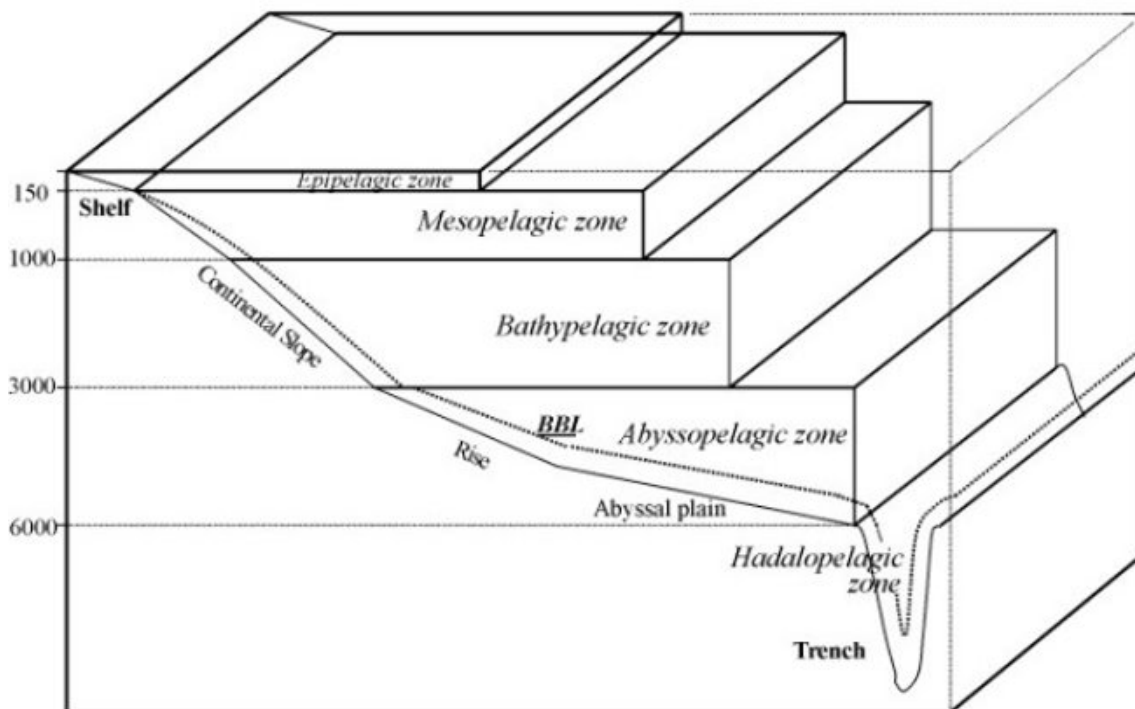

Figure 2. The main pelagic zones where the pelagic macrofauna is distributed.

Migrations of mesopelagic macrofauna (e.g. Pasiphaeidae, or Sergestidae among crustaceans, or Myctophidae among fishes) are mainly of a daily periodicity and mainly

ontogenic among the bathypelagic fauna (e.g. the deep-sea Oplophoridae shrimps). However, probably both time scales are mixed in determining migration in all these species. In general, bathypelagic macrofauna do not climb up to the surface layers and concentrations at depths of around 400 m can be observed at night. Some species, taxa or individuals only partially migrate or they are even non-migrants. Figure 3 shows the model of *ladder* migrations, a general scheme of the complex migratory patterns of zooplankton species.

Daily migrations are a regular phenomenon that can be observed following the ecosounding image of the Deep Scattering Layer (DSL). The DSL signal represent animal concentrations, though animal densities are not proportional to ecosounding signals because organisms with gas-filled floats (e.g. siphonophores, Myctophidae) give overestimated signals. This layer is regularly situated at depths of 200 to 700, at 800 to 1000 m or even at 2000 m at the daytime, whereas by night the DSL may reach the surface layers of the epipelagic zone, crossing the thermocline. Migrations must be, however, interpreted more as an statistical rather than an individual phenomenon, because part of the population may only partially, or even may not, migrate. The upward evening and the downward morning migrations may both be very fast and the speed of the downward migration may reach 108 m/h in mesopelagic decapods.
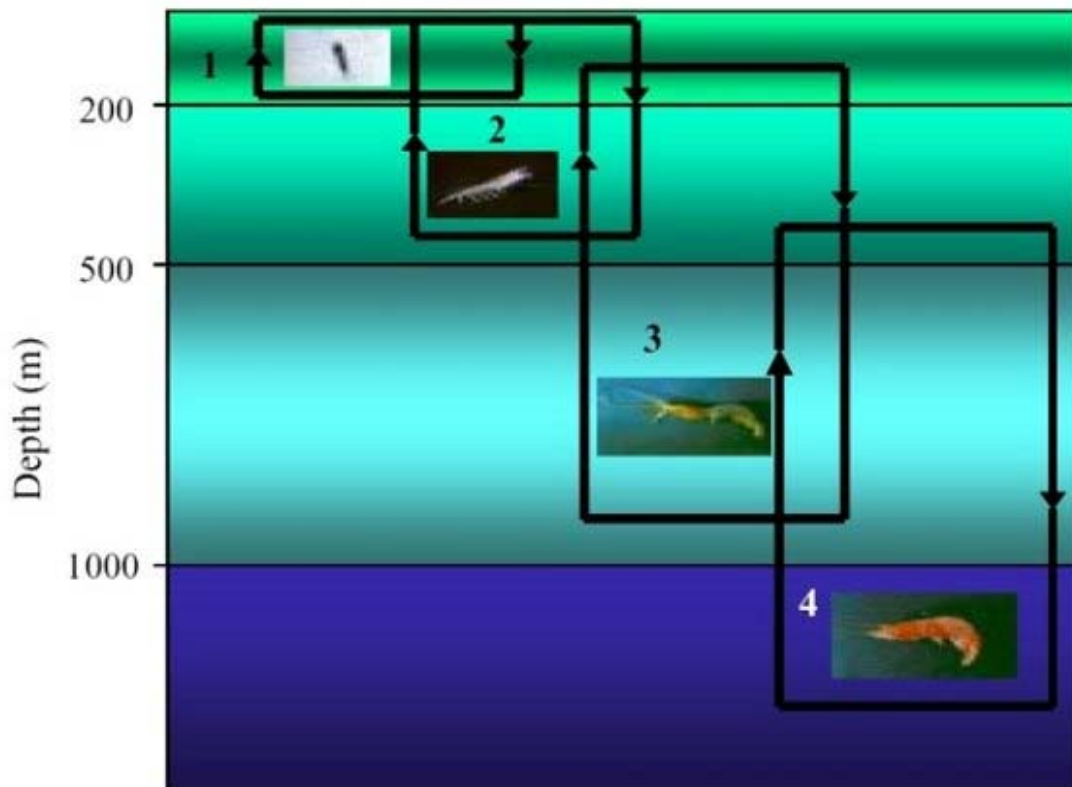

Figure 3 A general simplified scheme of the migratory patterns of zooplankton (a model proposed by Vinogradov) in a temperate area. 1 and 2: Migration of epipelagic and upper mesopelagic zooplankton (basically copepods); 3: Migratory patterns of Euphausiacea, Decapoda Natantia and mesopelagic fishes (e.g. Myctophidae); 4: migratory pattern of bathypelagic species (Oplophorid shrimps and Mysidacea).

Vertical migrations have been documented for a variety of macroplankton groups. In the neritic zone (on the continental shelf) isopods of *Eurycope* spp. (e.g. *E. truncata*) feed at night on neustonic prey, immobilized prey such as insects (e.g. dipterans) trapped at the surface, while they remain burrowed in the sediment at daytime. These migratory movements are also effected by other neritic peracarids (e.g. cumaceans, mysids), mainly by adult-natatory males. In the open sea, lanternfish (Myctophidae) exhibit a peak abundance in the water column between 300 and 1200 m by day and between 10 and 100 m at night, parallel to that of the DSL.

Many species of siphonophores undergo vertical migrations over ranges of 200 to 250 m. Epi- and mesopelagic euphausiids migrate with this same pattern through distances regurlarly ranging from 200 to 500 m. However, certain epipelagic *Stylocheiron* species and the bathypelagic species *Bentheuphausia amblyops* do not migrate. The general pattern of the daily migration of a species may be modified by different factors. Larvae often have different migratory patterns from adults, occurring closer to the surface at all times of the daily cycle; this is the case for most euphausiids. Juveniles of the mesopelagic decapod *Pasiphaea* migrate upward from the BBL at night whereas adults remain close to the bottom, adopting more benthopelagic habits.

The influence of environmental physico-chemical parameters in the vertical migrations are not conclusively established. The daily migration is considered to be controlled by endogenous rhythms, but changes in the density of water masses, light and pressure have been discussed as regulating factors of this phenomenon. The presence of a thermocline appears to restrict upward migrations and this is probably related to the increase of food in this interface.

It has been demonstrated that changes in light intensity derived from moonlight or solar eclipses can change the migratory patterns in euphausiids and decapods. Adaptative reasons that would cause an evolutionary development of daily vertical migrations are related to the search for higher food availability. Several euphausiids have been closely associated with clorophyll maximum layers in the epipelagic zone, and this has been clearly interpreted as a feeding response. Also, adult specimens of decapods and lanternfish usually have empty stomachs when they are captured at daytime close to the bottom, while stomachs are full in midwater samples taken at night. Where there is a sustained difference in temperature between surface and deep waters, it may be an optimal adaptative strategy to eat in surficial, usually warmer, waters and to grow in deep-colder waters.

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Biographical Sketch

Joan E. Cartes is a marine biologist, graduated at *Universitat de Barcelona* in June 1985, and achieving the title of Doctor in October 1991 at *Universitat Politècnica de Catalunya – C.S.I.C.* His PhD Thesis, entitled *Análisis de las comunidades y estructura trófica de los crustáceos decápodos batiales del Mar Catalán,* focused on the study of communities and the trophic role of deep-water decapods (mainly shrimps and prawns) in the deep Mediterranean (to depths of 2200 m). He is currently contracted by the programm *Ramón y Cajal* (call 2001) of the Spanish Governement (Ministry of Science and Technology- *M.C.Y T.*). His research interest was progressively directed to the topic of Trophodynamics and modelling of deep-sea benthopelagic food webs. The author was particularly interested to know how deep water species are distributed in the sediment-water interface (the *Benthic Boundary Layer*) and the important role of these species which channelize the energy flux derived from surface production (primary production – flux of particles). Seeing the importance of the interface natatory fauna dwelling immediately above the bottom – the so-called suprabenthos or hyperbenthos – in the diet of bathyal organims, he worked—with the help of expertise from laboratories in France (*CNRS*)—on adopting and developing methods to catch and quantify the hyperbenthos. Trophodynamics includes those aspects such as the quantification of diets, the secondary production (*P*) of benthopelagic fauna, and the amount of food consumed (the so-called *daily ration*: *DR*) by distinct trophic levels. Variables such as *DR*, *P*, and *P/B ratios*, are basic to understanding the trophodynamics of exploited systems and in modeling them, both from a conceptual and numerical approach. All these aspects are even more important in systems where food is the main limiting factor, as in deep bathyal systems, which moreover are now being submitted to increasing levels of fishery exploitation and anthropogenic impact.