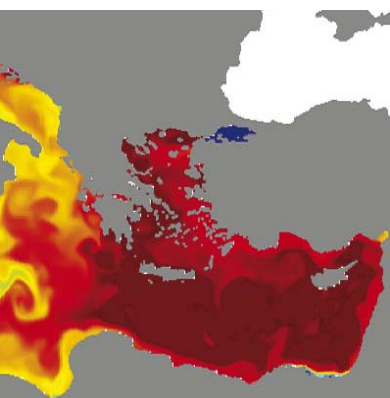




Mediterranean Pelagic Habitat

Oceanographic and Biological Processes, An Overview

Maurizio Würtz



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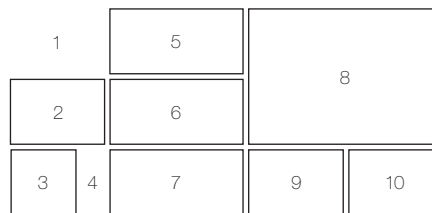
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Mediterranean Pelagic Habitat

Oceanographic and Biological Processes, An Overview

Maurizio Würtz

Dipartimento di Biologia, Università di Genova, ITALY
April 2010



Cover pictures:

- 1 Loggerhead turtle (*Caretta caretta*).
- 2 Striped dolphin (*Stenella coeruleoalba*).
- 3 Copepod, female of *Centropages kroyeri*.
Photo: Stéphane Gasparini, Laboratoire d'Océanographie de Villefranche.
- 4 Jewell squid (*Histioteuthis reversa*).
- 5 Atlantic, Strait of Gibraltar and Alboran Sea. Image SeaWiFS (S1997361123941.png)
<http://visibleearth.nasa.gov>
- 6 Higher salinity increases water density, as in water leaving the Mediterranean. In the eastern basin, denser water flows down and westward at intermediate level, below the lighter incoming Atlantic water (AW).
<http://www.mercator-ocean.fr>
- 7 The desert meets the southern coast of the Mediterranean, while the northern coasts are mainly constituted of more productive lands. Dust inputs from the southern coast via atmosphere dynamics, is important to the functioning of the Mediterranean pelagic ecosystem (e.g. nutrient input).
Provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE.
- 8 Common dolphinfish (*Coryphaena hippurus*), by Vincent Fossat, 1879.
Coll. Muséum d'Histoire naturelle de Nice.
- 9 Atlantic and mediterranean Devil fish (*Mobula mobular*).
- 10 Jellyfish (*Cotylorhiza tuberculata*).
Photo: Ignacio Franco, Centro Oceanográfico de Murcia.

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Abstract

The Mediterranean Sea is a highly variable and dynamic environment, with very high biologic diversity. Between 4% and 18% of the world's marine species are found in the Mediterranean, even though it represents only 0.82% in surface area and 0.32% in volume of the world oceans : more than a quarter of these species are endemic to the Mediterranean. The Mediterranean Sea and its pelagic environment are also of great economic importance to the surrounding countries.

This document is the first part of a project conducted by The World Conservation Union, IUCN, in an attempt to describe the functioning of the Mediterranean Sea and the threats to the ecosystem, and further to discuss solutions and provide a model for formulating protection plans. The high variability of the Mediterranean ecosystem brings the need for special actions and dynamic protection.

The high level of biodiversity in the Mediterranean Sea can be explained by its geological history, in which the rate of environmental change, and thus species occurrence, has been exceptionally high. Moreover, the present variety of climatic and hydrologic situations found within the Mediterranean pelagic ecosystem allows for the presence of both temperate and subtropical species.

The Mediterranean Sea is unique, being a semi-enclosed sea connected to the Atlantic Ocean through the narrow Strait of Gibraltar, to the Red Sea by the man-made Suez Canal and to the smaller enclosed Black Sea via the narrow Bosphorus Strait. The Mediterranean Sea exchanges water, salt, heat, and other properties with the North Atlantic Ocean, and is thus an important actor, affecting global water formation processes and variability and subsequently the stability of the global thermohaline state of equilibrium.

Water from the Atlantic enters the Mediterranean Sea through the Gibraltar Strait, circulates in Mediterranean basins, undergoing evaporation and depletion of nutrients, sinking in certain areas and becoming transformed into the salty, nutrient-poor Mediterranean water that later returns to the Atlantic through the Strait of Gibraltar.

Mediterranean circulation is driven by water exchange through the various straits, by wind stress, and by freshwater and heat fluxes causing buoyancy flux on the surface. The patterns and processes are complex and highly dynamic, including free or boundary currents and jets, bifurcating, meandering, growing and shedding ring vortices. These features create a landscape of dynamic habitats whose location, extent and shape changes through time. There are also permanent and recurrent sub-basin scale cyclonic and anticyclonic gyres, ocean fronts, upwelling areas, and small but energetic mesoscale eddies. All these hydrographical structures are associated to various transition domains, i.e. narrow regions of strong temperature and salinity gradient. Transition domains are of particular biological and ecological importance, maybe most significantly as being breeding and nursery grounds for a wide range of organisms. They are also associated with a high and predictable primary production, making them important foraging areas with high prey aggregation, and with changes in type and abundance of marine organisms. These structures also serve as migration routes for highly mobile species, such as marine mammals and other top predators.

Human activities have a large impact on physical, chemical and biological environment, which leads to ecological changes, and sometimes to permanent ecosystem shifts. Given the variability of the Mediterranean pelagic ecosystem and its dynamic habitats, a broad-based, dynamic conservation approach is needed to preserve essential ecological processes and services, and to protect economic and cultural resources for future generations. Hence, this project aims to apply a process approach to habitat conservation, seeking to ensure that not only the pelagic marine species, but also the dynamic pelagic habitats upon which they depend, are considered when Marine Protected Areas (MPAs) are formed. A particular aim of this project is trying to characterize which physical and biological characteristics make certain ocean habitats more suitable than others, and to determine if the processes are persistent and predictable enough in space and time to warrant designation as MPAs.

1. Introduction

What do we mean by *pelagic*? The online version of the Merriam-Webster Dictionary defines the term *pelagic* as: *of, relating to, or living or occurring in the open sea*. The term *pelagic domain* generally refers to those ocean portions off the continental shelf, while the areas within the shelf are known as *neritic*.

High Seas is also used instead of *pelagic*: the term is, however, more properly applicable to the maritime jurisdiction together with other definitions such as exclusive economic zone (EEZ), territorial sea, fishing zone, ecological protection zone and historic bays.

In this overview, which takes into account the physiographic and biological features of the Mediterranean Sea, it is preferred to use the term *pelagic* to describe the water column features and the organisms living there. However, organisms living at the bottom of the sea are referred to as *benthic*.

The pelagic ecosystem contains hundreds of kinds of organisms including bacteria, phytoplankton, zooplankton, fishes, reptiles, mammals and birds. These different groups are linked by energy and nutrient flows, interacting with each other and with the physical environment as a functional unit. All these components are thus connected in a complex food web characterized by evolving interactions (Etnoyer *et al.*, 2004).

Ecosystems carry out a diverse array of processes providing goods and services to humans. Every ecosystem is dynamic and even if all organisms affect their environment, human activities could have a significantly larger impact on ecological changes (Folke *et al.*, 2004; Elmquist *et al.*, 2003). It is therefore crucial to dispose of a reliable picture of the ecosystem's functioning in order to define the ecosystem's *resilience*, ie. its capacity to tolerate and recover from extreme situations (e.g. human impacts), returning to any of its dynamic states without losing important functions (Holling, 1973).

One or more *habitats* can be identified within an ecosystem. According to the ICES Working Group on Marine Habitat Mapping, a *habitat* is: *A recognizable space that can be distinguished by its abiotic characteristics and associated biological assemblage, operating at particular spatial and temporal scales* (ICES, 2005).

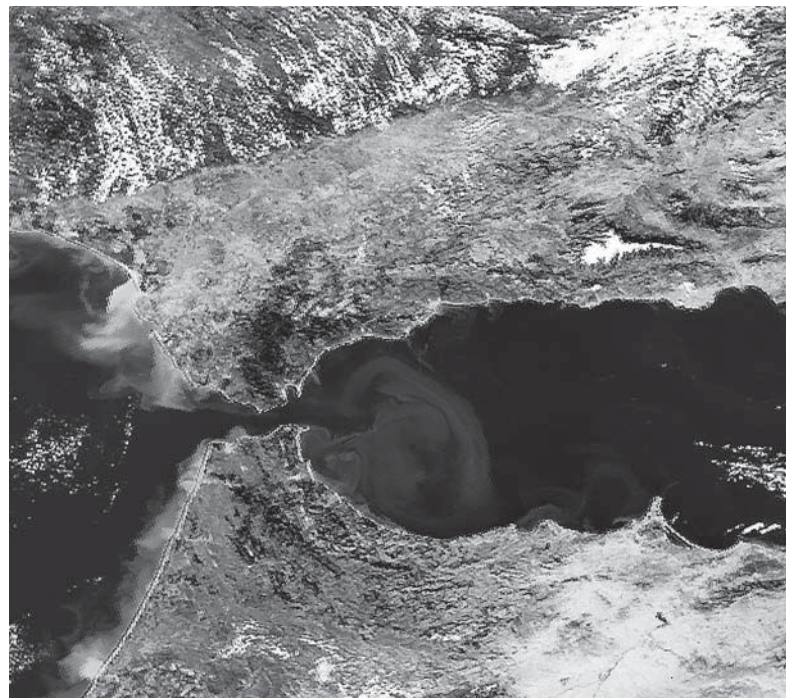


Fig. 1 (see color plate p. 76): Strait of Gibraltar and Western Alboran Sea. Atlantic water (AW) generates strong eddies as passes through the Strait of Gibraltar. AW undergoes intense mixing causing a loss in heat before it reaches the Alboran Sea. Here upwellings are set mainly on the Spanish side, while clockwise (anticyclonic) eddies generate convergence (downwelling) off the African coast. Image SeaWiFS (S1997361123941.png) <http://visibleearth.nasa.gov>

Some authors use the term *seascape* (or *marine landscape*), focusing on the physiographic and oceanographic elements and excluding biotic structure.

Mediterranean Sea circulation is complex (Fig. 1) and its interaction with biological processes defines a variety of marine pelagic habitats, from the surface to the deeper waters. Offshore waters are typically considered as *oligotrophic*, or nutrient-poor. Nevertheless the enrichment of surface layers is assured by upwelling and water mixing, by the concentration and retention

of nutrients by eddies and front action. All these oceanographic features determine favourable conditions both for primary production and for the autotrophic and heterotrophic microbial processes. Microbe food webs exceed a thousand times over the production of the "*classic food web*" (phytoplankton-zooplankton-fishes) which "*can now be considered as a variable phenomenon in a sea of microbes*" (Karl, 1999; Pomeroy, 2001), thus enhancing the ecosystem's carrying capacity. Furthermore, reduced continental shelves, steep slopes, canyons and seamounts accelerate through space and time the energy flow and the turnover from the sea bottom to the surface, as well as from coastal to pelagic waters (and vice versa). The presence and abundance of top predators in relation to specific topographic and oceanographic structures seem to confirm this new scenario of pelagic productivity.

The aim of this document is to review existing knowledge about the Mediterranean pelagic ecosystem, in order to help identify potential areas for protection. The pelagic domain needs a new perspective in order to revise the current paradigm about Marine Protected Areas as a tool for conservation. In fact, while for demersal or benthic species, protected areas can be defined using fixed borders depending on the substrate, for pelagic species there are certain difficulties in defining a particular area/water mass with fixed and permanent geographical limits. This limitation is due to the system's intrinsic variability, but also

to the interpretation of properties that link the occurrence of a given species in a given pelagic environment, which is, at best, poor (Verity *et al.*, 2002).

The size of an ecosystem is not necessarily correlated to its importance, diversity or complexity, but it is of certain interest from the perspective of environmental conservation. A large size ecosystem, such as the marine pelagic environment, could potentially absorb huge impacts. For centuries, this hypothesis dominated the attitude towards the use of the ecosystem among marine scientists (Roberts and Hawkins, 1999). However, when an ecosystem of this size starts showing signs of adverse impact, the situation may be urgent, as processes of ecological change may already have started. In such a situation, the ecosystem could be restored only if the symptoms are recognized early on, the diagnosis is accurate, and the relationships between organisms and their environment are well understood (Verity *et al.*, 2002).

2. Uniqueness of the Mediterranean

The Mediterranean is a semi-enclosed sea, connected to the Atlantic Ocean through the narrow Strait of Gibraltar, to the Red Sea by the man-made Suez Canal and to the smaller enclosed Black Sea via the narrow Bosphorus Strait. The offshore pelagic zone comprises 75% of the total Mediterranean and Black Sea surface area.

The same processes which are fundamental to the general circulation of the oceans also occur within the Mediterranean. The Mediterranean Sea exchanges water, salt, heat and other properties with the North Atlantic Ocean. Since the North Atlantic Ocean plays an important role in global *thermohaline* circulation (density-driven circulation of waters with different temperatures and levels of salinity), salt water originating from the Mediterranean may affect global water formation processes.

In the Mediterranean Sea, two basins of almost equal size can be identified: the western basin and the eastern basin, connected by the Strait of Sicily. The Adriatic Sea extends northward between Italy and the Balkans, communicating with the eastern Mediterranean basin through the Strait of Otranto. The Aegean Sea lies between Greece and Turkey, connected to the eastern basin through several straits within the Grecian Island arc. Mediterranean circulation is driven by water exchange through the various straits, by wind stress, by freshwater and heat fluxes causing buoyancy flux on the surface.

The limited exchange of Atlantic and Mediterranean waters plays an important role in the circulation and productivity of the Mediterranean Sea. Through the Strait of Gibraltar warm surface water, already stripped of much of its nutrients by phytoplankton growth in the Atlantic, flows into the Mediterranean, returning approximately 80–100 years later, after circulating the Mediterranean basin in a counter-clockwise (cyclonic) direction.

Once in the Mediterranean, as the water passes eastward, the nutrient level in phytoplankton production decreases (Bethoux *et al.*, 1997). At the same time salinity increases to up to 39.1‰, due to climatic factors such as evaporation (evaporation exceeding precipitation and river runoff) (Milliman *et al.*, 1992).

Higher salinity increases water density : thus the water leaving the Mediterranean, Mediterranean Deep Water (MDW), flows below the lighter incoming Atlantic water (AW). The decreasing west-to-east gradient of nutrients (Krom *et al.*, 1991) results in a gradual west-to-east reduction in productivity. The satellite image shows Mediterranean waters, clear and poor in pigment, and the west-to-east gradient (Fig. 2).

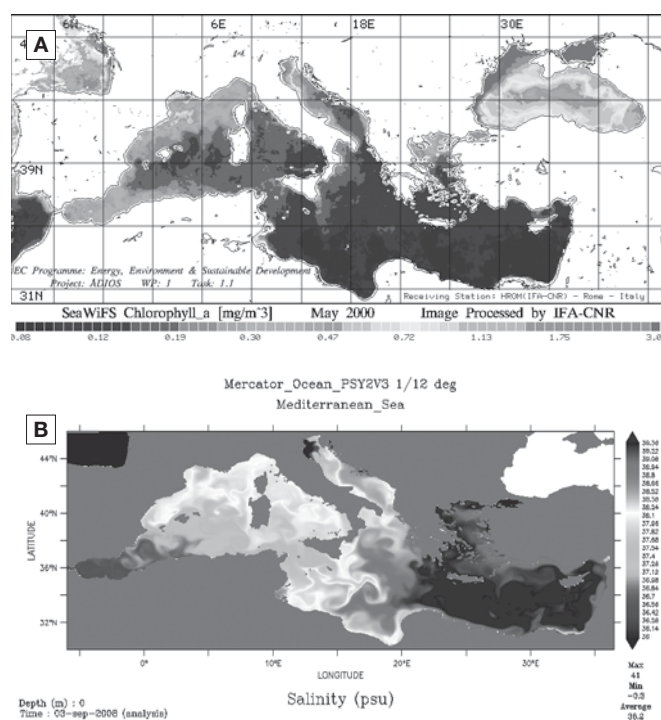


Fig. 2 (see color plate p. 76):

A) The west-to-east decreasing gradient of nutrients results in a gradual west-to-east reduction in productivity. The satellite image shows the eastern Mediterranean waters poor in pigment and the west-east gradient. Primary production in the northwestern basin of the Mediterranean is on average 3 times higher than that in the eastern basin.

B) Higher salinity increases water density, as in water leaving the Mediterranean. In the eastern basin, denser water flows down and westward at intermediate level, below the lighter incoming Atlantic water (AW).

Socio-economic, political and religious differences between northern and southern Mediterranean regions are other issues that may significantly influence the future development and management of the Mediterranean ecosystem. Additionally, there is a difference between the two regions in climate and geomorphology, and subsequently in vegetation and land-use (Jeftic *et al.*, 1992; Jeftic *et al.*, 1996), which is clearly demonstrated in the SeaWiFS image (Fig. 3). While the desert meets the southern coast of the Mediterranean, the northern coasts host more productive lands. Inputs from the southern coasts through the atmosphere (dust deposition) may also play an important role in the functioning of the Mediterranean ecosystem. Most of the dust deposition occurs during episodic events, carrying many trace elements, e.g. Fe (iron), Mn (manganese), Be (beryllium) and Al (aluminium). Eolian input of iron, which is an important element for phytoplankton growth, is one of the highest recorded globally, possibly exceeding the river input (Guerzoni *et al.*, 1997; Krom *et al.*, 1991).

The importance of dust deposition in controlling ocean productivity has only recently received attention. Moreover dust can influence the climate, e.g. by regulating radiation entering and leaving the atmosphere.

Global climate change (global warming) may increase the areas of desert and consequently more dust could be entering the biogeochemical and sedimentary marine cycles. The effects of this process are largely unknown (Turley, 1999).

2.1. MEDITERRANEAN SEA. GENERAL FEATURES

2.1.1. Area, depth and volume

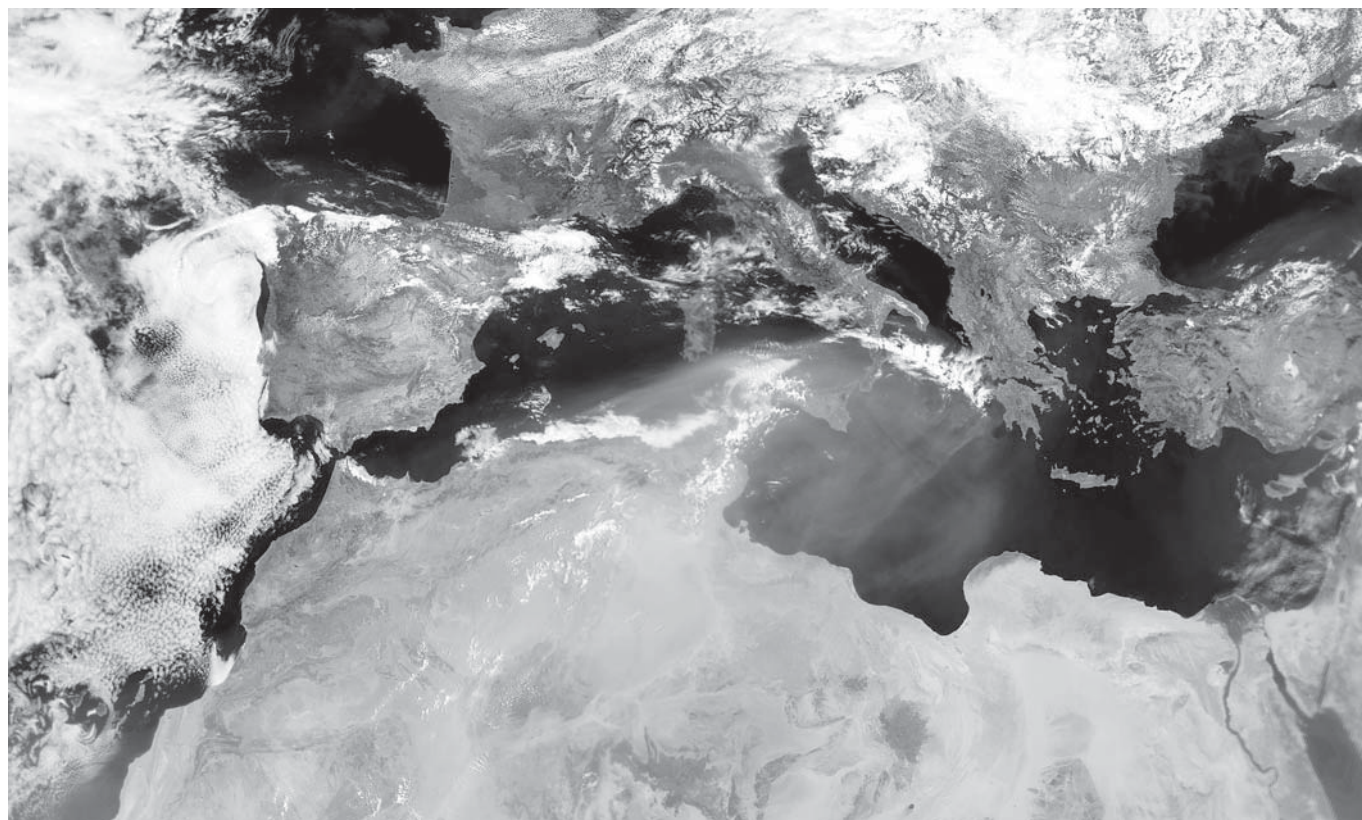
The Mediterranean Sea has a total area of about 2,536,000 km². It extends horizontally for 3860 km and its maximum width is 1600 km.

The principal rivers entering the Mediterranean are the Nile from Africa, and the Po, Rhone and Ebro from Europe.

The western basin is separated from the eastern by a bank crossing the strait between Sicily and Cape Bon, where water is no deeper than 366 m. Mean depth of the western basin is estimated to be 1612 m, and the deepest sounding ever recorded is 3733 m. In the eastern Mediterranean the maximum depth is 5150 m, reached off the southern coast of Greece. The steepest slope observed is situated close to the island of Sapienza, near Navarino, where a depth of 4978 m is reached only 10 miles from land. The mean Sicilian-Ionian sub-basin depth is 1620 m., while the Levant sub-basin has a mean depth of 1451 m.

The total volume of the Mediterranean basins is approximately 3,750,000 cubic kilometres.

Fig. 3 (see color plate p. 77): The desert meets the southern coast of the Mediterranean, while the northern coasts are mainly constituted of more productive lands. Dust inputs from the southern coast via atmosphere dynamics, is important to the functioning of the Mediterranean pelagic ecosystem (e.g. nutrient input). Provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE.



Depth zone (m)	Area (Km ²)
0 - 200	578,000
200 - 1000	720,000
1000 - 2000	230,000
2000 - 3500	951,000
Over 3500	57,000
Total	2,536,000

	Basin Volume (Km ³)	Mean Depth (m)
Western Mediterranean	1,357,000	1612
Sicilian-Ionian basin	1,243,000	1620
Levantine	1,117,000	1451
Adriatic Sea	33,000	243
Total	3,750,000	

2.1.2. Meteorology

The Mediterranean region forms a distinct climatic unit. The prevailing winds in this region are westerly, but during the winter the sea itself causes the formation of bands of low barometric pressure, frequently developing cyclonic disturbances. During the summer, the region comes under the influence of the polar margin of the tropical high-pressure belt and the weather is very stable.

The Mediterranean region is, hence, characteristically affected by winter rains. This characteristic becomes more clearly defined from south to north and the total annual rainfall increases in the same direction. From west to east, the climate becomes more continental (as opposed to maritime), even though with great local irregularities. The temperature in the Mediterranean region varies greatly, with annual means ranging from -14° C to 25° C. The Atlantic influence limits the average annual temperature to about 10-12° C in the west, while it can reach 36-40° C in the east.

Autumn is warmer than spring, particularly in the coastal regions. This difference is enhanced in the eastern part of the region by local land winds replacing the cool sea breezes of summer. Local winds develop in nearly all the coastal areas of the Mediterranean, especially during the winter, as a result of the rapid change of temperature from the sea to the snow-clad hinterland. Cold, dry and very strong winds occur in Liguria (*Tramontana*), in Istria and Dalmatia (*Bora*), the Rhone valley (*Mistral*) and in the western Caucasus. In summer, a north-west trade wind called *Maestro* occurs in the Adriatic. The *Scirocco* is a cyclonic wind characteristic of the rainy winter season. In the Tyrrhenian and Adriatic regions it is usually accompanied by clouds, moisture and rain. In Sicily and southern Italy, however, the same wind blows year-round, a dry and dusty wind from the south-east or south-west. It brings dust mainly from the Sahara. Similar winds occur also in Spain (*Leveche*), in Egypt (*Khamsin*) and in Algeria and Syria (*Simooms*), where their greatest development can be seen.

2.1.3. Temperature

The mean surface temperature of Mediterranean waters ranges from over 21° C (eastern basin) to an average of 15.5° C (coast of the Gulf of Lion in the western basin). The 18°C isothermal line runs from Gibraltar to the north of Sardinia, passing through the Strait of Messina up to the Gulf of Corinth. Similarly, at a depth of 200 m, temperature falls from 15.5° C in the eastern basin to 12.7° C in the Alboran Sea. Below 200 m, temperature remains practically uniform down to the bottom, 13.6° C in the eastern basin and 12.7-13.2° C in the western basin.

2.1.4. Salinity

The salinity of the surface water of the Mediterranean increases eastwards from 36‰ in Gibraltar to 37.6‰ east of Sardinia and 39‰ and upwards in the eastern basin. Deep-water salinity in the western Mediterranean is likely to be between 38‰ and 38.5‰. The saltier waters tend to flow westward.

2.1.5. Deposits

Much of the Mediterranean seabed is covered in blue mud, often presenting a yellow upper layer, which contains a considerable proportion of lime carbonate (calcium carbonate, CaCO₃). This portion of carbonate mainly originates from shells of pelagic Foraminifera. In many areas, particularly in the eastern basin, a 1-8 cm calcareous or siliceous crust can be found.

3. Pelagic predators, prey and process: a multidimensional approach to pelagic habitat conservation

The marine pelagic ecosystem is the greatest in size among all ecosystems on the earth. It encompasses 99% of the total biosphere volume and is generally considered to have high resilience. This seems also to be true in the Mediterranean Sea, which can be conceived as a small-scale ocean. In fact, despite thousands years of exploitation and alteration of both its pelagic and coastal environments, it is quite surprising that it still hosts very large resident and transient populations of top pelagic predators (tuna, swordfish, dolphins, whales, etc.). However, some alarming signs lead to emerging issues: pollution, biological invasions, harmful algal blooms, ecosystem changes due to unsustainable fishing and aquaculture, ecosystem loss and alteration by coastal urbanization (EEA, 2007).

It can be expected that, in coming years, growing anthropogenic impacts will be enhanced by climate change. The so-called *tropicalization* of the Mediterranean Sea is striking evidence of global warming. Thus it is generally recognized that the Mediterranean Sea environment is under considerable stress and that effective conservation measures must be undertaken as quickly as possible.

Amongst the various possible conservation initiatives (international agreements, laws, research, education, dissemination, etc.), the use of Marine Protected Areas (MPAs) is widely accepted as a valuable tool to reduce biodiversity and habitat loss, as well as to improve public awareness. MPAs have historically focused on benthic systems, which nowadays constitute the vast majority of existing marine reserves worldwide (Agardy, 1994; Murray *et al.*, 1999). Nearshore reserves in bounded areas have been effective for conservation of benthic habitats and sessile (sedentary) species with restricted ranges (Halpern and Warner, 2002). Pioneering studies by Hooker *et al.* (1999, 2002) and concept papers by Duffus and Dearden (1995) and Hyrenbach *et al.* (2000) have presented a basis for ecosystem-level pelagic protected areas. However, conservation of mobile marine vertebrates still largely relies on single-species based management, including regulations (e.g. quotas) and fishing gear modifications (e.g. bycatch mitigation).

In the Mediterranean Sea the only established protected pelagic area is the Pelagos International Sanctuary for marine

mammals. Recently, a series of protected pelagic areas have been proposed by ACCOBAMS and NGOs (Fig. 4). As in the case of larger IWC Whale Sanctuaries in the Indian and Southern Oceans, which have been recently addressed by Gerber *et al.* (2005), these protected Mediterranean areas could suffer from the same limitations: arbitrary boundaries, narrow focus, lack of an adaptive population design and a need for baselines. In fact, static boundaries could not encompass the species distribution shift or the habitat preferences of the exiting sub-population as a consequence of prey availability caused by climatic and oceanographic variations, if they are established on a political basis.

As stressed by Verity *et al.* (2002), new approaches largely depend on our ability to describe and predict the effects of natural and anthropogenic changes on the species' health and distribution in pelagic habitats. It has to be considered that current conceptual models of pelagic ecosystem structure and functioning have failed to provide the basis for accurate prediction of pelagic communities' patterns. This means that it is still difficult to know why, where and when specific organisms occur. If the policy is to achieve effective environmental conservation, it is crucial to understand the role of predation pressure in shaping the pelagic ecosystem. For this reason a revised paradigm of its structure and functioning has to incorporate both resource availability and predation.

A process approach to conservation has been presented by Pederson *et al.* (2004). It seeks to ensure that pelagic marine species and the dynamic pelagic habitats, upon which they depend, are considered within the context of conservation initiative planning. In particular, it seeks to characterize which physical and biological features make certain ocean habitats more suitable than others. Then, if those processes are persistent and predictable enough in space and time, they could be used for the designation of protected areas. Therefore, with a multi-species-process and ecosystem approach, it could be possible to consider complementary habitat metrics and selection criteria, in order to accommodate the location, size, shape and number of protected areas to the natural variability of the considered ecosystems (Hyrenbach *et al.*, 2000).

Regions within a pelagic ecosystem are usually inhomogeneous. An effective approach in designing pelagic MPAs will need to consider the differences in water mass distribution (e.g. influence of the Atlantic Current), physical forcing (intensity of coastal upwelling, etc.) and food-web structure (e.g. species composition), which characterize each region, as well as the ecological significance of areas and habitats on a smaller scale. Each regional domain contains different pelagic habitats, associated to upwelling centres and other mesoscale (10s–100s km) hydrographic features such as fronts and eddies, or bathymetric structures (morphological structures with differing water depth) such as canyons, seamounts and steep slopes.

The basis of this approach is belief in the connectivity of predator-prey processes within the ecosystem. This leads to global or partial models which have been proved to be of limited utility because there is always too little information for their adequate parameterization.

Boyd *et al.* (2006) start from another concept: as the dynamics of the system have too many complex properties, there may be no choice (from the point of view of cost-benefit ratio) other than considering the outputs of the energy flow through the food webs. This means using the upper-trophic level predators (top predators) as indicators of the ecosystem status and performances. This is possible because their feeding and breeding grounds frequently represent biodiversity hotspots, associated with topographic and oceanographic features. Their distribution and aggregation may be effectively used in pelagic habitat mapping, even if a whole-system approach could be the proper strategy and the top predators approach could be part of a set of insights and interpretations used for management measures.

Three types of pelagic hotspots have been identified (Hyrenbach *et al.*, 2000): **ephemeral habitats**, including wind – current driven upwelling, eddies and water filaments; **persistent hydrographic systems**, like currents, gyres and thermal fronts, and **static systems**, such as seamounts, canyons and other continental slope features. Moreover, among these hotspots some migratory corridors could exist and persist both in location and in time. While static systems can be protected by establishing boundaries, the persistent and ephemeral habitats are much more problematic as regards the conservation issue. The problems derived from the inter-annual, seasonal and even daily variability of the geographical position of such oceanographic structures can be avoided by delimiting an area, which encompasses all these fluctuations (Hooker, 2006). Nevertheless, the resulting area could be too large for effective patrolling and thus reliable protection.

The Mediterranean pelagic realm has a highly variable four-dimensional structure (time-variable water volumes) associated with a complex of biological processes with a series of non-linear relationships. During the last two decades, thanks to technical development of remote sensing and *in situ* sampling, we dispose of useful tools for describing and forecasting sea and atmosphere dynamics. However our knowledge about the biological component of the pelagic system is still poor, both for drawing descriptive mapping and for implementing species-environment interaction models. It is clear that most of the future research effort should be devoted to filling this gap.

3.1. EFFECT OF CIRCULATION ON THE BIOLOGICAL COMPONENTS

3.1.1. Ephemeral hydrographic features

A network of isolated protected pelagic areas could protect species associated with predictable and fixed bathymetric and hydrographic features. However, many ecologically important marine environments are neither fixed in space nor persistent. Ephemeral hydrographic features are defined by short-living gradients in water properties, features that vanish once they mix with the surrounding waters. Highly mobile pelagic species can find and exploit ephemeral hydrographic features insofar as far as they persist (Hyrenbach *et al.*, 2000).

Upwelling forcing is one of the best-understood ephemeral processes responsible for the creation of transient gradients in water properties. It provides nutrients to the surface layer and enhances primary production by vertically transporting cool, nutrient-rich water from the depths. Upwelling is temporally predictable and occurs seasonally in response to favourable wind conditions and counter-clockwise rotation of a current flow (cyclonic eddies). The centre of a cyclonic eddy is characterized by upwelling of nutrient-rich waters while along the periphery, downwelling can generate retention fields. The interaction of upwelling water with the dominant flow gives rise to ephemeral fronts, which are characterized by strong gradients in physical and biological properties (Fig. 5A).

In anticyclonic eddies, where the rotation pattern is clockwise, the aggregation of marine predators and their prey is mediated by convergence and downwelling at the core (Fig. 5B). On a larger scale, evidence shows that when cyclonic and anticyclonic eddies act as contiguous enrichment-retention structures, the region is characterized by elevated primary production. This results in a high zooplankton biomass and aggregation of pelagic fish, seabirds and marine mammals.

In addition to coastal upwelling and eddies, wind forcing, deep convection and buoyancy fluxes can create small-scale fronts and convergence zones. These features promote patchiness by aggregating floating objects and weakly swimming zooplankton. Although the ecological significance of these ephemeral fronts is poorly understood, they appear to constitute important nurseries and foraging habitats for many pelagic species, including sea turtles and billfishes (Hyrenbach *et al.*, 2000).

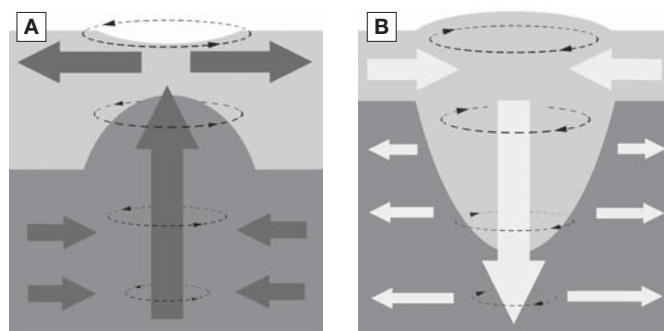


Fig. 5: Schematic representation of water masses upwelling (A) and downwelling (B) generated by eddy dynamics.

Eddies are dynamic hydrographic features, with diameters in the order of tens to hundreds of kilometres and lifespans of up to several months. As long as they are trapped by topography, they are defined as "*forced eddies*" and show the properties described above. Nevertheless, they can drift away from their original location, then becoming "*free eddies*". In this case their effect on water masses is the inverse. Thus, a cyclonic eddy has a downwelling effect at its core, while an anticyclonic eddy generates an upwelling at its centre.

3.1.2. Persistent hydrographic features

Persistent hydrographic features, such as gyres and frontal systems, comprise some of the best-known oceanographic patterns.

Gyres are spiral currents driven primarily by large-scale wind systems and constrained by the topography of land surrounding the basins. Large, permanent mesoscale eddies can be defined as gyres even if they may have seasonal topography in location and intensity. The direction of a gyre's rotation is determined by the effect of prevailing winds on the mainstream flow. Figure 6 schematically shows wind-driven gyres during winter in the Mediterranean Sea (Pinardi and Masetti, 2000). Their overall effect on water mass dynamics can be the same as explained above for eddies. It must be taken into account that a gyre can encompass two or more eddies with different effects.

The high predictability and the persistence of oceanic fronts make them ideal signposts and highways, delineating the migratory routes of pelagic species in otherwise featureless water masses (Hyrenbach *et al.*, 2000). Along the frontal system, a narrow region of strong temperature and salinity gradient is termed *Transition Domain*: it is of particular biological and ecological importance. As a matter of fact, it is a breeding and nursery ground for a wide range of organisms.

Surface fronts delineate boundaries between two different surface water types. Mixing processes near the interface between these water masses of different densities produces a new water type of intermediate density. This water tends to flow (downwards)

under the less dense surface water type. Thus, both surface water types contribute to the formation of a mass of mixed water, which slowly sinks at the interface between them. Even in the case of two water types with equal densities, the mixture of the two will tend to have higher density due to a process known as *cabbeling*. The buoyancy-driven flows that supply this mixed water formation are directed from each of the water types toward the interface, resulting in a zone of convergence that acts to maintain the distinct frontal character of the boundary (Fig. 7).

Small weakly swimming organisms, being passively transported by a horizontal ocean flow, may nonetheless be able to control their depth level. Hence, such organisms will accumulate in the slowly sinking waters of the convergent frontal zone and pelagic predators may find the opportunity for high food intake at low foraging cost. Characteristically, this leads to the multi-trophic-level blooming of productivity.

The importance of processes occurring in or near ocean fronts appears to be exemplified by the evident attraction of a wide range of fish species and other marine animals to floating objects.

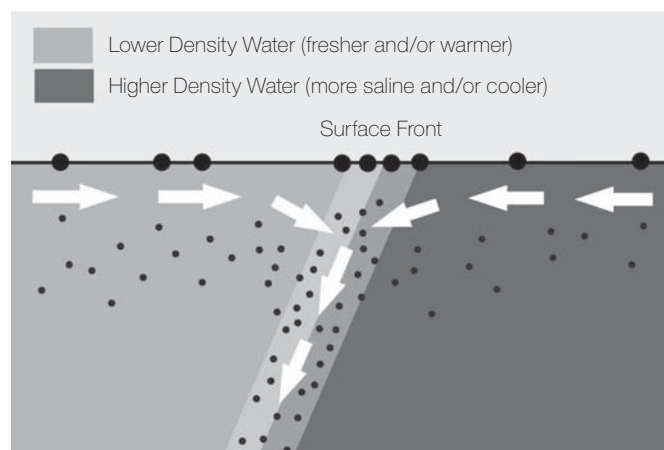


Fig. 7: Schematic representation of a front structure, its effect on floating objects (larger black dots) at the surface and on suspended crop (smaller black dots).

Fig. 6: Gyres and eddies generated by wind stress (Mistral) along the longitudinal axis of the Mediterranean Sea.

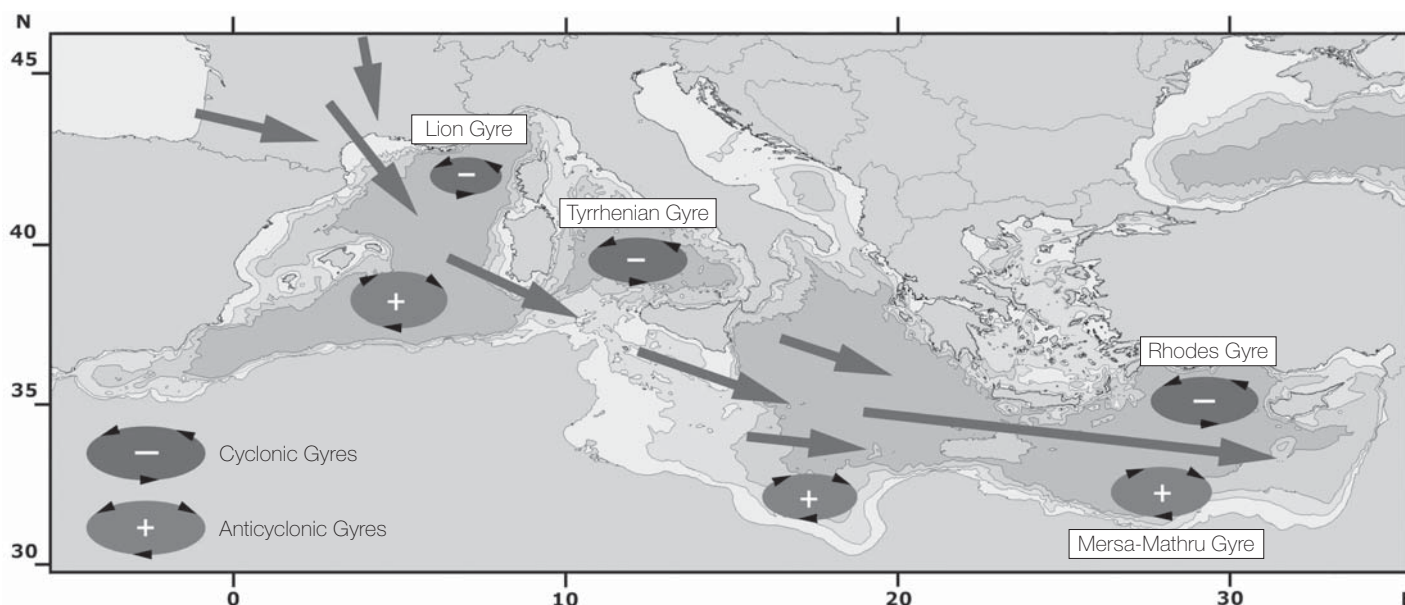




Fig. 8 (see color plate p. 77): Floating objects can be attractive for young pelagic stages of off-shore benthic species such as *Polyprior americanus* as well as for larger predators (e.g. dolphin fish, billfishes, bluefin tuna, tuna-like species, etc.)..

Moreover, biological distributions (i.e. of potential preys) tend to be so patchy in the ocean that a fish looking for its preys may find very little indication of relative favourability. However, drifting objects floating on the ocean surface tend to be carried into, and to accumulate within, convergent frontal structures.

An innate attraction to drifting objects (i.e. an instinctive “level of comfort” in their vicinity having evolved through Darwinian selection) would serve to automatically position the fish within convergent zones with enhanced biological activity and possibly favourable feeding opportunities. The use of Fish Aggregating Devices (FADs) - floating rafts of logs or other materials, allowed to drift freely or anchored in convenient locations, in order to attract and concentrate fishes and thereby enhancing fishing success - is one way that modern fisheries exploit this behavioural pattern (Fig. 8).

3.1.3. Ocean Triads

The Mediterranean is generally recognized as an oligotrophic sea, considering its relatively low average primary production. However, it hosts a variety of resident and migratory top predators, which find enough food there to sometimes sustain a very large population. To explain this higher level of productivity in the food web, a series of mechanisms enhancing fertility has been proposed, which act at certain times of the year in connection with hydrographic structures.

Nutrient input into the system, with resulting primary production, may be a necessary condition for fish stock development, but it is not sufficient to yield high levels of fish stock productivity alone. As a matter of fact, regions where satellite images display high chlorophyll concentrations are not always regions of high fish productivity (Bakun, 1998).

A recently emerging concept, which seems to have substantial explanatory power, addresses *ocean triads*. A series of comparative studies on the climatology and geography of known preferred spawning areas (Parrish *et al.*, 1983; Cury and Roy, 1989; Bakun and Parrish, 1990; Bakun, 1996, 1998; Durand *et al.*, 1998) have served to identify three major classes of physical processes combining to yield favourable reproductive habitats for coastal pelagic fish as well as many other types of fish:

- enrichment processes (upwelling, mixing, etc.)
- concentration processes (convergence, frontal formation, water column stability)
- processes favouring retention within (or drift toward) appropriate habitats.

Bakun (1996) called these three elements the ‘fundamental triad’ of factors underlying favourable fish reproduction habitats. Subsequently, oceanic areas where the three elements exist in mutually supportive configurations are sometimes referred to as *ocean triads* (Bakun, 1998).

Winds blowing along the axis of an elongated basin (such as the Mediterranean) induce transport away from one coast. They thus cause a divergent flow which results in a ‘coastal upwelling’, while towards the opposite coast convergence and downwelling occur. Ekman Transport (Ekman, 1905) causes a water flow from the zone of upwelling and nutrient enrichment towards the area of convergence and downwelling, resulting in concentration (Franks, 1992) and retention, all together producing a natural *ocean triad*.

Mountainous coastal topography may offer sheltered locations where wind intensity can increase turbulent mixing-allowing processes, as for the concentration of food for fish larvae. Inflows of less saline waters from rivers, the Black Sea and the Atlantic Ocean yield additional enrichment and concentration mechanisms, contributing to *ocean triad* configurations in the Mediterranean (Agostini and Bakun, 2002).

4. Coupling between biological processes and circulation within the mediterranean pelagic ecosystem

4.1. OVERALL VIEW OF MEDITERRANEAN CIRCULATION PATTERNS

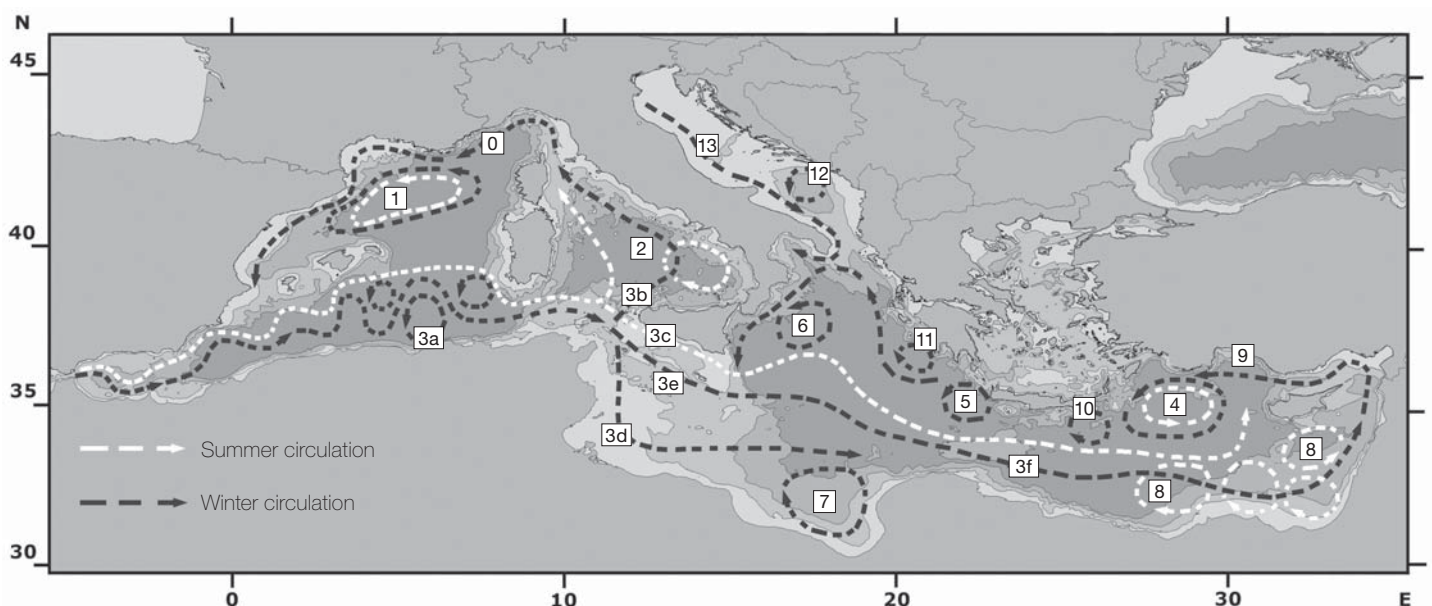
The Mediterranean Sea is already known to have a complex and multi-scale circulation, driven by wind, water flux, thermohaline and topographic features of its basins. The basic functioning of the sea, transforming Atlantic Water (AW) into Mediterranean Waters (MWs), is understood, as well as the process of dense water formation, making Atlantic Water sink offshore in specific northern zones of the western and eastern basins. However, the more detailed patterns of the circulation, mainly on basin scale, are very complex and still debated (Pinardi and Masetti, 2000, Robinson *et al.*, 2001).

The overall circulation structure is summarized in Fig. 9 for the surface water, and in Fig. 10 for the intermediate depths. In both the western and eastern basins, the AW current (100-200 m deep) flows along slopes, creating counter-clockwise (cyclonic) gyres, which can meander, bifurcate into veins or form branches because of seabed and coastal topography. To the south of each basin, parts of these gyres are markedly unstable and generate mesoscale anticyclonic eddies.

Fig. 9:

Simplified scheme of the Mediterranean's general circulation.

- 0) Ligurian-Provençal current,
 - 1) Lion Gyre,
 - 2) Tyrrhenian cyclonic circulation with summer weakening and eastern anticyclone,
 - 3a) Algerian current eddies,
 - 3b-e) Atlantic-Ionian stream branches,
 - 3f) Mid-Mediterranean jet,
 - 4) Rhodes Gyre,
 - 5) Western Cretan Gyre,
 - 6) Western Ionian Gyre,
 - 7) Gulf of Syrte anticyclonic eddy,
 - 8) Shikmona and Mersa Matruh gyre system,
 - 9) Cilician and Asia Minor current,
 - 10) Iera-Petra Gyre,
 - 11) Pelops Gyre,
 - 12) Southern Adriatic Gyre,
 - 13) Western Adriatic coast current
- (from Pinardi and Masetti, 2000, modified).



Circulation at intermediate depths (Fig. 10) emanates from the Rhodes gyre, which is the major formation area of Levantine Intermediate Water, LIW (Lascaratos *et al.*, 1999), spreading westward and northward.

If the Strait of Gibraltar were to be closed, the level of the Mediterranean Sea would drop by 0.5-1 m each year. The rain and river runoff does not balance the evaporation loss, so there is a sea-level difference between the Atlantic Ocean and the Mediterranean Sea. As a result, there is an AW flow into the Mediterranean Sea at a rate of ~ 1 Sverdrup ($1 \text{ Sv} = 10^6 \text{ m}^3\text{s}^{-1}$). Typical values for incoming AW measured at Gibraltar give a temperature (T) of approximately $15\text{--}16^\circ\text{C}$, salinity of $36\text{--}37\text{‰}$ and density of $1.026\text{--}1.027 \text{ g/cm}^3$ ($\sigma = \sim 26\text{--}27$).

All along its course, AW is continuously modified, seasonally warmed (up to $20\text{--}28^\circ\text{C}$ in the mixed layer) or cooled (down to $\sim 13^\circ\text{C}$, or locally less) but, overall, its salt content increases (up to $38\text{--}39\text{‰}$) and it is thus made denser (up to $\sigma \sim 28\text{--}29$). This happens in winter, when cold and dry air masses, caused by relatively brief episodes of strong northerly winds, induce marked evaporation (increased salinity) and direct cooling of AW. This dramatic increase of its density (above 29) makes the AW sink. Sinking occurs in a series of specific zones: the Rhodes Gyre, the Southern-Aegean, the Southern-Adriatic, the Gulf of Lion and the Ligurian Sea.

In the western basin, intermediate (WIW) and deep (WMDW) waters are formed in the Gulf of Lion and, during winter, in the Ligurian Sea, by the action of wind blowing from the north (Mistral and Tramontane respectively). After having circulated and accumulated at depths greater than 2000m in the Algero-Provençal basin, these waters flow towards the deep Tyrrhenian Sea ($\sim 3900\text{m}$) (Millot, 1999; Robinson *et al.*, 2001).

Deep water for the eastern basin is produced in the southern Adriatic (ADW), descending through the Otranto Straits. The Aegean, previously contributing to the deep waters only to a modest extent, has gradually become more important as a source of deep and bottom waters (AeDW) in the eastern Mediterranean, providing a warmer, more saline, and denser deep-water mass (than that existing previously).

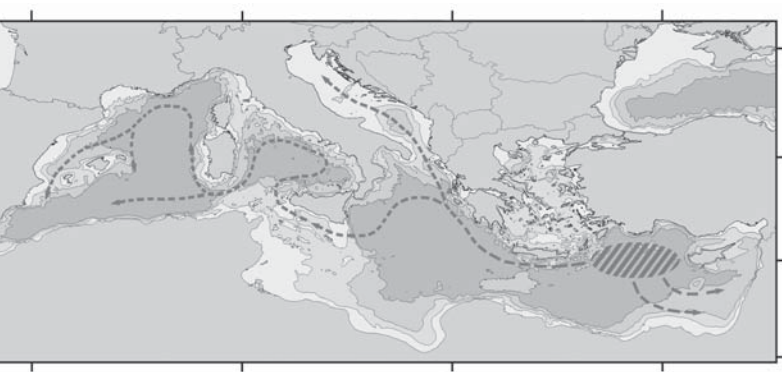


Fig. 10: Simplified scheme of Levantine Intermediate Water (LIW) formation site and dispersal pathways according to recent modelling and observation (Pinardi and Masetti, 2000, modified).

These intermediate and deep MWs can still be identified after leaving their zone of origin, but as they circulate they continuously mix. Finally (the average residence time is 50-100 years), they flow through the Strait of Gibraltar as rather homogeneous water ("the" Mediterranean Water). Thus, Mediterranean Sea circulation transforms surface AW into denser water, which can be recognised at a depth of 1000-1200 m in most of the northern Atlantic Ocean (Millot and Taupier-Letage, 2004).

On the basis of the general characteristics of Mediterranean Sea circulation and using a set of recent satellite imagery (Sea surface temperature: SST, Sea surface height: SSH, Chlorophyll concentration, Current direction and intensity, Salinity, etc.), it is possible to identify offshore areas where divergence and convergence actions generate favourable conditions for the development of pelagic life. Reduced SST, by about $1\text{--}2^\circ\text{C}$ at the core of cyclonically rotating eddies, as well as negative SSH, with respect to the surrounding ambient, together with increases in pigment concentrations, allow us to follow the dynamics of the enrichment processes.

Indeed, upwelling and downwelling maps for the whole Mediterranean have been already provided by Bakun and Agostini (2001) from the Comprehensive Ocean-Atmosphere Data Set database (Fig 11). The upwelling signatures by cyclonic eddy interactions with other oceanographic structures (anticyclonic vortexes, fronts, bottom topography, chlorophyll concentration, etc.) can also be deduced from more recent satellite imagery. The general patterns, as obtained from Mercator Ocean and NASA's Giovanni satellite images for the year 2007, are presented and discussed in the following paragraphs.

4.1.1. Circulation effects in the western basin

In this chapter, in order to better describe circulation effects on the biological components (e.g. primary production), we will use SST and Chlorophyll concentration on SSH satellite data collected during the year 2007. By overlapping all these maps, the effects of circulation on vertical transport and open sea productivity seem to fit the above-mentioned patterns quite well (Fig. 12, Fig. 13, Fig. 14).

As AW passes through the Strait of Gibraltar it undergoes intense mixing, causing a loss in heat before it reaches the Alboran Sea. Here upwellings are mainly set on the Spanish side, while one or two clockwise (anticyclonic) eddies generate convergence (downwelling) off the African coast (Fig. 1). From February, the area with high Chlorophyll concentration enlarges eastwards, probably because cyclonic eddies generate upwellings on the eastern Alboran side, enriching the upper layers until late summer (August) between Almeria and Oran.

The water flow, leaving the Alboran, restructures itself along the Algerian coast, mainly thanks to the Coriolis effect and it remains along slope. During the winter, wind forcing maintains downwelling close to the African coast, where relatively small and short-lived anticyclonic eddies characterize AW circulation. Chlorophyll hotspots appear in February off the eastern coast of Algeria. They are likely to be correlated to surface divergence. Approaching the summer months, the AW current generates a meander, embedding an anticyclonic eddy (50-100 km in

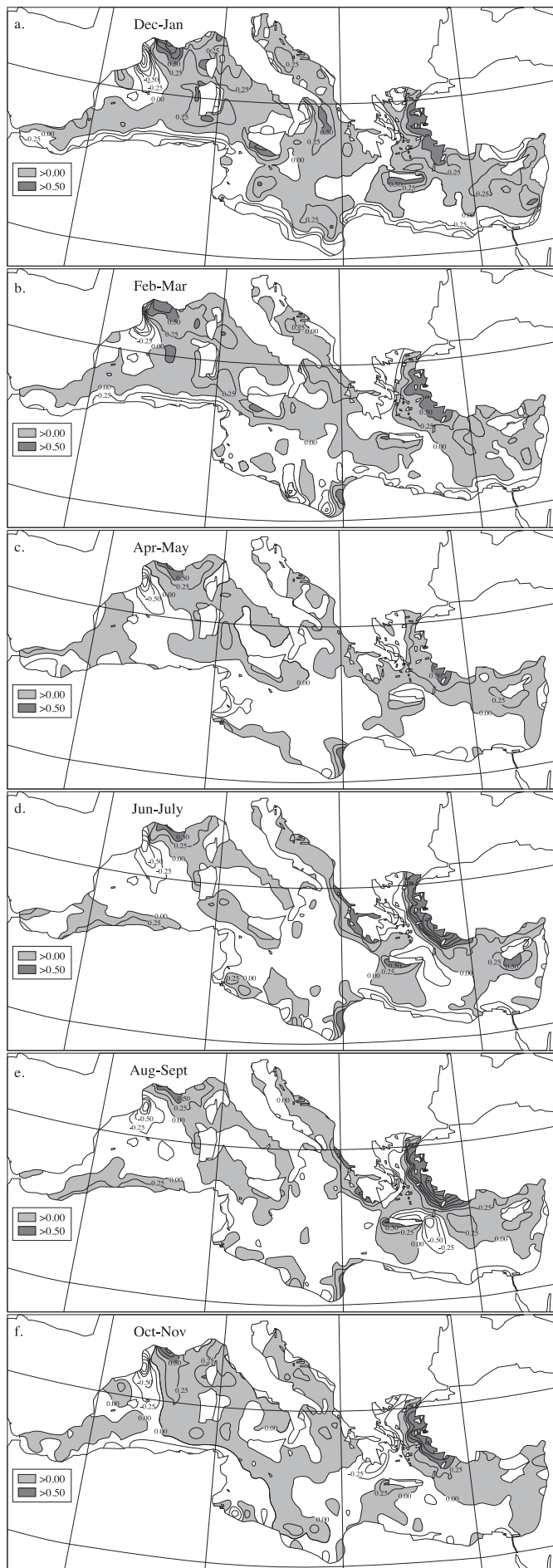


Fig. 11: Seasonal variation of wind-driven upwelling zones (shaded areas) and downwelling (unshaded areas) in the Mediterranean Sea. Darker shading indicates greater upward velocities (from Bakun and Agostini, 2001, Fig. 4 pages 252-253).

diameter), which propagates eastwards. These occurrences are too large and deep to continue through the Channel of Sardinia (south): once stopped by the Tunisian and Sardinian shelves, they drift northwards guided by the topography, mainly towards the Balearic Islands. AW dispersed in meandering-eddy events spreads towards the Provençal and Catalan areas, forming the North-Balearic front.

As AW flow reaches the western border of the Channel of Sicily, it forms three branches: the west-Corsica vein, which flows northwards to the Ligurian Sea; the north-Tunisia vein, which flows along slope through the Channel of Sicily feeding the eastern basin, and finally the Tyrrhenian vein. This last continues flowing counter-clockwise around the Tyrrhenian Sea, along Northern Sicily and the Italian peninsula before entering the Channel of Corsica. The Tyrrhenian vein thus makes the south Tyrrhenian a key place for mixing and transformation of the water masses. When the Tyrrhenian vein joins the west-Corsica vein, the AW flow reorganises itself again as the western basin gyre. The gyre continues along slope in the Ligurian, Provençal and Catalan Seas, entering the Alboran where the circle is closed.

In the Ligurian, Provençal and Catalan areas, the northern current is characterised by a maximum speed of several 10 cm/s at its core, a width of a few 10s km and a depth of a few 100s m. It displays a marked seasonal variability, because of the link with the dense water formation process, which also contributes to form WIW and WDMW, when the Mistral and the Tramontane winds blow in winter. Surface divergence persists off the northwestern coast year around, but the effects of upwelling enrichment are more evident during spring months. At this time of the year, Chlorophyll concentration heights are clearly visible at the core of the Ligurian Sea, in northern and south-western parts of the Gulf of Lion and between the Catalan coast and Balearic Islands.

Where the AW closes its western gyre along the Spanish coast, near the border between the Alboran and Algerian areas, water that has circulated inside the whole basin encounters water that is just flowing in. The result is the formation of a large horizontal gradient. Since the incoming flow is more intense, it forms the Almeria-Oran jet, well delimited on its left-hand side by the Almeria-Oran front, with effects on productivity described above (Millot and Taupier-Letage, 2004).

The various islands (with associated shelves) located in the western Mediterranean can significantly affect water circulation. The marked orography between Sardinia and Corsica (Strait of Bonifacio) creates a funnelling effect for the western winds, which are the continuation of the Mistral and Tramontane. This specific wind field induces east to the Central Tyrrhenian Sea cyclonic eddies carrying a clear upwelling SST and Chlorophyll concentration signatures.

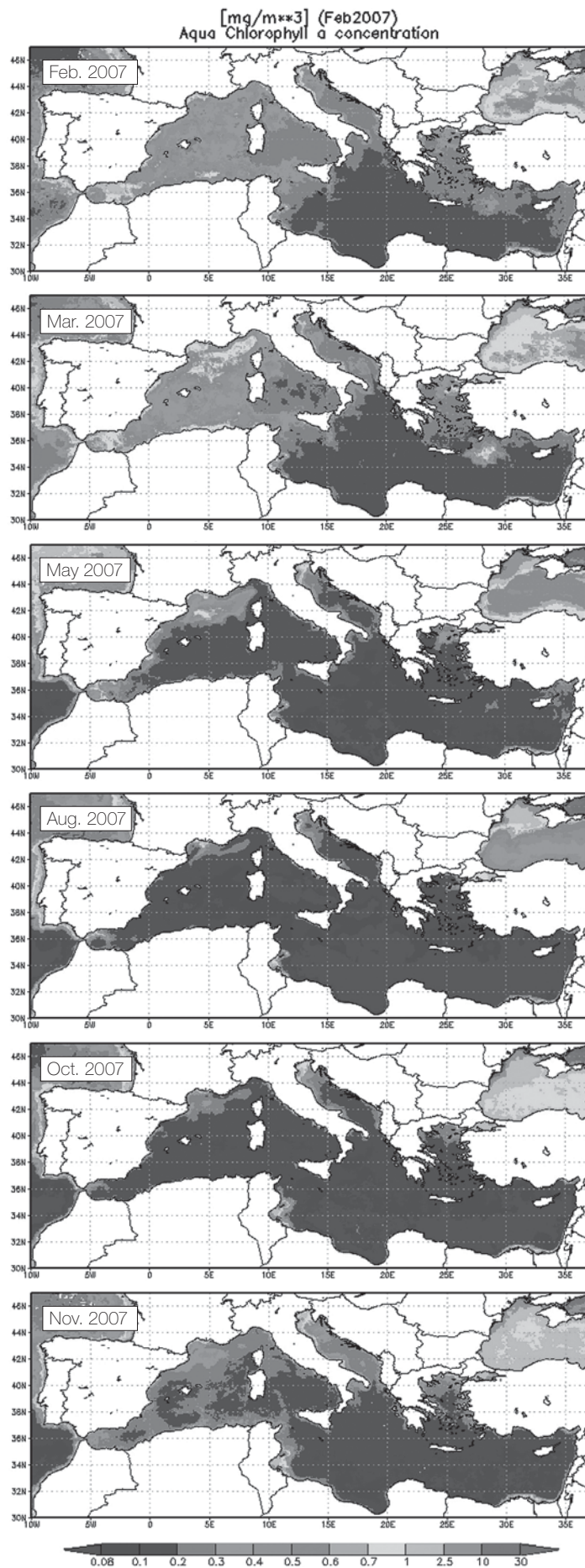


Fig. 12 (see color plate p. 78): Chlorophyll concentrations during the year 2007 (from NASA Giovanni).

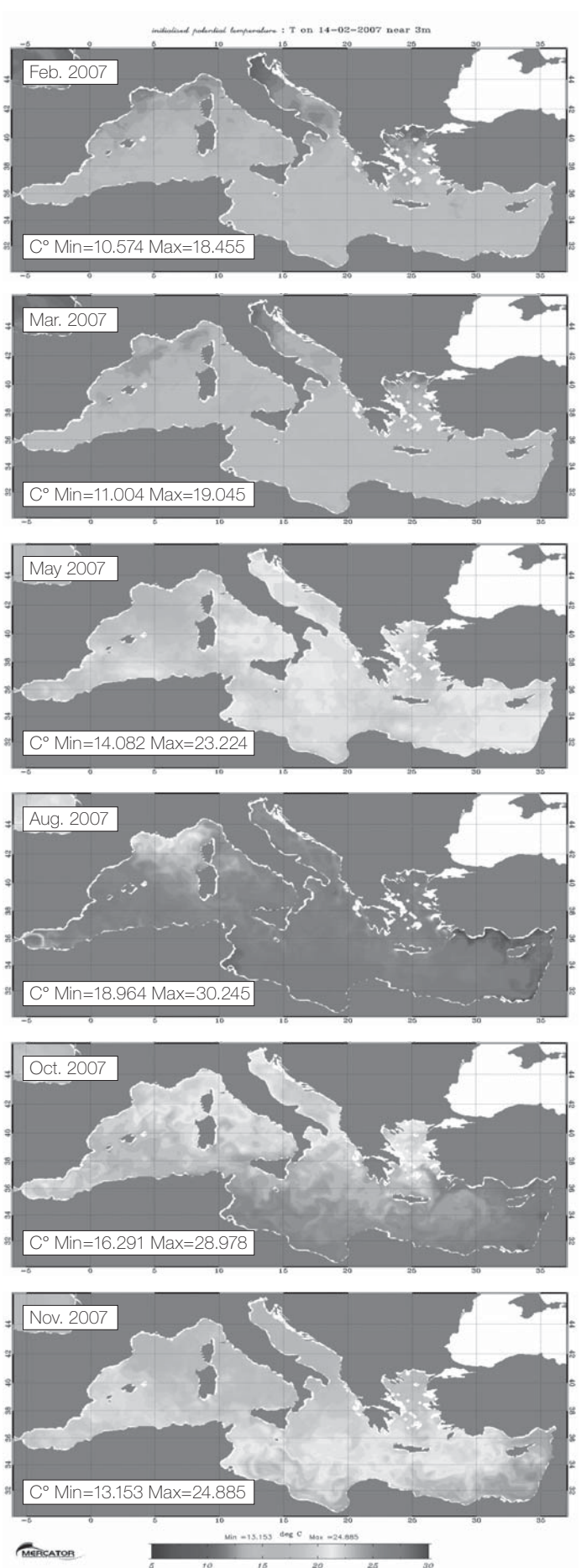


Fig. 13 (see color plate p. 78): Sea surface temperature (SST), year 2007 (from Mercator-Ocean).

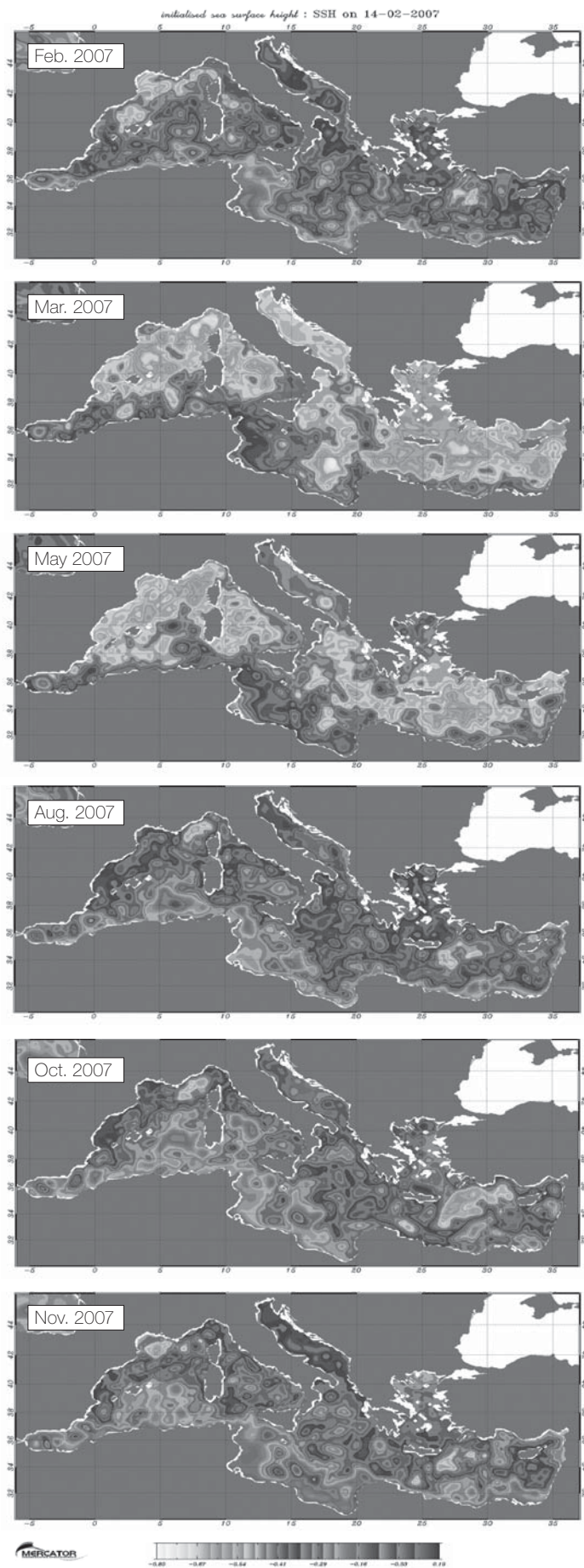


Fig. 14 (see color plate p. 79): Sea Level Height (SSH), year 2007 (from Mercator-Ocean).

4.1.2. Circulation effects in the eastern basin

As AW in the Northern Tunisia vein enters through the Channel of Sicily, it splits into two branches. The north-eastward branch, associated with interannual variability, flows off the southern Sicilian coast and spreads into the north Ionian sea. Along the northern side of the current, small cyclonic eddies enrich the surface waters near Sciacca, where a Chlorophyll maximum was located in April 2007. In the following months, on the southern side of the branch, anticyclonic eddies created retention cores west of Malta and off Capo Passero.

The second more regular branch (the south-Tunisia vein) flows mostly along the edge of the Tunisian shelf, with only a minor (upper) part following the Tunisian coast. Once it exits the channel, mesoscale eddies tend to drift into the central part of the Ionian while the numerous islands and banks, the large width of the channel and the northwest winds induce intense mixing and upwelling east of Malta (Millot and Taupier-Letage, 2004), but with low effects on Chlorophyll concentration. From $\sim 15^\circ\text{E}$, the south-Tunisia vein continues eastwards along the Libyan slope: while generating mesoscale eddies, it rapidly detaches from the coast spreading seawards, due to the coast and sea-bottom topography. These eddies, together with those formed at the channel exit, constitute a complex eddy field in the whole southern Ionian.

From northern Cirenaica to the western part of the Nile delta, this current (now the Libyo-Egyptian Current) generates well-structured and energetic anticyclonic eddies (150-250 km diameter) that tend to propagate downstream during the summer-fall period.

During the winter, passing the Nile delta, the restructured eastern basin gyre generates cyclonic eddies and divergence close to the central and northern Middle East coast. This passage is followed by a higher Chlorophyll concentration strip (Fig. 13). As the flow shifts far from the coast during the summer, anticyclonic eddies become stronger, thus feeding the Shikmona and Mersa-Matruh gyre system (Fig. 9, Fig. 14).

The eastern basin stream continues along the Turkish slope and generates, mainly by wind stress, the cyclonic Rhodes gyre. This permanent gyre is located east of Crete Island and is stronger in winter-spring. In 2007, its effects on primary production were more evident from March to April. Beside this aspect, the Rhodes gyre is the area where heating and evaporation mainly form Levantine Intermediate Water (LIW). The anticyclonic eddy systems, which surround the area (wind-induced Pelops, Ierapetra and likely Shikmona and Mers a-Matruh), incorporate LIW, making it sink and flow into all the eastern and western basins at intermediate depths (Fig. 9, Fig. 14). LIW appears to play an important role in the functioning of the Mediterranean Sea: it is the warmest and saltiest among MWs, it also forms in the largest amounts and is involved in the offshore formation of all deep MWs (AeDW, AdDW, WMDW). Due to its relatively low density, it is found just below AW and hence it mixes with AW as soon as the latter starts sinking. The LIW flowing into the Atlantic can still be recognised along the western Spanish continental slope (Millot and Taupier-Letage, 2004).

The island of Rhodes divides the eastern basin stream into a north-western and south-western vein. The north-western vein penetrates into the Aegean, where the complex topography induces a second bifurcation, with one sub-vein continuing into the Northern-Aegean, joining the Black Sea outflow. From winter to spring, cyclonic eddies characterize circulation off the western Turkish coast, where upwellings generate spring phytoplankton bloom. At the same time, on the Greek side, convergence can be associated with the dense water formation process that involves AW and LIW to form Aegean Deep Water (AeDW).

Atlantic Water continues northwards in the north-eastern Ionian where it re-constitutes the eastern gyre before bifurcating again into a northern and western vein at the entrance to the Adriatic.

The northern vein penetrates into the Adriatic and continues northwards, mixing with runoffs from the Po and other rivers. The northern vein is associated with the Adriatic Deep Water (AdDW) formation in the southern part of the sub-basin. Chlorophyll concentration is mainly evident along the coast, nevertheless during March a cyclonic eddy corresponds to phytoplankton bloom signature in the centre of the southern Adriatic. The water, which leaves the Adriatic, rejoins the western vein, closing the circuit of the eastern basin circulation.

4.1.3. Overall view of productivity in the Mediterranean pelagic environment

Even if the two previous paragraphs describe the seasonal influence of circulation on primary production in the Mediterranean pelagic waters during a single year, its overall pattern fits the circulation models proposed by other authors (Robinson *et al.*, 2001; Pinardi and Masetti, 2000; Millot and Taupier-Letage, 2004). Therefore some general aspects can be stressed for a better understanding of Mediterranean pelagic ecosystem functioning.

Firstly, from Figure 13 there is an evident eastward decrease in nutrient levels. This feature is the result of superimposing the general circulation patterns, the detritus fallout due to biological activity and the remineralization processes. The Mediterranean is known to be the largest oligotrophic area in the world where interactions between deep water and coastal areas are unusually direct. The nutrient-rich Atlantic water entering through the Gibraltar Strait flows eastward in the surface layer of the Mediterranean Sea. Along this path, nutrients are assimilated by primary producers and transformed into detritus, which sinks out of the euphotic layer. This downward flux reduces the total amount of nutrients reaching the Eastern Mediterranean. At the same time, below the surface layer the LIW nutrient content increases as the water spreads westwards, due to the mineralization of incoming detritus and the mixing with deep waters.

In describing the oligotrophic conditions of the Mediterranean Sea, both surface and subsurface production need to be considered. In fact, both these processes are subject to periods of mixing and stratification, with consequent variability in nutrient concentrations

and light intensity. There are strong seasonal variations in all Mediterranean surface waters and production peaks occur during winter and spring. In the Eastern Mediterranean, winter conditions are characterised by a depth-integrated chlorophyll density in the upper 200 m. Values found near the Rhodes area are similar to those found in the Ligurian Sea. The greatest depth of Deep-Chlorophyll Maximum (DCM) is found in these more oligotrophic areas. Trophic conditions are different in the Adriatic and Aegean seas, where the shelves are well developed and where external sources (the Po and other Italian and Albanian rivers in the North Adriatic, the Black Sea inflow in the North Aegean) act to mitigate the oligotrophy (Fig. 13). However, these regional riverine inflows do not significantly affect the pelagic ecosystem on a basin scale: the only direct discharges into the main basin are the Rhone, Ebro and Nile rivers.

The second aspect concerns the consequences of the overall eddies dynamic. From Figure 14, it can be easily noted that surface divergence, due to cyclonic eddies, characterizes the northern areas of both the basins, while anticyclonic eddies that generate convergence are mainly set off the southern shelves. Together with other factors, this pattern contributes to concentrate primary production in the northern sector of the basins. Furthermore in winter-spring months northern winds force cyclonic eddies southward, while during summer and fall southern anticyclonic eddies tend to expand northward. Therefore, thermal fronts can be located in the middle of the two basins as well. As explained by Agostini and Bakun (2002), a special relationship between enrichment (upwelling) and concentration (convergence, fronts) has favourable effects if their ephemeral life spans sufficiently (retention) to give time for biological processes to occur (zooplankton growth, fish eggs and larvae development, prey-predator concentration, etc.). Agostini and Bakun (2002) have drawn a map of five selected segments of the Mediterranean basin where "triads" occur, mainly concerning their potential effects on small pelagic species (Fig. 15). Nevertheless, it must be considered that the whole ecosystem is highly variable on an inter-annual as well as on a longer time scale. The variability and relatively fast response of the Mediterranean Sea to external conditions suggest that physical and ecological interactions at the basin scale may have a strong influence in determining the evolution of the ecosystem.

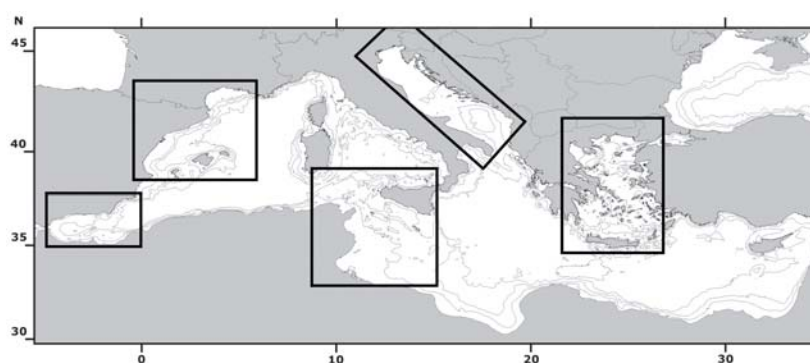


Fig. 15: Five selected sectors of the Mediterranean Sea where regional scale "Triads" occur (from Agostini and Bakun, 2002, modified).

5. Static pelagic habitats

5.1. BATHYMETRIC FEATURES

Many pelagic predators aggregate (especially to forage) as a result of static bathymetric features such as seamounts, submarine canyons, shelf breaks and in the lee (downstream) of islands. Irregularities of the sea floor often alter water flow above them, enhancing mixing and promoting upwelling of nutrient-rich waters. In turn, increased turbulence and water-column mixing promote high primary production and localized production of higher trophic levels. The process of aggregation of planktonic preys is consequently produced elsewhere, in secondary convergence zones, persistent eddies and fronts. In addition, there is evidence that shallow shelves and ledges adjacent to deep-water areas trap vertically migrating zooplankton in shallower waters (Fig. 16). Here it becomes accessible to near-surface and diving predators.

Many pelagic vertebrates, including seabirds, cetaceans and swordfish, forage in these areas, exploiting the elevated primary production and high standing stocks of zooplankton, fish and squid. The closed circulation associated with these features is likely to retain the enhanced local production near the surface and much of it is transferred to first levels of the pelagic food web, which in turn supports dense aggregations of mobile top predators. In addition, seamounts often serve as mating and spawning areas for a wide range of pelagic species. These predictable mating and foraging aggregations of pelagic species are susceptible to destructive pulse fisheries, which frequently also damage slow-growing resident fish and invertebrate communities (Hyrenbach *et al.* 2000).

5.2. SEAMOUNTS

Seamounts are typically cone-shaped undersea mountains that never emerge above sea level. Seamounts can be very large, in terms of height as well as in terms of area. They often occur in chains or clusters that are probably linked to seafloor hotspots and the associated volcanic activity. Their steep slopes, often current-swept and predominated by hard exposed rock surfaces, provide a marked contrast with the characteristically

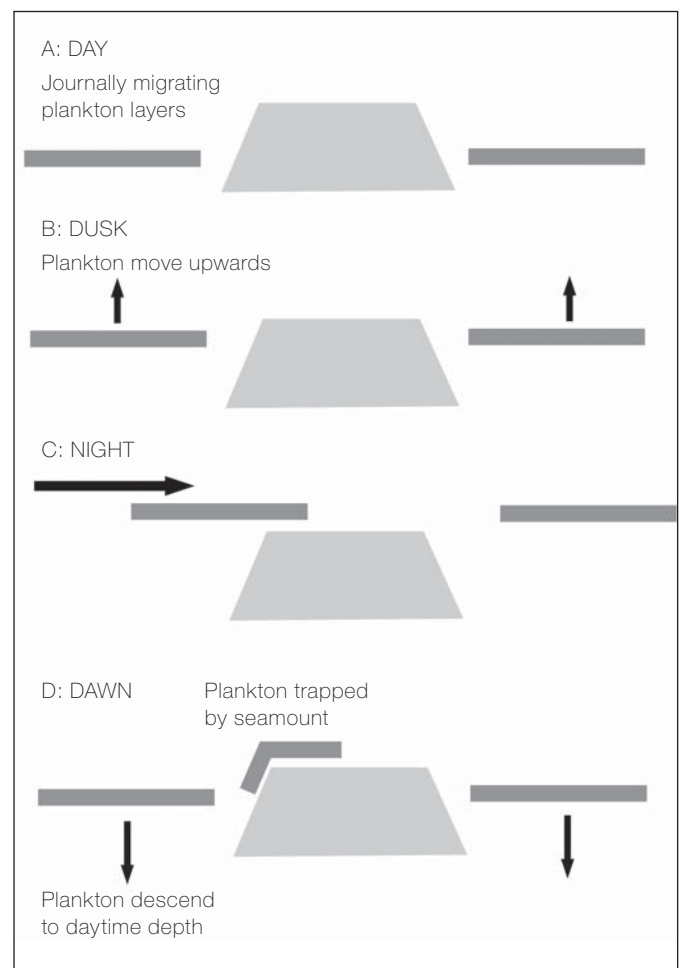


Fig. 16: Schematic representation of the trapping effect on migrating Plankton by a seamount.

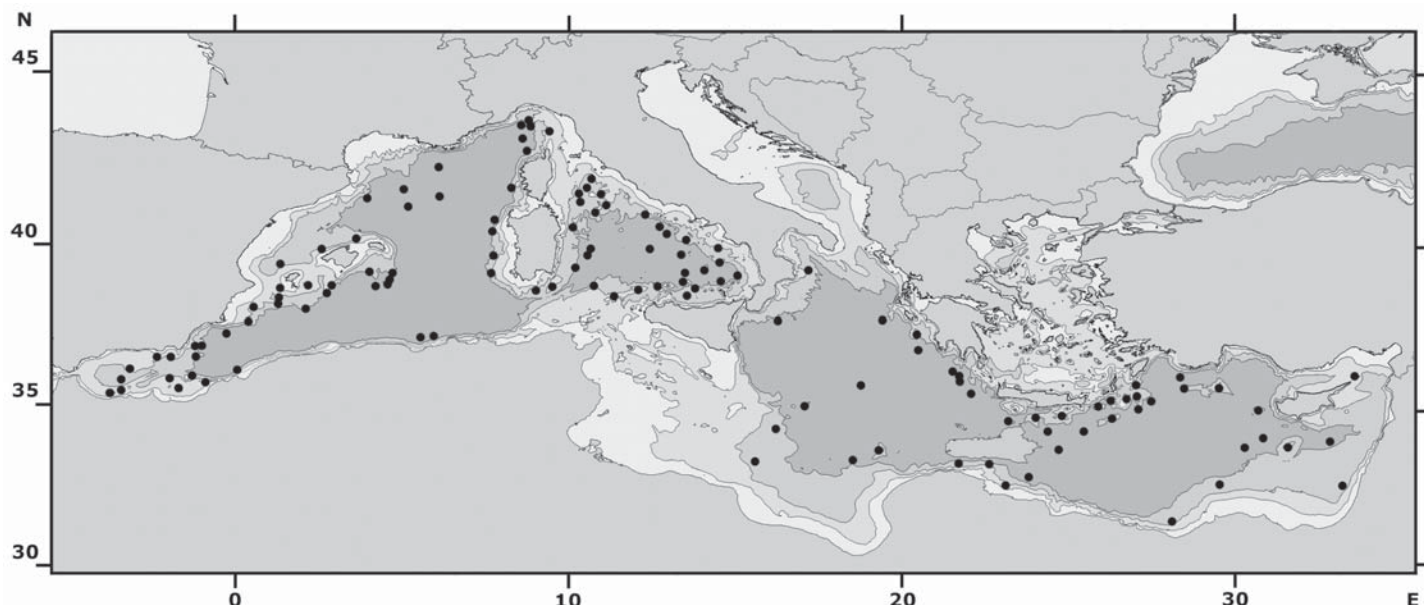


Fig. 17: Approximate seamount positions in the Mediterranean sea (see text for explanations).

flat and sediment-covered abyssal plain. Moreover, their elevated profile affects the circulation of water in the surrounding area, for example by deflecting currents as well as by leading to the formation of trapped waves, jets and eddies. Some of these eddies are known to be trapped over seamounts and to form closed circulations (*Taylor columns*) which have been observed to persist for several weeks.

Studies of pelagic communities above seamounts have revealed both qualitative and quantitative differences compared to the pelagic fauna and flora found in surrounding waters. Planktonic biomass is often higher over seamounts than in surrounding areas (Fig. 16): this probably results from upwelling around the seamount. However, the opposite situation has been observed in other cases, which can be possibly explained by intensive grazing by predators or downward migration during the day. Nekton that are usually located at deep waters during the day (500-600 m in the case of Myctophids of the *Diaphus* genus) have been observed, thanks to acoustic observations and trawls, moving over seamounts at a depth of 80-150 m at night. This Myctophid feeds on diurnally migrating oceanic plankton and is an important component of the diet of large fish species and small odontocetes (dolphins), which are often much more abundant around seamounts than in the surrounding oceanic waters. The ecology of seamounts in the Mediterranean Sea is poorly investigated, as a matter of fact some seamounts are even better known by sport and commercial fishermen than by researchers. Considering those sites with an elevation greater than 1000 m from the surrounding depths and within five miles on bottoms deeper than 2000 m, it is possible to identify almost one hundred seamounts in both the Mediterranean basins (Fig. 17). Some are known as banks (e.g. Banco des Cabliers, Banco Avenzoar, el Secho des los Olivos) others as mounts (e.g. Monte Aguilas, Calypso hills, Monte Magnaghi, Monte Vasilov, Monte Marsili, Eratosthenes Seamount). For the latter, the concentration of pelagic species is documented (Clark *et al.*, 2006; Abdulla *et al.*, 2009), nevertheless their overall influence on the pelagic ecosystem also needs further investigation.

5.3. SUBMARINE CANYONS

The continental slope is a steep, narrow fringe separating the coastal zone from the deep ocean. During phases of low sea levels in the Mediterranean, dense sediment-loaded flows and slides erode the outer continental shelf and the continental slope, leading to the formation of submarine canyons. These canyons funnel large volumes of sediment and organic matter from shallow regions to the deep ocean. During periods of high sea level (such as at present), occasional sediment gravity flows still occur in the canyons, possibly triggered by sediment failure, river flooding or dense shelf water cascading (DSWC), a type of current driven only by density seawater contrast. DSWC can transport large amounts of water and sediment, reshape submarine canyon floors and rapidly affect the deep-sea environment (Fig. 18).

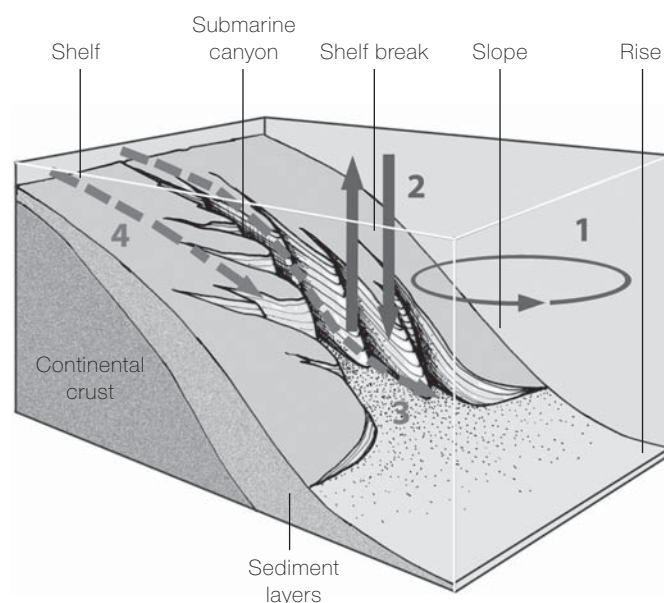


Fig. 18 (see color plate p. 77): Submarine canyon processes scheme. 1) Eddy formation; 2) Up- and down-welling; 3) Slumps, turbidity currents; 4) Off-shelf currents.

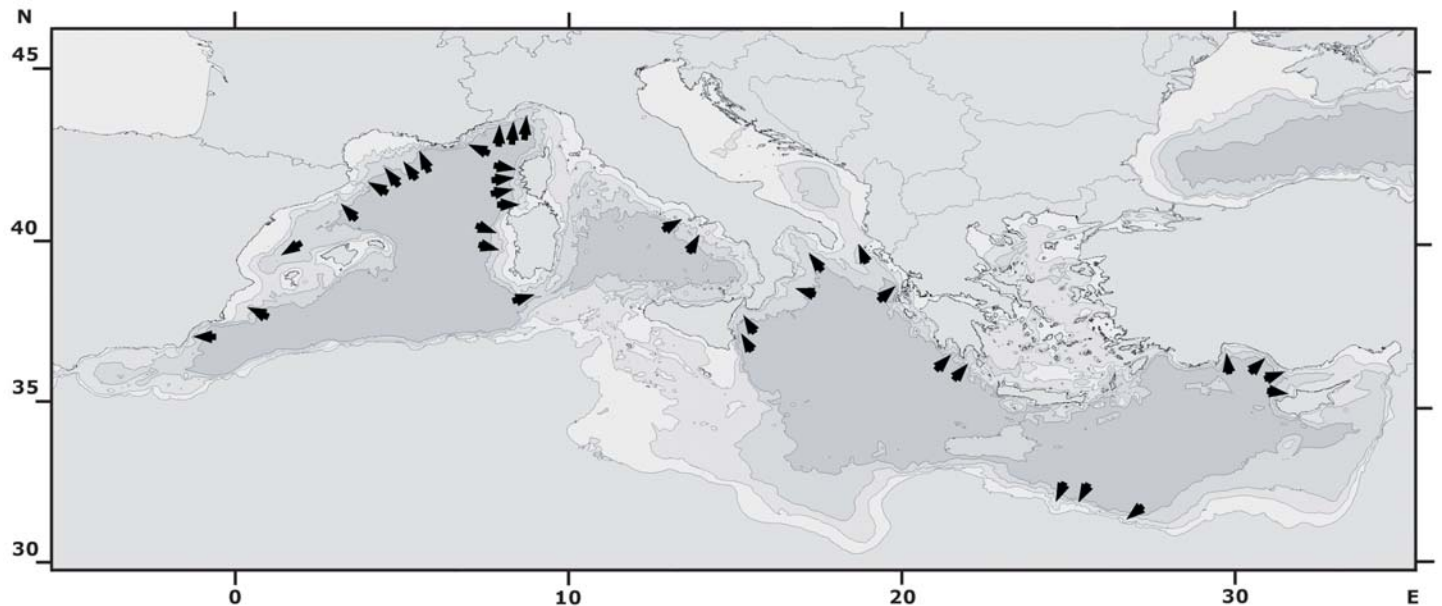


Fig. 19: Approximate positions of the main submarine canyons in the Mediterranean Sea.

Cascading is seasonal; resulting from the formation of dense water accordingly cooling and/or evaporation, it occurs on both high- and low-latitude continental margins. Furthermore, changes in the frequency and intensity of DSWC, driven by interannual and seasonal weather variability and future climate change, may have a significant impact on the supply of organic matter to deep-sea ecosystems and on the amount of carbon stored on continental margins and in ocean basins. The effects of submarine canyons vary according to canyon morphology: slumps, turbidity currents, upwelling, downwelling and eddies may be generated, particularly in the outer part of the canyon, generally resulting in an accelerated and concentrated transport from the shelf to the bathyal layers via off-shelf currents (Canals *et al.*, 2006).

As for seamounts, scientific information about Mediterranean submarine canyons (Fig. 19) is lacking, even though top predator (e.g. sperm whale) affinity for such structures has been investigated in some areas (David, 2000). Because of the above-mentioned geological processes, submarine canyons are mainly located in the northern sectors of the two basins. In this area, submarine canyons sometimes form a system (e.g. Polcevera and Bisagno canyons off Genoa). Because of the Coriolis effect on ancient river-mouth flows, the longitudinal axis of the canyons runs more or less westward, from the coast to the deeper part of the slope, where it enters valleys or plains. The shelf then abruptly extends seaward and the slope may form a wall intersecting the mouth of the submarine canyon. It thus creates a trough or a basin, which may have effects on the anticyclonic flow of the AW stream and other water masses (e.g. LIW). In these areas, swordfishes (e.g. *Xiphias gladius* and *Tetrapturus belone*) and cetaceans (e.g. *Ziphius cavirostris*, *Physeter catodon*, etc.) may find their preferred food, such as Histioteuthids and other mesopelagic squids (Moulins *et al.*, 2007).

6. Pelagic biodiversity

Biodiversity, as defined by the Convention on Biological Diversity, is: *the variability among living organisms from all sources, including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems* (Heip and Gattuso, 2006).

All three domains of life, bacteria, archaea (single cell organisms lacking membrane-bound nucleus and organelles) and eukarya (all more complex organisms, single- or multicellular, having membrane-bound cellular nucleus and organelles) are present in the marine environment. A fourth domain consists of viruses; however, since they lack their own metabolism, they are often not considered as being living organisms. Approximately 230,000 species of plants, animals and a few thousand bacteria and archaea have been scientifically described in the marine environment, even though they represent only a small fraction of existing species. A large proportion of the yet unknown species are likely to be found in the world oceans.

The oceanic pelagic environment seems to have low species diversity if compared to both terrestrial and marine benthic diversity. However, thanks to the recent exploration of pelagic environments difficult to access (e.g. deep-sea) and to the application of new technologies, new species and higher taxonomic categories (even up to phylum level) of both animals and microbes are constantly being discovered. The availability of rapid gene sequencing technologies has made it possible to show that microbial diversity, is extremely high and that tens of thousands of species may co-occur in a single litre of sea water.

Pelagic habitats are difficult to define in numbers, because of the great variability of the pelagic environment and finer discontinuities being revealed in the water column. The pelagic environment appears homogenous but it may be very deep. As the potential for exploration and observation increases, so will the number of known marine habitats, on many different scales. As these habitats do often host species specifically adapted to environmental conditions, it is also likely that the discovery of new species will increase (Heip and Gattuso, 2006).

6.1. THE ORIGIN AND DEVELOPMENT OF MEDITERRANEAN BIODIVERSITY

The Mediterranean Sea is a remnant of the Tethys Ocean, an extensive, wedge-shaped, equatorial water-body, open towards the east, that indented Pangea during the Triassic. After the opening of the Atlantic Ocean in the Cretaceous, the Tethys connected the newly born ocean to the older Indo-Pacific Ocean, through an uninterrupted equatorial belt. The Tethys at this time harboured a highly diverse warm-water fauna, comparable to that found nowadays in the tropical Indo-west Pacific. The shrinking of the Tethys Ocean in the Oligocene (30 Ma), with subsequent diminution of its warming influence on the world oceans, produced cold-water conditions in other areas and may have resulted in higher extinction rates. During Miocene orogeny (around 10 Ma), the Isthmus of Suez was formed, separating the Mediterranean from the Indo-Pacific. Towards the end of the Miocene (about 6 Ma), the connection with the Atlantic also closed, completely isolating the Mediterranean Sea. The negative water balance of the Mediterranean probably transformed the sea into a series of large evaporitic lakes. This period is known as the "salinity crisis" in the Messinian Stage: desiccation drove the Tethyan biota to extinction, or at least severely reduced it. The Mediterranean Sea was repopulated by species of Atlantic origin only in the early Pliocene (5 Ma) thanks to the re-opening of the Straits of Gibraltar. During the whole Quaternary, the alternation of the ice ages (Fig. 20) and warm interglacial periods resulted in different immigration occurrences of Atlantic fauna, respectively of boreal or subtropical origin (Bianchi and Morri, 2000; Emig and Geistdoerfer, 2004).

As a consequence, the biogeographic characteristics of the Mediterranean Sea could be described as those of an Atlantic province (Briggs, 1974). Considering the complex history of the Mediterranean, it can be concluded that its high species richness is principally due to its long evolutionary history throughout the Tertiary, as well as the post-Pliocene diversity pump from the Atlantic. As a result, the present marine biota of the Mediterranean is composed of species belonging to several biogeographic categories:

- temperate Atlantic-Mediterranean species
- cosmopolitan or *pan-oceanic* (existing in all oceans) species
- endemic elements, comprising both *paleo-endemic* (endemic due to extinction elsewhere) species (possibly of Tethyan origin) and *neo-endemic* (endemic due to local evolution) species (mainly of Pliocene origin)
- subtropical Atlantic species (interglacial remnants)
- boreal Atlantic species (ice-ages remnants, especially of the Würm glacial)
- Red Sea migrants (especially into the Levant Sea)
- eastern Atlantic migrants (especially into the Alboran Sea)

The categories above are more or less abundant in different parts of the Mediterranean, and ten biogeographic sectors can be distinguished within the sea (Fig. 21). The most “typical” Mediterranean flora and fauna are found in the central parts of this sea, particularly in the western basin. The Alboran Sea, immediately east of Gibraltar, shows stronger Atlantic affinities, while the Levant Sea is now experiencing an important influx of Red Sea species after the opening of the Suez Canal. This is a phenomenon known as Lessepsian invasion in recognition of Ferdinand de Lesseps, the French diplomat who promoted the cutting of the Canal (Galil, 1993).

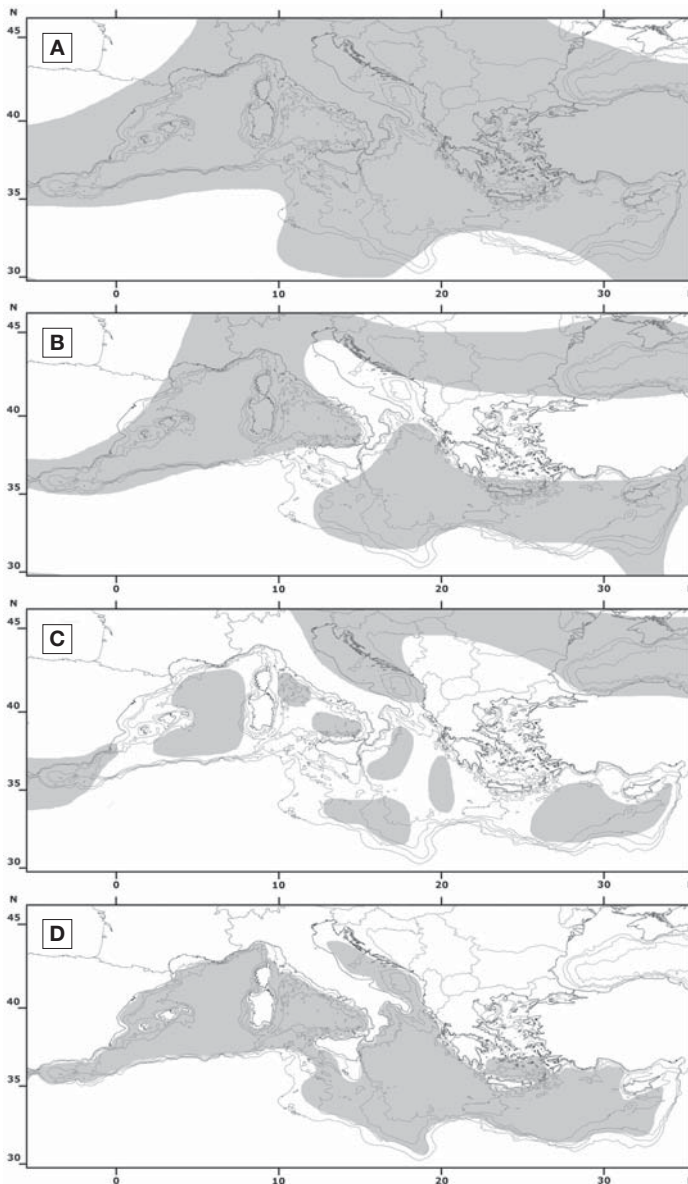


Fig. 20: Some phases in the geological evolution of the Mediterranean Sea.

- A) Cretaceous, 120 my BP;
- B) Oligocene, 30 my BP;
- C) Late Miocene (Messinian Stage), 6 my BP;
- D) Late Pleistocene (Würm glacial), 20,000 y BP.

Land in white, sea in grey. Land masses are represented in their relative position of today, plate movements are neglected (from Bianchi and Morri, 2000, Fig. 1 modified).

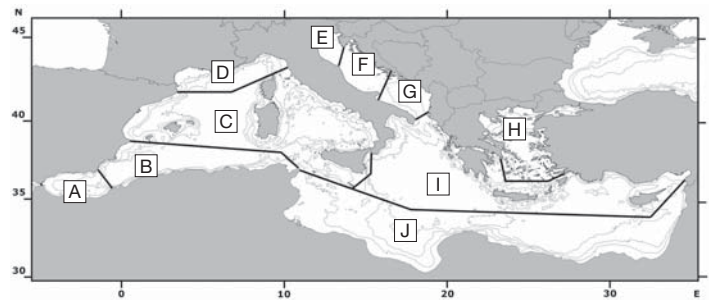


Fig. 21: Biogeographic sectors within the Mediterranean Sea.

- A) Alboran Sea,
 - B) Algeria and Southern Spain,
 - C) Balearic and Tyrrhenian Sea,
 - D) Gulf of Lion and Ligurian Sea,
 - E) North Adriatic,
 - F) Central Adriatic,
 - G) South Adriatic,
 - H) North Aegean,
 - I) Ionian and South Aegean,
 - J) Gulf of Gabès and Levant Sea
- (from Bianchi and Morri, 2000, modified).

6.2. PELAGIC SPECIES RICHNESS IN THE MEDITERRANEAN SEA

The Mediterranean Sea hosts more than 8,500 species of macroscopic marine organisms, of which approximately 30% can be considered pelagic, (Fredj *et al.*, 1988, 1992; Fischer *et al.*, 1987; Ribera *et al.*, 1992). This percentage could be higher because it has to be considered that many benthic species have pelagic larvae and juveniles (meroplankton). Comparing this estimate to global estimates (Wilson, 1988), between 4% and 18% of the world marine species (with large differences between groups) are found in the Mediterranean Sea. This is particularly impressive as the Mediterranean Sea represents only 0.82% in surface area and 0.32% in volume of the world ocean (Defant, 1961). Moreover, more than a quarter of all Mediterranean species are endemic, i.e. living exclusively in the Mediterranean, (Tortonese, 1985; Fredj *et al.*, 1992).

A simple reason that could explain this high number of species in the Mediterranean may be that this sea has been studied more intensively than most other oceans. There are also other convincing explanations for this high level of marine biodiversity. One of them is that the Mediterranean's geological history, in which the rate of environmental change, and hence species occurrence, has been exceptionally active. Another is the present-day variety of climatic and hydrologic situations found within the Mediterranean pelagic ecosystem, resulting in the presence of both temperate and subtropical biota (Sarà, 1985).

6.3. PELAGIC LIFE

The diversity of life in the complete pelagic province is difficult to describe, in both qualitative and quantitative terms, because of the variability of the environment and our limited capacity to perform efficient sampling.

Very small-size plankton ($< 200 \mu\text{m}$) can be sampled by using a set of bottles, while larger zooplankton can be caught in nets with calibrated mesh size and openings of different diameters. Sampling procedure (i.e. opening and closing at a defined depth) is species-specific. Species composition encompassing vertical migration patterns over 24 hours, for macroplankton and micronekton, can be studied using *Isaacs-Kidd Mid-water Trawl (IKMT)* tow and a multiple opening and closing net called *BIONESS* (Sameoto *et al.*, 1980).

The major limit of the gear mentioned above is that fast-swimming animals cannot be caught with a tow whose speed is generally kept lower than 3 knots (1 knot $\approx$ 1 nautical mile/hour). Thus, these methods give only a partial picture of the effective species composition and patterns within the water column.

Nektonic species can be also sampled using fishing gear: pelagic nets, long lines, traps, fish aggregating devices (FADs) etc. However, they are selective on a small number of target species. Of course, pelagic life can be described in detail by underwater cameras and through direct observations on board a research submarine, but the obvious economical and operational limits make extensive use of these techniques impossible (Laval *et al.*, 1989).

Studying the feeding ecology of pelagic predators can help us to investigate the abundance of a set of species, from macroplankton to fast-swimming nekton. Gut contents and faeces studies, as well as fatty-acid analyses, give very interesting pictures of prey species composition. Unfortunately, in the case of very efficient predators such as ceatceans, stomach contents can be sampled only from dead animals (fished or stranded) and faeces are not always easy to sample properly, whereas fatty acids can be sampled also through biopsies from free-ranging animals, though not always in a non-invasive way.

6.3.1. The diversity of pelagic organisms

Pelagic organisms could be divided into two main groups: Plankton and Nekton.

Plankton includes viruses, bacteria, plants and animals with locomotive powers, which cannot prevent passive movement by currents. Plankton can be: Holoplankton, when the organism's entire life cycle is spent in the plankton or Meroplankton, when only a temporary stage of life is spent in the plankton (e.g. 70% of benthic species have larval stages in the plankton).

According to size classes, Plankton can be divided into: femtoplankton (0.02-0.2 μm), picoplankton (0.2-2 μm), nanoplankton (2-20 μm), microplankton (20-200 μm), mesoplankton (0.2-20 mm), macroplankton (2-20 cm), megaplankton (20-200 cm).

Viruses are a current research area. They are typically femtoplankton. Virus infection leads to cell lyses and may control phytoplankton bloom dynamics.

Heterotrophic and autotrophic bacteria are cells without nuclear membrane (Prokaryote), seldom observed as rods. Typically, their concentration is 5×10^6 cells/ml in euphotic zone and 10^3 cells/ml in the deep ocean. Their role in the microbial loop is to break down particulate detritus (dead organisms, phytodetritus and faeces) and utilise dissolved organic material excreted or exuded by plankton. Bacteria bloom often follows phytoplankton bloom. Bacteria are grazed by nanoplankton and especially by zooflagellates: microbes are thus linked to higher trophic levels. Nevertheless when they aggregate in rods or flocks (sea snow) they can be ingested by microplankton and even by mesoplankton.

Cyanobacteria, previously known as Blue Green Algae, can be considered as the link organism between bacteria and green plants. Their cells contain chlorophyll and other accessory pigments, therefore they carry out photosynthesis. For this reason Cyanobacteria can be included in the Phytoplankton category together with unicellular algae such as Diatoms, Dinoflagellates, Coccolithophorids and Silicoflagellates.

Zooplankton includes (as described below **very roughly**):

Protozoa (Fig. 22)

- Zooflagellates, unicellular with flagella. They may be 20-80% of nanoplankton feeding on bacteria and detritus.
- Foraminifera, amoebae with calcareous perforated test catch on bacteria, phytoplankton and small zooplankton.
- Radiolaria, unicellular with central perforated silica capsule with branched axopodia feeding on bacteria, phytoplankton and other protists.
- Ciliates feeding on bacteria, diatoms, phytoplankton and zooflagellates using cilia for locomotion and feeding. The group includes Tintinnids, which have a vase-like external shell of protein, and may consume up to 60% of primary production.

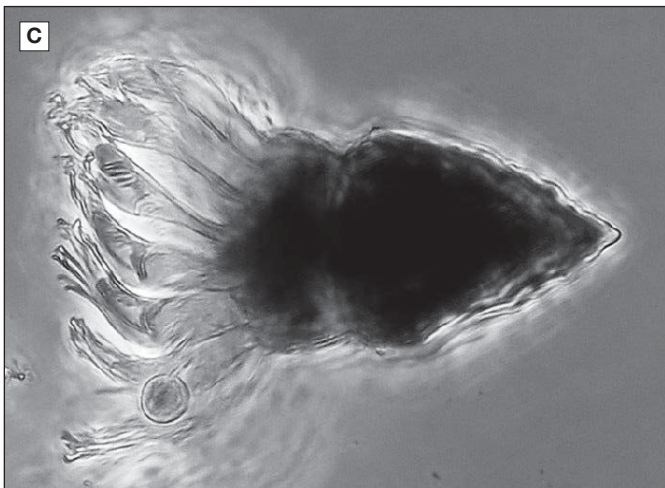
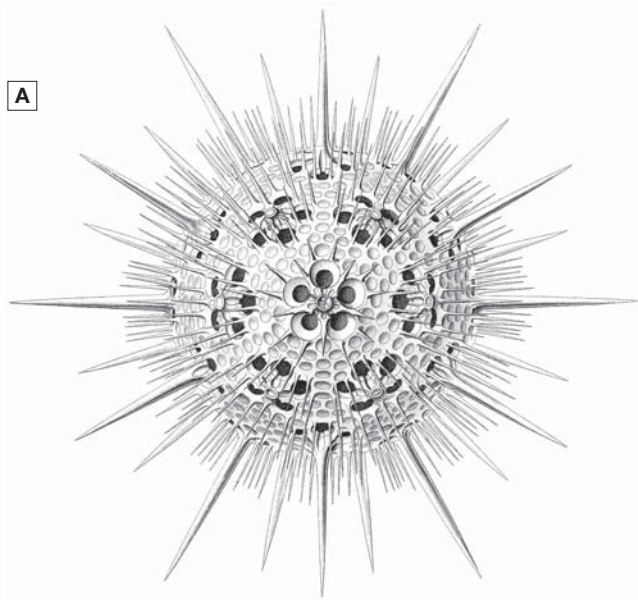


Fig. 22 (see color plate p. 79): Protozoans:

A) Radiolaria: *Haeckeliana porcellana*, from Ernst Haeckel. *Kunstformen Der Natur*, Leipzig-Wien, 1899-1904. Modified).

B) Foraminifera: *Challengeron willemoesii*.

C) Ciliates: a swimming oligotrich ciliate with its prey.

Photos: John Dolan, Station zoologique de Villefranche-sur-Mer, <http://www.obs-vlfr.fr/LOV/aquaparadox>

Cnidaria (Fig. 23)

- Medusae capture zooplankton by tentacles with nematocysts (See box).
- Siphonophores, a colony of specialised individuals.

Ctenophora. Gelatinous transparent animals with no nematocysts (Fig. 24).

Chaetognatha. Transparent, less than 4 cm long with chitinous hooks around mouth, feeding on small zooplankton (Fig. 25).

Annelida. Pelagic Polychaete worms (Fig. 26).

Mollusca (Fig. 27)

- Heteropods have eyes and chitinous teeth, swim with fins, feed on other molluscs, copepods and salps (see below).
- Pteropods have calcareous shells, swim with paired wings, suspension feed for phytoplankton, small zooplankton and detritus using mucous web.
- Cephalopoda (see box).

Urochordata (Fig. 28)

- Appendicularians – tadpole-like body in mucous house, which filters out particulates. The house is discarded when clogged, adding to marine snow. Catch nanoplankton and bacteria.
- Salps and other tunicates. Cylindrical gelatinous body, internal mucous net catching phytoplankton and bacteria.

Arthropoda – Crustacea class (Fig. 29)

- Copepods form 70% of netted plankton.
- Euphausiids – shrimp-like, up to 50 mm, e.g. *Meganyctiphanes norvegica* (northern krill). Key species, feeding on phytoplankton, detritus and zooplankton.
- Amphipods – laterally compressed body, feeding on other crustaceans.
- Isopods – free swimming, but also parasitic on pelagic vertebrates (fishes, mammals and turtles)
- Ostracods – bivalve exoskeleton which animal withdraws into.
- Mysids – shrimp-like, pelagic at night.
- Decapods – includes pelagic shrimps as well as larval stages of benthic species.

Nekton (Fig. 30) includes all the pelagic animals capable of swimming against a current. This category is dominated by fish (bony fishes, sharks, rays) varying in size, trophic level and depth adaptation (see box *Small mesopelagic fishes*), but it also includes reptiles (turtles), crustaceans (crabs and shrimps), cephalopods (squids and octopuses) (see box *Mesopelagic cephalopods*), and mammals (whales, seals, dolphins).

Seabirds are not part of the pelagic fauna, but some species spend their whole life foraging, feeding and resting at sea, thus being in some cases totally dependent on marine food resources. Some seabirds feed near the surface at night, taking advantage of the vertical migration of plankton. Others species feed on preys which are forced to the surface by other large predators, such as dolphins and tuna (see box *Pelagic birds*).

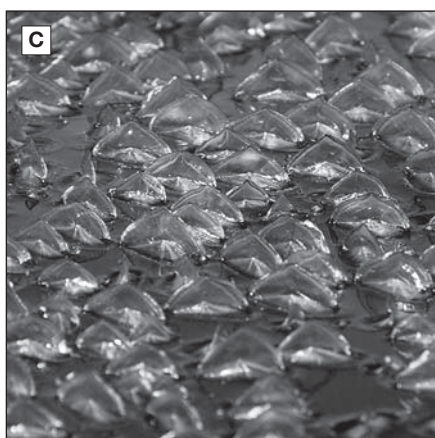
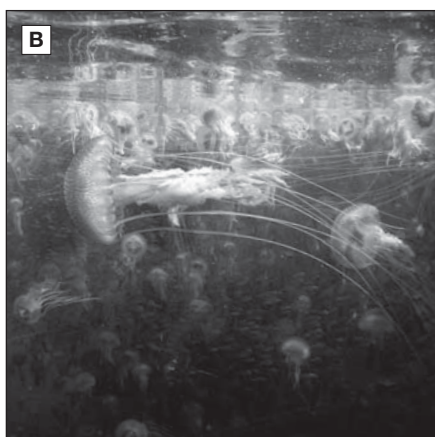
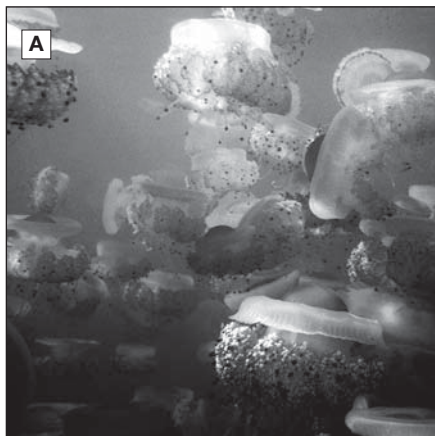


Fig. 23 (see color plate p. 80): Cnidaria.

- A) *Cylindrorhiza tuberculata*.
Photo: Ignacio Franco,
Centro Oceanográfico de Murcia.
B) *Pelagia noctiluca*.
Photo: Sandrine Ruitton.
C) *Velella velella*.
Photo: M. Rosso, DIBIO, Unige.

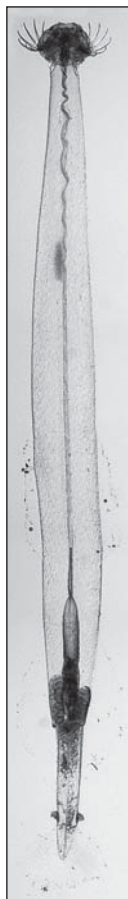


Fig. 25 (see color plate p. 80):

Chaetognath, Flaccisagitta enflata. Size: 2 cm.
Photo: Yvan Perez,
Institut Méditerranéen d'Écologie et de Paléoécologie.

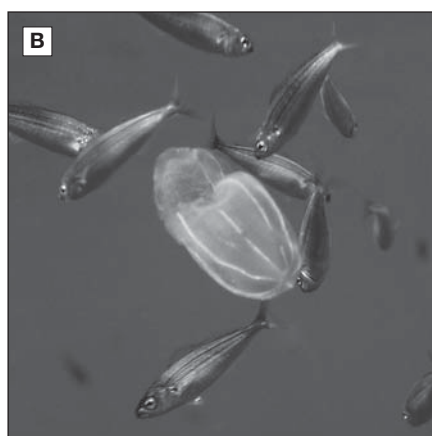
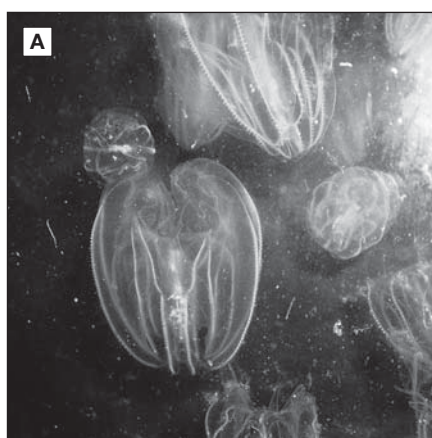


Fig. 24 (see color plate p. 80):

- Ctenophora.
A) *Mnemiopsis leidyi*. In the Eighties, it has
been introduced into the Black Sea through
tanker ballast waters, now is proliferating in
the Mediterranean with a strong impact on
fish eggs and larvae. Photo: Prof. Hans Ulrik
Riisgård, Marine Biological Research Centre
(University of Southern Denmark).
B) *Beroe* sp. Photo: Olivier Le Corre, [http://
www.olivierlecorre.com/](http://www.olivierlecorre.com/)

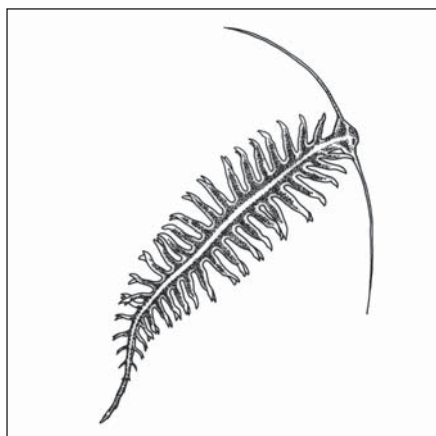


Fig. 26:
Pelagic Polychaete worm.

Fig. 28 (see color plate p. 81):

Urochordata.

A) Appendicularians: *Oikopleura dioica*. Photo: Maurice Loir,
<http://www.diatomloir.eu/Siteplancton/Tunicier.html>

B) Salps, Photo: Olivier Le Corre.

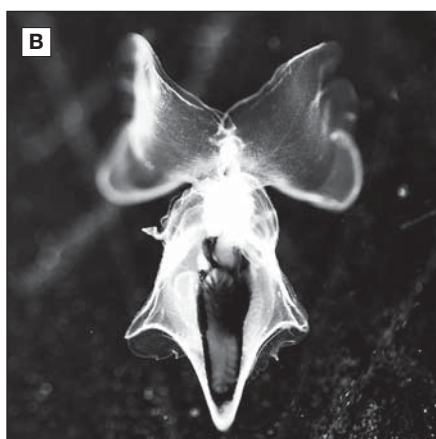
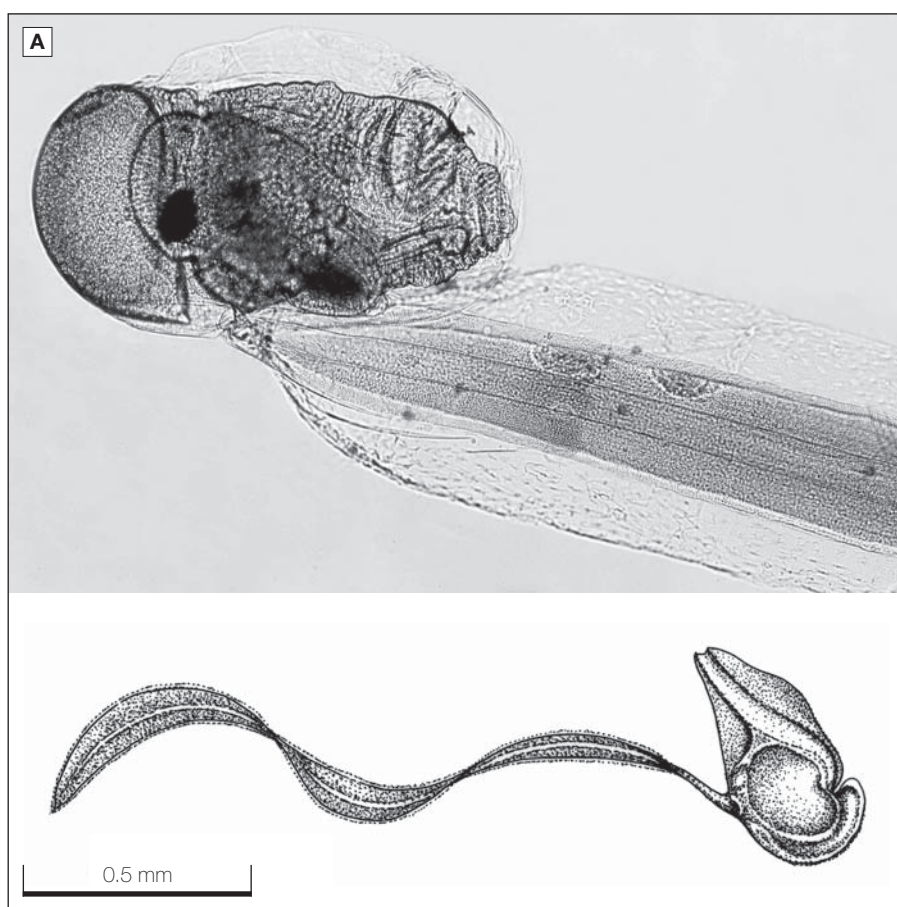
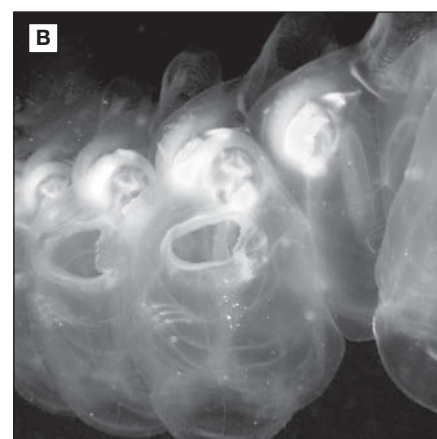


Fig. 27 (see color plate p. 81):

A) Heteropods Molluscs, *Pterotrachea* sp.
Photo: Olivier Le Corre.

B) Pteropods Molluscs: Adult of *Cavolinia inflexa* collected in the Villefranche-sur-Mer bay. Photo: S. Comeau, Observatoire
Océanologique de Villefranche.



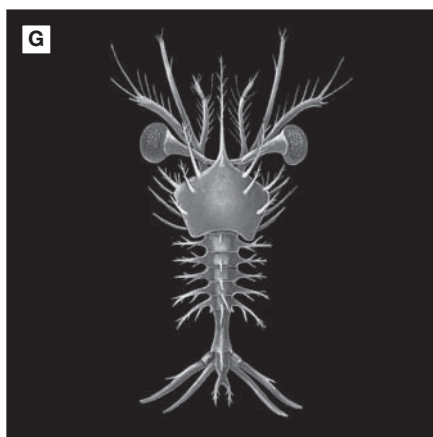
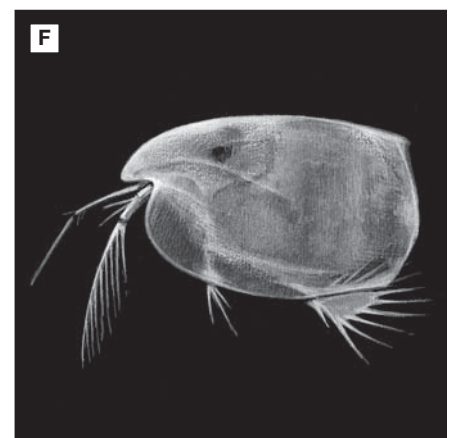
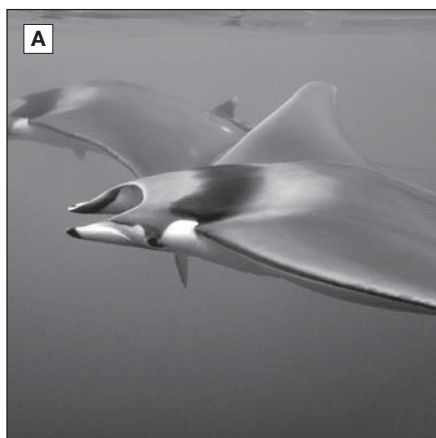


Fig. 29 (see color plate p. 82):

Crustacea:

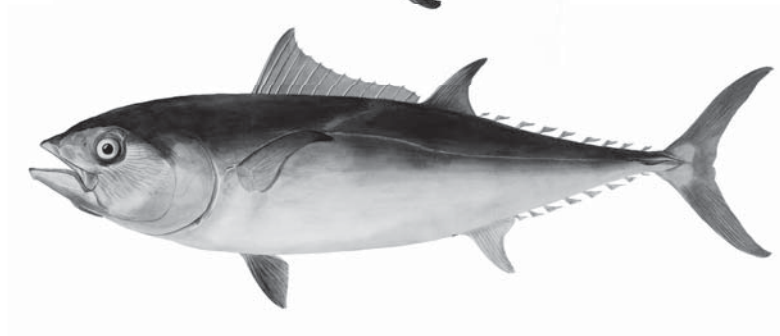
- A) Copepods,
female of *Centropages kroyeri*.
Photo: Stéphane Gasparini, Laboratoire
d'Océanographie de Villefranche.
- B) Euphausiids,
- C) Amphipods,
- D) Isopods,
- E) Mysids,
- F) Ostracods,
- G) Decapods (larval stage of *Sergestes* sp.)



B



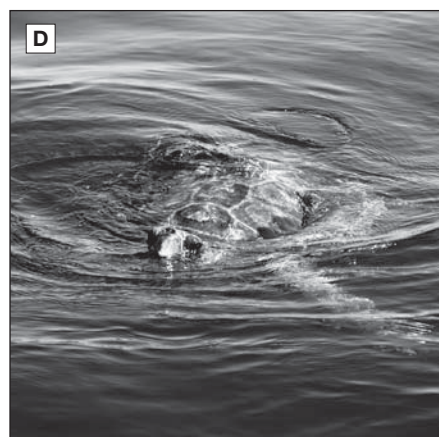
C



E



F



D

Fig. 30 (see color plate p. 83):

Nectonic species.

A) *Mobula mobular*;

B) *Mola mola*, by V. Fossat, 1878. Coll. Muséum d'Histoire naturelle de Nice;

C) *Thunnus thynnus*, by V. Fossat, 1878. Coll. MHNN;

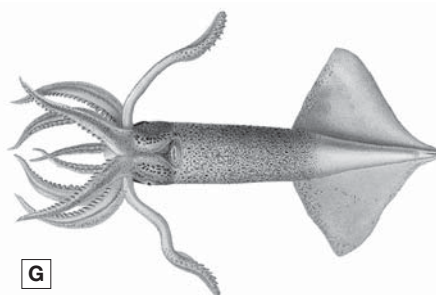
D) *Caretta caretta*,

E) *Prionace glauca*, by V. Fossat, 1879. Coll. MHNN;

F) *Coryphaena hippurus*, by V. Fossat, 1879. Coll. MHNN;

G) *Onychoteuthis banksii*. Joubin, L., 1900. Céphalopodes provenant des campagnes de la Princesse-Alice. Résultats des campagnes scientifiques accomplies sur son yacht par Albert I^{er} prince souverain de Monaco, Fascicule XVII, planche XII;

H) *Stenella coeruleoalba*.



G



H

Jellyfishes (Fig. 31)

Gelatinous macroplankton are dominated by three main phyla, the carnivorous Cnidaria and Ctenophora and the herbivorous Tunicata.

At present, the division of Cnidaria into four classes is generally accepted by specialists: the Anthozoa class which does not have medusa stages, the Scyphozoa, Cubozoa and Hydrozoa classes, with medusa stages.

The most common pelagic jellyfishes, *Pelagia noctiluca*, *Aurelia aurita*, *Cotylorhiza tuberculata* and *Rizostoma pulmo*, all belong to Scyphozoa, while *Aequorea forskalea* and *Velella velella* are Hydrozoa. The adult stage of this latter species lives at the surface and its distribution is typically regulated much more by prevailing winds than by currents. The other five species are found in the epipelagic layer, mostly between 0 and 50m, seasonally in very high densities.

All the Ctenophora species are marine. At least 32 species belong to the Mediterranean fauna and most of them are *holoplanktonic*, though this figure is likely to be largely incomplete. The diversity of Ctenophora species appears to be higher in the epipelagic zone, where *Cestum veneris* and *Beroe* sp. are very common in spring plankton samples.

Pelagic tunicates (salps, appendicularians, pyrosomas and doliolids) are exclusively marine organisms. They are all filter feeders, which means that they filter the entire size range from very small colloids to large phytoplankton chains. Smaller appendicularians, however, are usually considered *microphageous* (feeding on small particles) (Sommer and Stibor, 2002).

Tunicates are the only marine metazoans which feed on particles of similar sizes as protozoa (less than 2 μm) (Bone *et al.*, 1997). The reproduction cycle is complex, including sexual and asexual generations, with high nativity rates. Under good food conditions, tunicates show population growth rates ranking at the top of the metazoans (Bone,

1998). *Thalia democratica*, *Salpa fusiformis*, *Pyrosoma atlanticum*, *Pangea confoederata* are the most represented species in pelagic samples.

Gelatinous macroplankton represents a successful morphotype, and several hypotheses attempt to give plausible explanations. A transparent gelatinous body, together with the low nutritive value of the body tissues, may provide efficient protection from predation (Verity and Smetacek, 1996; Johnsen, 2000). However, transparency gives no advantage in the deep sea and, besides, many tunicates exhibit bioluminescence or are non-transparent (Harbison, 1992). There are also specialized predators of gelatinous zooplankton, and recent research indicates that medusae, ctenophores and tunicates may be a good food resource for some fish (Harbison, 1998). *Mola mola*, *Schedophilus ovalis*, *Centrolophus niger*, *Caretta caretta* (Parker *et al.*, 2005), *Dermochelis coriacea* and many other pelagic species feed on gelatinous macroplankton, which is an abundant and easily accessible food source (Arai, 2005).

Anyway, a gelatinous body may allow survival in low food concentrations typical of open oceans (Harbison, 1992; Acuna, 2001).

Moreover, by acting as a floating gelatine substratum in the Mediterranean Sea, the jellyfishes capture and agglutinate suspended organic matters, thereby slowing down the sinking process. Hence, they can enhance, together with microbiota, the trophic potential of the open sea environment (Jacques, 1989). On the other hand, Cnidaria and Ctenophora play, as predators, an important role in evolution and ecology of small zooplankton and early pelagic stages of many marine species (Boero *et al.*, 2005).

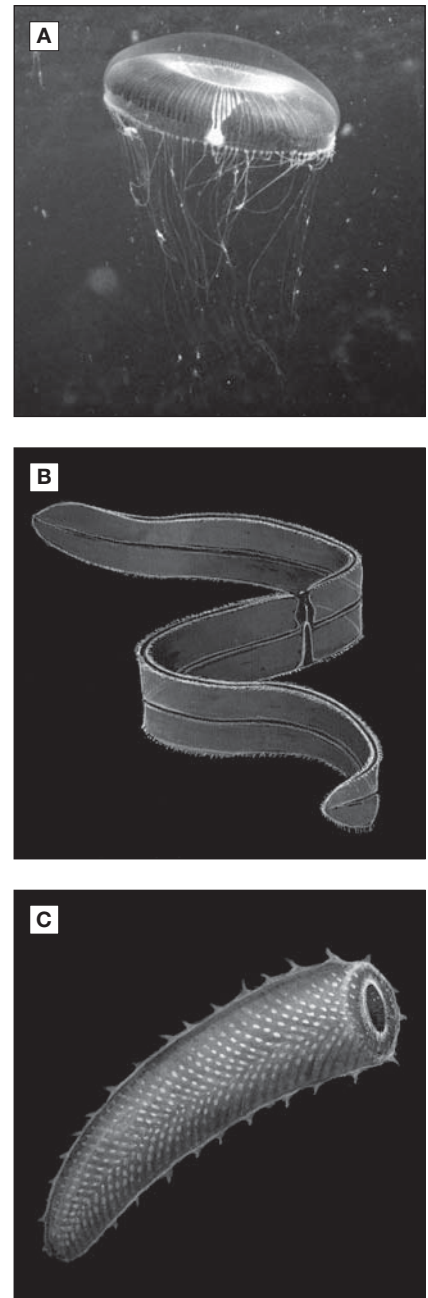


Fig. 31 (see color plate p. 84):

A) Cnidaria, *Aequorea forskalea*. Photo: Olivier Le Corre.

B) Ctenophores, *Cestum veneris*.

C) Urochordata (tunicates), *Pyrosoma* sp.

Small mesopelagic fishes (Fig. 32)

Lanternfishes (families: Myctophidae and Neoscopelidae) are ubiquitous and species-rich, with approximately 249 species grouped in 30 genera. Up to half of fish larvae collected in the open ocean are Myctophid fishes: this indicates that they may have the greatest biomass of all vertebrate families.

Myctophids are often a major element in the deep scattering layer and they are key members of the oceanic food web, because they are the prey of some commercially important and protected pelagic species such as swordfish, tuna and cetaceans. Most Myctophids exhibit a diel vertical migration between the mesopelagic and epipelagic zones, feeding on zooplankton in the upper 200 m depth.

The proximity of the deep-sea basins to coastal and epipelagic waters increases the probability of interaction of these abundant fishes with a variety of other organisms. The forage role of Myctophids, Gonostomatids, Sternoptychids and Chauliodontids make them a vital link between the zooplankton community and the larger vertebrate predators. These small mid-water fishes, especially lanternfishes, appear to occupy a position in the trophic structure of offshore basin waters similar to that occupied by northern anchovy in more inshore, shallower pelagic waters.

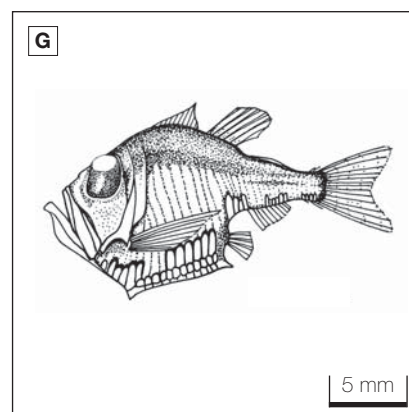
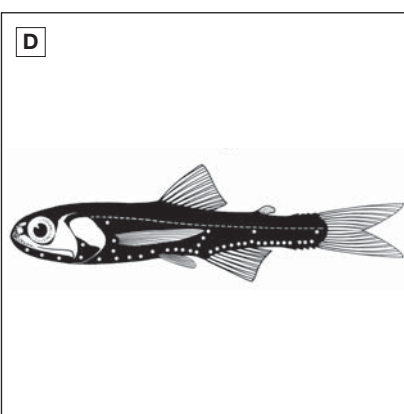
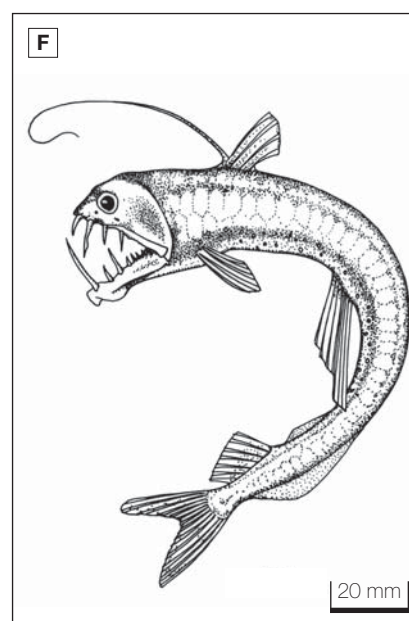
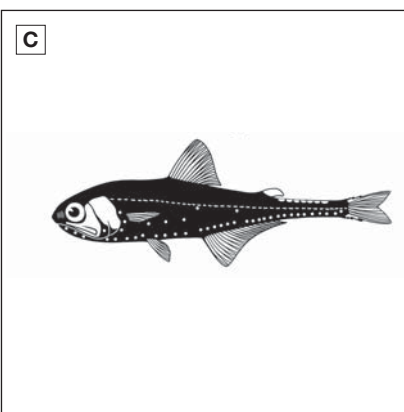
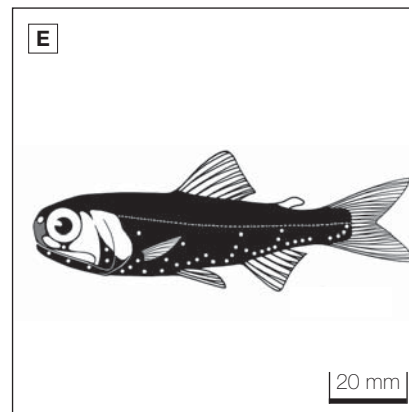
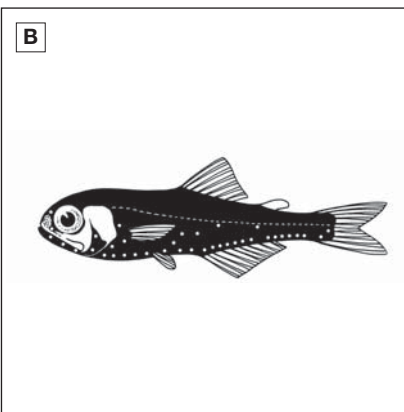
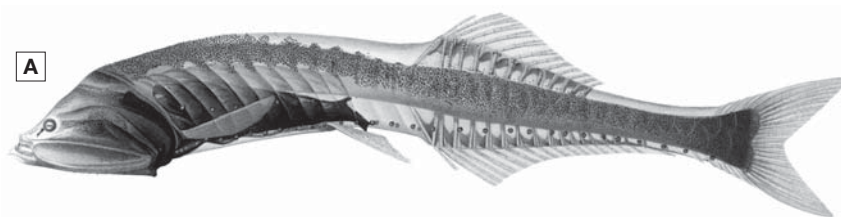


Fig. 32: Mesopelagic fishes.

A) Gonostomatidae: *Cyclothone* sp.
(from Zugmayer, 1911).

(See color plate p. 84) ;

Myctophidae,

B) *Benthosema glaciale*;

C) *Gonichthys cocco*;

D) *Ceratoscopelus maderensis*;

E) *Diaphus* sp.;

F) Chauliodontidae: *Chauliodus sloani*;

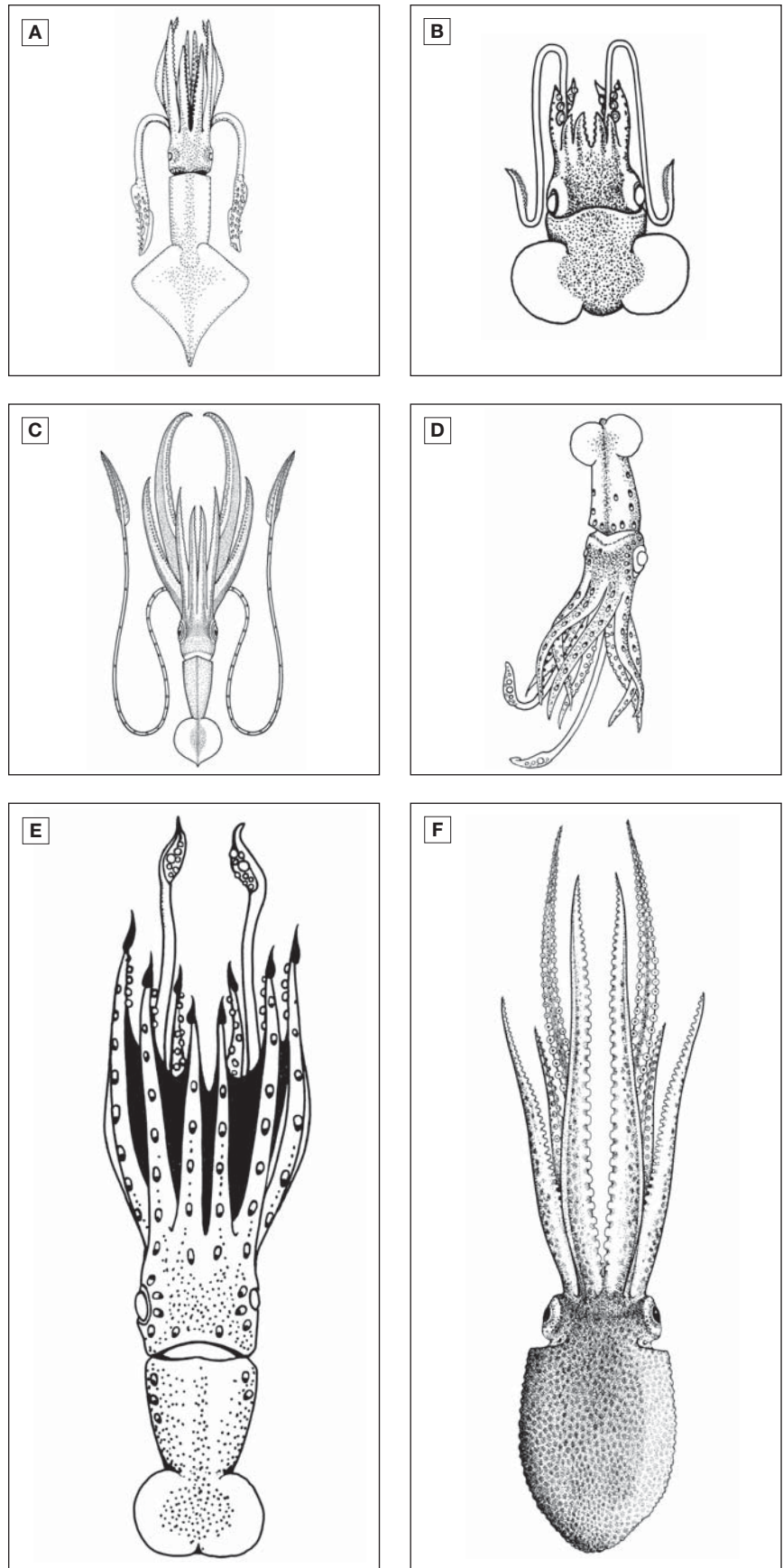
G) Sternoptychidae: *Argyropelecus hemigymnus*.

Mesopelagic Cephalopods (Fig. 33)

The apparently large biomass of cephalopods in the global oceans has generated worldwide interest for its importance in marine food webs, and to major international and regional fisheries. Commercial fisheries globally take up to 3 million tonnes of cephalopods annually, of which about 3% is landed in Mediterranean. This quantity has increased steadily over the last 30 years. During the same period of time, improved methods of species identification and size estimation of the cephalopods taken in the diet of many marine predators have suggested that total removal by predators is at least 100-fold greater than human fisheries. Rapid advances have been made in understanding key life-cycle processes of cephalopod development, feeding, growth, reproduction, and mortality- as well as interactions between these biotic factors and the physical environment. The studies mentioned above have shown that cephalopods may reach large individual body sizes and are extremely fast growing. Some important factors explaining their high growth rates are their exclusively predatory feeding habits and high growth efficiency (food conversion). They do not seem to attain asymptotic adult size before reaching reproductive maturity. Coastal cephalopods breed during a short period of time and die shortly afterwards. Essentially, they are annual species in which there is little overlap between generations. Thus, the biomass coming from any species is likely to be available to predators and fisheries for only a limited period of time (Boyle, 2002).

Fig. 33:

- A) *Ancistroteuthis lichtensteini*, DML 30 cm;
 - B) *Heteroteuthis dispar*, DML 3.5 cm;
 - C) *Chiroteuthis veranyi*, DML 20 cm;
 - D) *Histioteuthis reversa*, DML 20 cm;
 - E) *Histioteuthis bonnellii*, DML 33 cm;
 - F) *Ocythoe tuberculata*, DML 30 cm.
- DML: dorsal mantle length.



Pelagic birds (Fig. 34)

There are at least 13 species of marine birds in the Mediterranean which depend on marine resources, feed exclusively on marine preys and breed only on islands or the coastline (more restrictive than "seabirds"). They belong to the Procellariidae, Hydrobatidae, Sulidae, Phalacrocoracidae, Laridae, Sternidae and Alcidae families. Among them eight are endemic. Zotier *et al.* (1999) have estimated the population size for the species of the Alcidae family by observing that the total biomass and species diversity is lower in the Mediterranean than in the near Atlantic. The eastern Mediterranean hosts a lower number of marine bird taxa than the more productive western part. Species which mainly occur in the western and southern part of the Mediterranean migrate through the Straits of Gibraltar to spend winter in the southern Atlantic, while those species inhabiting the northern coastal basin of the Tyrrhenian and Balearic Seas are composed of less pelagic breeding species, that rear chicks during the productive season. The Mediterranean bird community includes large-body species (Cory's shearwater, *Calonectris diomedea*), breeding in large colonies in the central basin and foraging on the summer thermal front area. There are also small-body pelagic species (European storm petrel, *Hydrobates pelagicus*), which are present in small numbers throughout the western basin and which find food along the continental shelf. In particular, one species, the Sandwich tern (*Sterna sandvicensis*), is strictly dependent on an estuarine environment. Three species, shag (*Phalacrocorax aristotelis desmarestii*), Audouin's gull (*Larus audouinii*) and medium-sized pelagic Mediterranean shearwater (*Puffinus yelkouan mauretanicus*) are mainly confined to the productive northern basin. They are the most typical Mediterranean species in terms of endemism, being dependent on its resource dynamics.

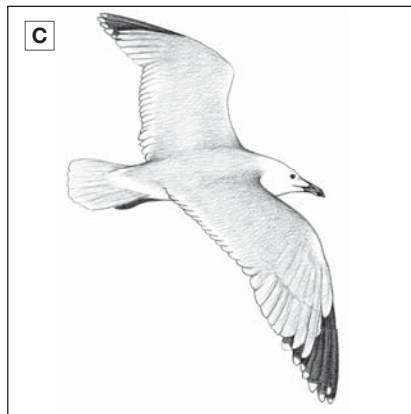
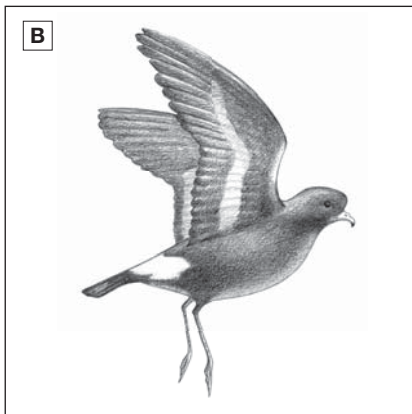
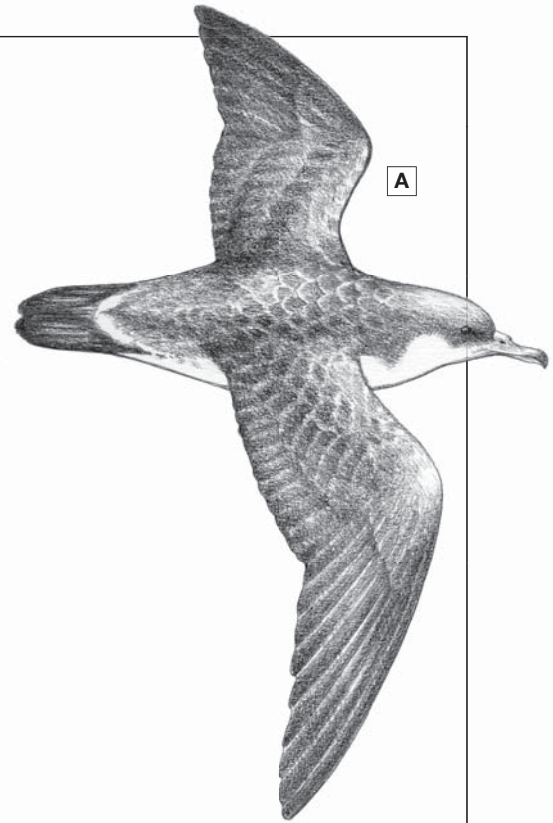


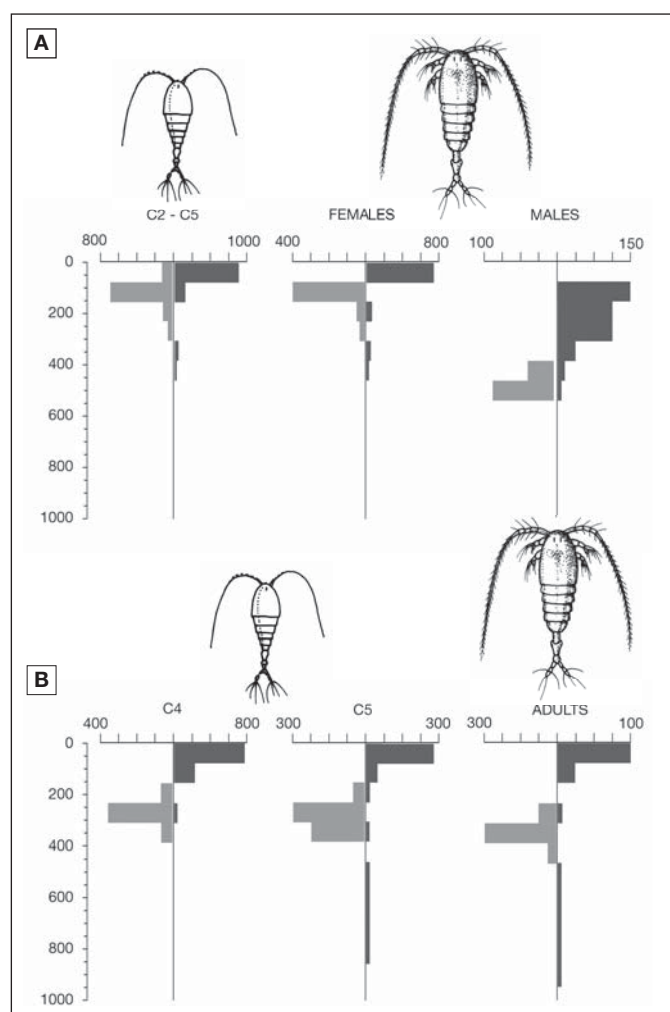
Fig. 34:

- A) *Calonectris diomedea*,
- B) *Hydrobates pelagicus*,
- C) *Larus audouinii*,
- D) *Puffinus yelkouan mauretanicus*,
- E) *Sterna sandvicensis*.

6.4. PELAGIC SPECIES COMPOSITION WITHIN THE WATER COLUMN, AS SEEN THROUGH RESEARCH SAMPLES AND THROUGH FISHERY.

Seasonal variability in abundance and (specific) species composition of the zooplankton community is relatively well documented for the western Mediterranean Sea. Available data are based on net sampling, collected monthly (Franqueville, 1971) and on a short-term scale, in order to investigate the effect of exogenous factors (i.e. physical forcing) on the vertical (diel) and *ontogenetic* (during development from egg to mature) migration of zooplankton (Andersen *et al.*, 2001a; Andersen *et al.*, 2001b; McGehee *et al.*, 2004; Warren *et al.*, 2004).

According to results of studies on the Zooplankton community in the open NW Mediterranean, *Calanus helgolandicus*, *Pleuromamma gracilis* and *Pleuromamma abdominalis* are the most abundant copepod species (Andersen *et al.*, 2001a). *C. helgolandicus* performs seasonal downward migration from surface layers (0-70m depth) in late spring, down to deeper waters (700-1000m) in July (Andersen *et al.*, 2001a). Adult *P. gracilis* and *P. abdominalis* both show a clear vertical (diel) migration and the latter also perform an ontogenetic migration, as the younger developing stages migrate within a shallower depth range than adults (Fig. 35).



Numerous micronekton species (euphausiids, mysids, decapod crustaceans and fishes) are known to undergo diel vertical migration (DVM) and much information on this phenomenon can be found in literature. Vertical distributions of micronekton in the Northwestern Mediterranean Sea have been investigated by Casanova (1970, 1977), Franqueville (1970, 1971) and Goodyear *et al.* (1972) using non-closing nets and sampling with large depth intervals. The development of techniques, such as multiple opening/closing net systems that subdivide long tows into many consecutive sub-samples, has made it possible to describe the vertical distribution of these organisms more accurately (Andersen and Sardou, 1992).

Labat and Cuzin-Roudy (1996) have described population dynamics of the northern krill *Meganyctiphanes norvegica* in the Ligurian Sea. Here, this euphausiid is the primary food source of many predator species (e.g. tuna, fin whales, basking shark). A Bimodal length frequency distribution was observed for the most of the samples, except for the first months of the year. The mode corresponding to the adults was present throughout the annual cycle, while the first occurrence of juveniles was recorded in March. Temporal changes in macroplankton and micronekton show maximum abundance in spring and minimum in the period June-September (Andersen *et al.*, 2001a). Marked changes in euphausiid populations can be due to the differences in diet among species (Mauchline, 1980): the omnivorous *M. norvegica* decrease in abundance from April while the carnivorous *Nematoscelis megalops* is present in higher numbers from April-May.

Young stages of the two euphausiid species above seem to be non-migrant, remaining (in high densities) in the upper 150m of the water column during day and night, while the adults perform very large DVM.

The Euphausiid community also shows differences between the western and eastern basins. From a set of Isaac-Kidd Midwater Trawl (IKMT) night collections taken at stations throughout the Mediterranean Sea, a faunal similarity analysis of the euphausiid community has shown differences in species composition, as well as in vertical distribution, between geographical areas. Although most species were widespread, three distinct patterns of abundance were apparent: *Euphausia krohnii*, *Nematoscelis megalops*, *Meganyctiphanes norvegica*, and *Stylocheiron abbreviatum* predominated in western basin areas west of the Tyrrhenian Sea; *Euphausia hemigibba*, *Thysanopoda aequalis*, and *Stylocheiron longicorne* predominated in the Tyrrhenian Sea and eastern Mediterranean Sea; *Euphausia brevis* and *Stylocheiron suhmii* predominated in the eastern Mediterranean Sea (Fig. 36).

Fig. 35: Vertical day and night distribution of two Copepod species.
A) *Neocalanus gracilis* (C2-C4 and C5 copepodite stages).
B) *Pleuromamma abdominalis* (C4 and C5 copepodite stages).
Frequencies are in n. of specimens/m³.

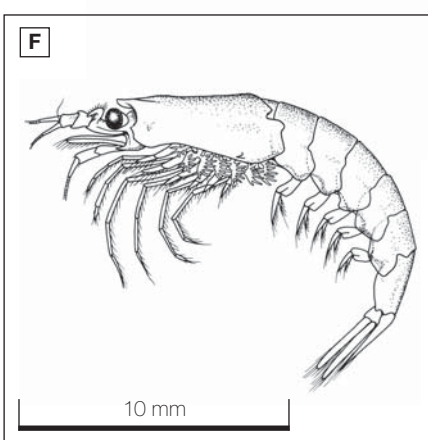
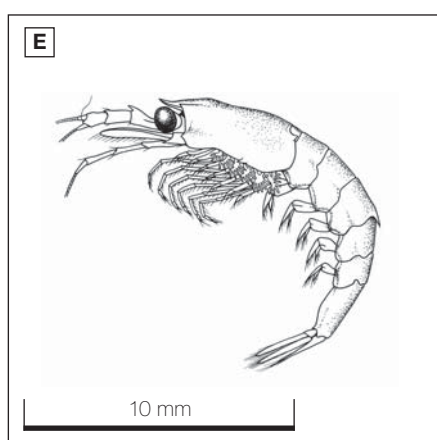
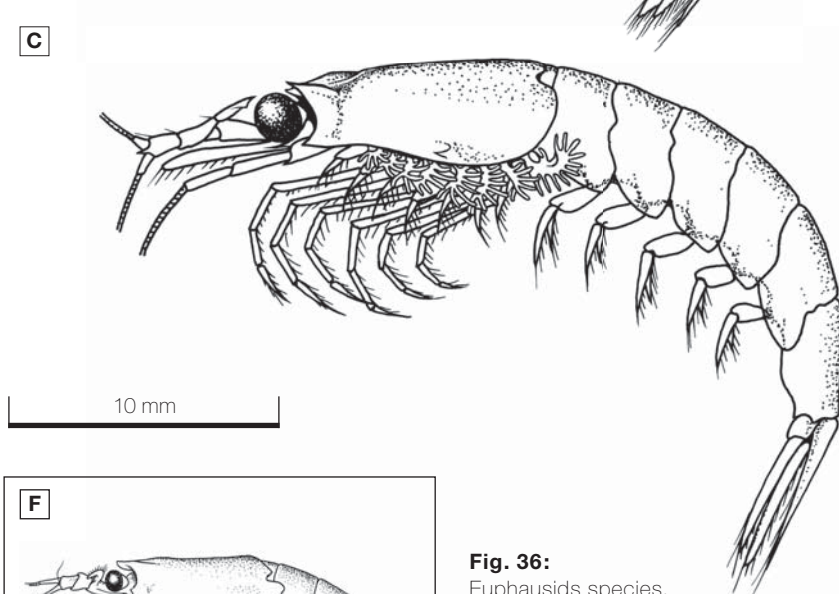
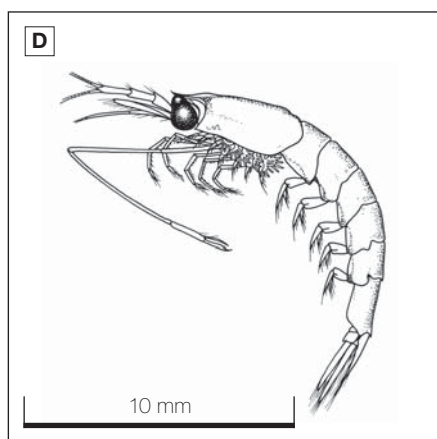
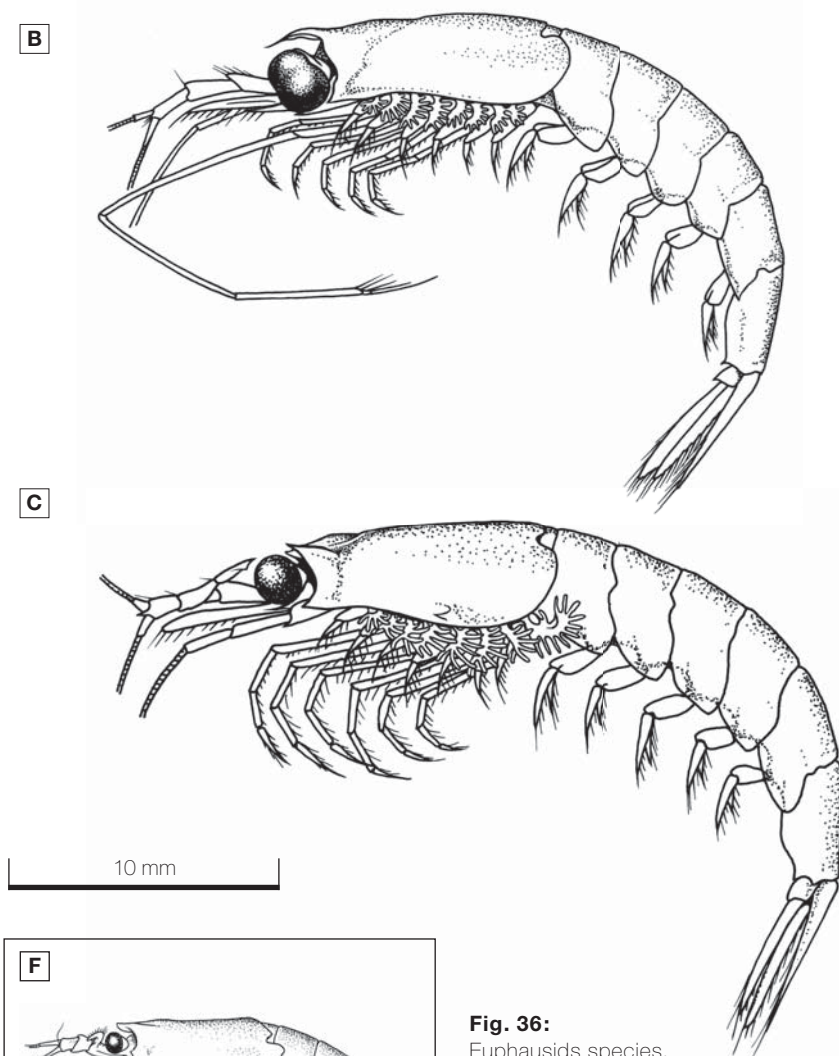
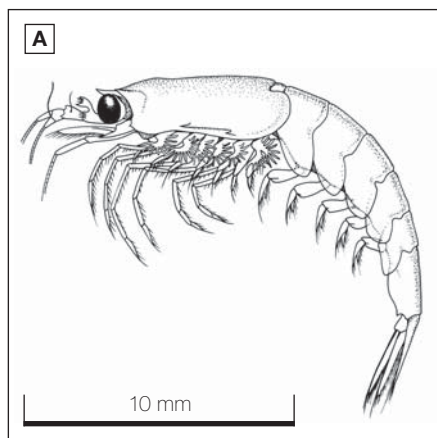
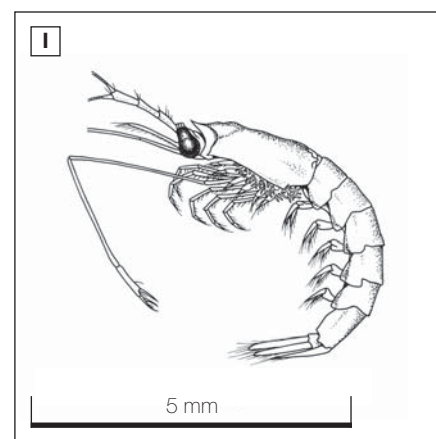
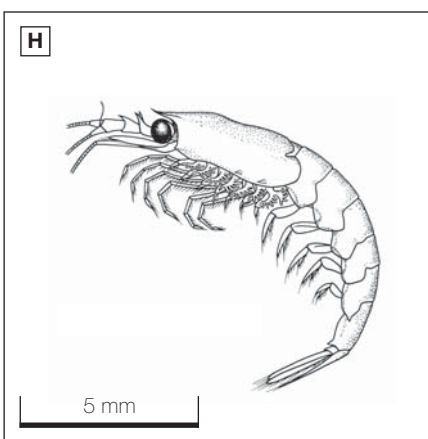
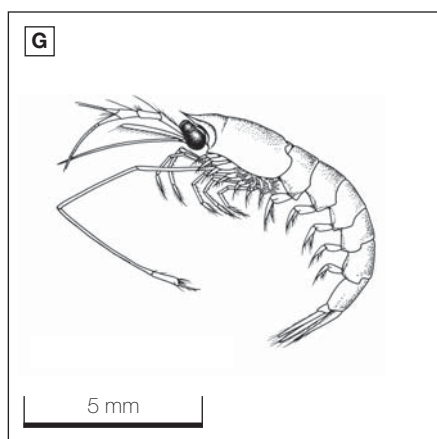


Fig. 36:
Euphausiids species.
A) *Euphausia krohnii*,
B) *Nematoscelis megalops*,
C) *Meganyctiphanes norvegica*,
D) *Stylocheiron abbreviatum*,
E) *Euphausia hemigibba*,
F) *Thysanopoda aequalis*,
G) *Stylocheiron longicorne*,
H) *Euphausia brevis*,
I) *Stylocheiron suhmii*.



Tyrrhenian Sea fauna at the time of the collections was more similar to eastern Mediterranean areas than to most other areas in the western basin. The degree of similarity was dependent, to some extent, on the depth at which the samples were collected. Anyway, the euphausiid species composition found above 150 m at night-time in this area was more similar to eastern basin areas, while the composition at larger depths rather resembled that of the rest of the western basin. Comparison of euphausiids collected at three points in the Balearic Sea, over a period of 60 years, shows greater similarity in species composition within the area than between adjacent areas in the western Mediterranean Sea (Wiebe and D'Abramo, 1972).

Eucopia unguiculata (Fig. 37) was almost the only mysid species caught in the samples carried out by Andersen and Sardou (1992) in the NW Mediterranean. It was of the same order as that of the most numerous euphausiid species, *N. megalops*. During the day, *E. unguiculata* was found between 550 m and 980 m (greatest sampling depth) below surface level, with maximum abundance in the 700-850 m interval. At night, the species migrated upwards in the water column, up to 350 m depth.

In the same study, Andersen and Sardou (1992) found four species of Crustacea Decapoda and fifteen species of fish. Four species of Crustacea Peneidea (*Gennadas elegans*, *Sergestes arcticus*, *Sergia robusta* and *Sergestes vigilax*), and three species of Crustacea Caridea (*Acanthephyra pelagica*, *Pasiphaea multidentata* and *Pasiphaea sivado*) (Fig. 38) were identified in the catches. However, only *G. elegans* (even though still with lower densities among micronekton) was abundant enough in the samples to allow a description of its vertical distribution. During the day, this species was found at depths between 550 and 980 m, with maximum density in the 700-850 m interval, while at night it extended upwards throughout the entire 0-980 m water column.

In the Mediterranean Sea, during the early 'seventies, investigations on jelly macroplankton (siphonophores, hydromedusae and pyrosomids, see box *Jellyfishes*) were essentially conducted with non-closing nets (Casanova, 1970; Franqueville, 1970, 1971) and in coastal areas (Palma, 1985). Franqueville (1971) began some direct observations with a limited number of dives in a manned submarine.

One of the most detailed studies on (DVM) of siphonophores in the Mediterranean is provided by a series of eight submersible dives performed by Laval *et al.* (1989). The DVM of *Solmissus albens* (Fig. 39), the most numerous narcomedusa in the western Mediterranean (endemic to the Mediterranean Sea), was first described by Benovic (1973). In this area, there are two existing detailed studies, by Mills and Goy (1988) and Laval *et al.* (1989), both based on submersible dives.

Andersen *et al.* (1992) give a detailed description of gelatinous macroplankton vertical distributions and diel migrations in the 0-1000 m water column in the Northwestern Mediterranean Sea. The three siphonophores *Abylopsis tetragona*, *Chelophyes appendiculata* and *Lensia conoidea*, one hydromedusa (*Solmissus albens*) (Fig. 39) and one tunicate (*Pyrosoma atlanticum*) are the most abundant. All five species performed extensive diel

vertical migration, most remarkable in *A. tetragona*, *S. albens* and *P. atlanticum*, where the major part of the population migrated as a compact unit. Highest migrating amplitude is seen in *P. atlanticum*, with a mean of 515 m. The migration pattern of *L. conoidea* was more complex. Its distribution during daytime was bimodal and at night part of the population ascended towards the surface, while the other part appeared to migrate downwards around 50 m. The migratory cycles presented a clear diurnal symmetry.

Studies of mesopelagic (related to water depths around 200-900 m) fish have long a tradition in the Mediterranean, with important contributions being presented as early as 1918 (Taning, 1918); however, quantitative data is still meager. Abundance was estimated through IKMT sampling by Goodyear *et al.* (1972), while Chapman *et al.* (1975) carried out acoustic studies. The resulting pattern indicates that the biomass is low (2.45×10^8 t), and lower in the eastern than in the western basin (Gjøsaeter and Tawaguchi, 1980). More recently, Lam and Pauly (2005) mapped the global biomass of mesopelagic fish and revised the estimates for the Mediterranean Sea in 3 million tons. Concentration in the western basin is 3 g/m², in the central 0.5 g/m² and in the eastern Mediterranean about 0.1 g/m² (Fig. 40).

Goodyear *et al.* (1972) also found that *Cyclothone braueri* gave the highest catch rates in all areas of the Mediterranean. Among the most important myctophids they found *Benthosema glaciale*, *Ceratoscopelus maderensis* and *Gonichthys coccoi*.

In a study by Aboussouan (1971), collecting fishes off the Provence coast using an IKMT, Sternoptychidae (*Argyropelecus hemigymnus*) made up 16% of the catches, Gonostomatidae (mostly *Cyclothone braueri*) 27%, and Myctophidae (most *Benthosema glaciale* and *Diaphus raphinesquei*) (Fig. 18) only 8%. Dekhnik and Sinyukova (1966) however, studying fish larvae, found that Gonostomatidae (*Cyclothone* and *Vinciguerria*) dominated, followed by Myctophidae (*Diaphus holti* and *Ceratoscopelus maderensis* in highest densities).

Among the fish species identified in IKMT catches performed by Andersen and Sardou (1992) in the Ligurian Sea, only *Cyclothone braueri*, *Cyclothone pygmaea* and, to a smaller extent, *A. hemigymnus* (Fig. 41) occurred in sufficiently large numbers, and showed a sufficiently regular pattern to allow for analysis of their vertical distributions. Nine micronektonic species were described in the study above, among which *C. braueri* and *C. pygmaea* largely dominated in numbers with *A. hemigymnus* proving to be the less abundant. *C. braueri* was found in significant numbers in the water layer at 350-700 m depth, with highest density in the 350-550 m interval during both night and day. Vertical distribution did not show any evidence for a DVM.

A. hemigymnus occurred daytime at depths between 250 and 550 m, with a clear maximum abundance in the 350-450 m stratum. At night, its vertical range shifted upwards, with maximum densities found between 150 and 350 m.

Another interesting picture of mesopelagic fauna can be provided using a larger IKMT (Fig. 42). During the CNR-ISSIA Open Sea

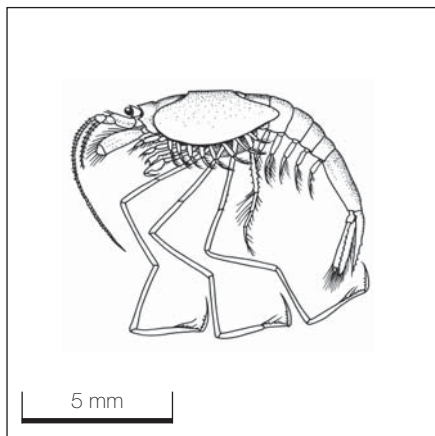
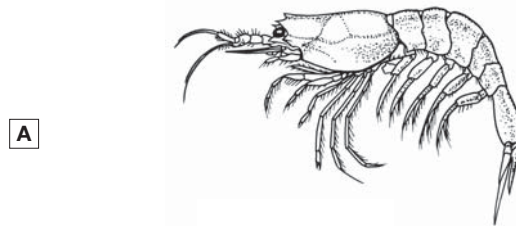


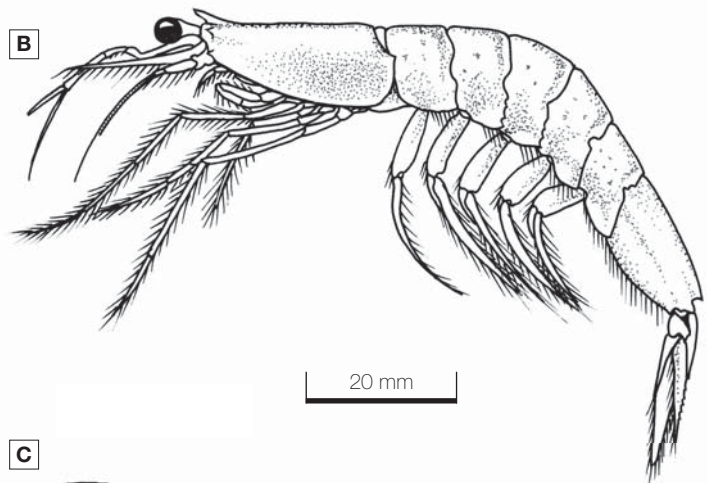
Fig. 37: Pelagic Mysid species *Eucopia unguiculata*.

Fig. 38 (see color plate p. 84):
Pelagic Decapod Crustaceans.

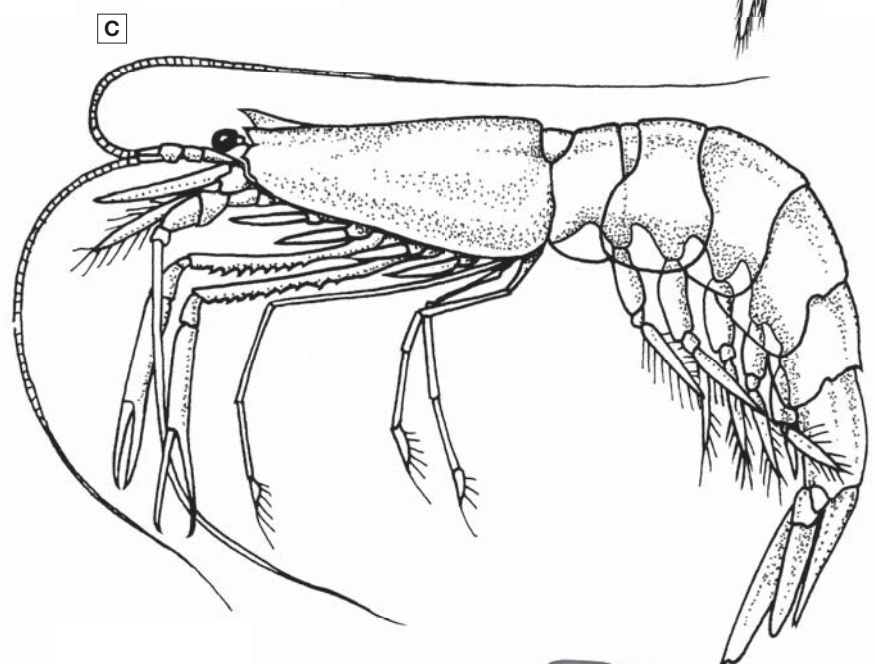
- A) *Gennadas elegans*,
- B) *Sergia robusta*,
- C) *Pasiphaea multidentata*,
- D) *AcanthePHYra pelagica*.



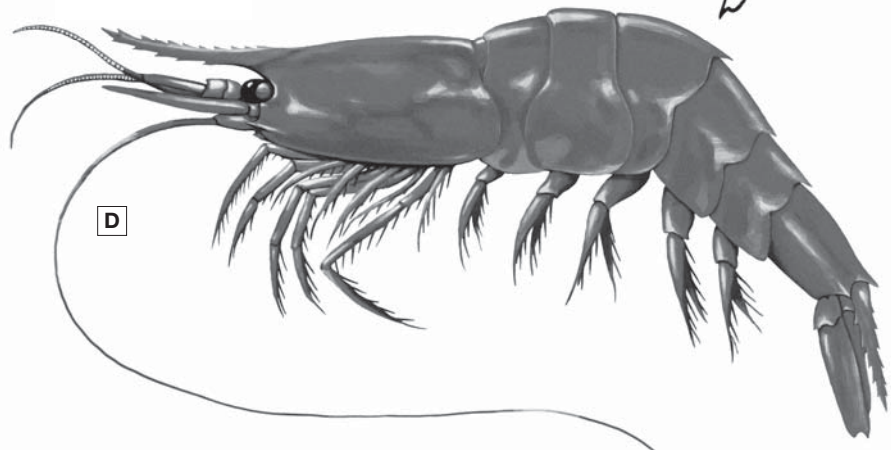
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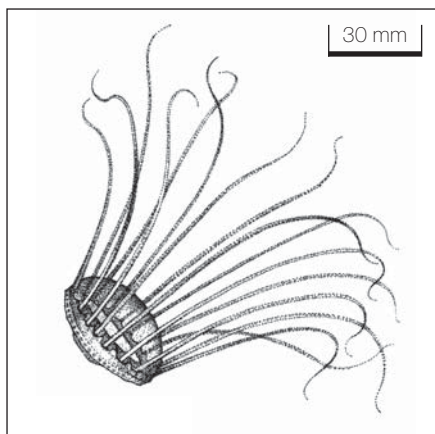


C



D

Fig. 39: Hydromedusa:
Solmissus albescens.



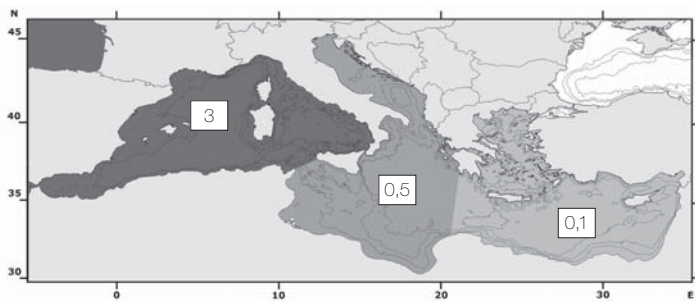


Fig. 40: Mesopelagic fish density (g/m²) in the Mediterranean Sea (From Lam and Pauly, 2005).

Laboratory ODAS campaign, various seasonal samplings were carried out at depths between 200 and 1000 m in the Ligurian Sea. Orsi Relini and Relini (1997) describe the composition of the samples by major systematic groups, listing more than 60 species of fishes, crustaceans and cephalopods (Tab. 1). During the same research project, large pelagic species were also observed at the surface around the oceanographic ODAS buoy (e.g. *Balaenoptera physalus*, *Stenella coeruleoalba*, *Globicephala melas*, *Grampus griseus*, *Thunnus thynnus*, *Coryphaena hippurus*, *Mola mola*).

Fishery can provide another insight into pelagic life. Fish generally classified as small pelagic species, e.g. anchovy (*Engraulis encrasicolus*), sardines (mainly *Sardina pilchardus* and *Sardinella aurita*), mackerels (*Scomber scombrus*, *Scomber colias*), horse mackerels (*Trachurus* sp.) and saury (*Scomberesox saurus*) (Fig. 43), are mainly caught in the *neritic* and *epipelagic* zones. Large pelagic species, however, migrate far from the coast, mainly over deeper bottoms. The *neritic* zone extends from low-tide sea surface level to the edge of the continental shelves. The *epipelagic* zone encompasses water masses from the surface down to ~200 m, where photosynthetic production can occur.

The target species of purse seiners, pelagic long-lines and other oceanic fishing gear are tuna (*Thunnus thynnus*) and tuna-like species (*Thunnus alalunga*, *Euthynnus alletteratus*, *Katsuwonus pelamis*, *Sarda sarda*, *Auxis rochei*) (Fig. 44), swordfish (*Xiphias gladius*), spearfishes (*Tetrapturus belone*, *T. albidus*) (Fig. 45), dolphin fish (*Coryphaena hippurus*, *C. equiselis*) and sharks (*Prionace glauca*, *Alopias vulpinus*, *Isurus oxyrinchus*) (Fig. 47). Other oceanic target species such as *Brama brama*, *Centrolophus niger*, *Schedophilus ovalis*, *Luvarus imperialis*, *Ruvettus pretiosus* (Fig. 46) and the shark *Lamna nasus* are less frequently present in the catches. Among the species caught accidentally, the largest bonyfish *Mola mola* (weighting up to 2 t), the devilfish *Mobula mobular* (fin diameter up to 6 m width) (Fig. 30), the basking shark *Cetorhinus maximus* (9.75 m the maximum recorded length), the pelagic stingray *Pteroplatytrygon violacea* (Fig. 47), the mesopelagic opah *Lampris guttatus*, *Luvarus imperialis* (Fig. 46) and sea turtles, mainly *Caretta caretta* (Fig. 30) and *Dermochelis coriacea* can be found (Fig. 47).

Osteichthyes		%
Gonostomatidae	<i>Cyclothone pygmaea</i>	23.47
	<i>Cyclothone braueri</i>	70.02
	<i>Gonostoma denudatum</i>	+
Photichthyidae	<i>Ichthyococcus ovatus</i>	0.02
	<i>Vinciguerria attenuata</i>	0.02
	<i>Vinciguerria powenae</i>	0.05
Sternoptychidae	<i>Argyropelecus hemigymnus</i>	3.96
	<i>Maurolucus muelleri</i>	+
Astronesthidae	<i>Borostomias antarcticus</i>	+
Melanostomiatidae	<i>Bathophilus nigerrimus</i>	0.01
Stomatidae	<i>Stomias boa</i>	0.02
Chauliodontidae	<i>Chauliodus sloanei</i>	0.37
Paralepididae	<i>Lestidiops jayakari</i>	0.28
	<i>Lestidiops sphyrenoides</i>	
	<i>Notolepis rissoi</i>	
	<i>Paralepis coregonoides</i>	
	<i>Sudis hyalina</i>	
Evermannellidae	<i>Evermannella balbo</i>	+
Myctophidae	<i>Electrona rissoi</i>	+
	<i>Hygophum hygomii</i>	+
	<i>Hygophum benoiti</i>	0.32
	<i>Benthosema glaciale</i>	0.42
	<i>Myctophum punctatum</i>	0.13
	<i>Symbolophorus veranyi</i>	0.07
	<i>Lobianchia dofleini</i>	0.02
	<i>Diaphus rafinesquei</i>	0.02
	<i>Diaphus holti</i>	+
	<i>Diaphus metopoclampus</i>	+
	<i>Lampanyctus crocodilus</i>	0.37
	<i>Lampanyctus pusillus</i>	0.04
Argentinidae	<i>Ceratoscopelus maderensis</i>	0.27
	<i>Notoscopelus kroeyeri</i>	+
	<i>Notoscopelus elongatus</i>	+
	<i>Microstoma microstoma</i>	+
Nemichthyidae	<i>Nansenia oblita</i>	+
	<i>Nemichthys scolopaceus</i>	0.01
Trachipteridae	<i>Zu cristatus</i>	+
	<i>Trachipterus trachipterus</i>	+
Regalecidae	<i>Regalecus glesne</i>	+
Zoarcidae	<i>Melanostigma atlanticum</i>	

Crustacea Decapoda		%
Aristeidae	<i>Gennadas elegans</i>	46.3
Penaeeidae	<i>Funchalia villosa</i>	0.13
	<i>Funchalia woodwardi</i>	0.06
Sergestidae	<i>Sergestes arcticus</i>	26
	<i>Sergestes henseni</i>	3.3
	<i>Sergestes sargassi</i>	2.6
	<i>Sergestes vigilax</i>	2.9
	<i>Sergia robusta</i>	2.7
Oplophoridae	<i>Acanthephyra pelagica</i>	2.3
	<i>Acanthephyra eximia</i>	+
Pasiphaeidae	<i>Pasiphaea multidentata</i>	9.3
	<i>Pasiphaea sivado</i>	4.1
Hippolytidae	<i>Ligur ensiferus</i>	+
Mollusca Cephalopoda		
Sepiolidae	<i>Heteroteuthis dispar</i>	21.5
	<i>Stoloteuthis leucoptera</i>	1.07
Enoploteuthidae	<i>Abralia veranyi</i>	1.07
	<i>Abraliopsis pfefferi</i>	2.15
Onychoteuthidae	<i>Onychoteuthis banksi</i>	1.07
	<i>Ancistroteuthis lichtensteini</i>	1.07
Histioteuthidae	<i>Histioteuthis bonnellii</i>	5.4
	<i>Histioteuthis reversa</i>	40.9
Ctenopterygidae	<i>Ctenopteryx sicula</i>	5.4
Ommastrephidae	<i>Todarodes sagittatus</i>	1.07
	<i>Illex coindetii</i>	1.07
	<i>Ommastrephes bartrami</i>	1.07
Cranchiidae	<i>Galiteuthis armata</i>	8.6
Octopodidae	<i>Pteroctopus tetracirrhus</i>	1.7
	<i>Octopus</i> sp.	3.2
Chiroteuthidae	<i>Chiroteuthis veranyi</i>	2.15
n.e.i. Cephalopoda		2.15
	Osteichthyes N = 26932	
	Decapoda N = 7135	
	Cephalopoda N = 93	

Tab.1: Mesopelagic fishes, decapod crustaceans and cephalopods caught by IKMT in the Ligurian Sea and their relative occurrence in the samples (Orsi Relini *et al.*, 1995).

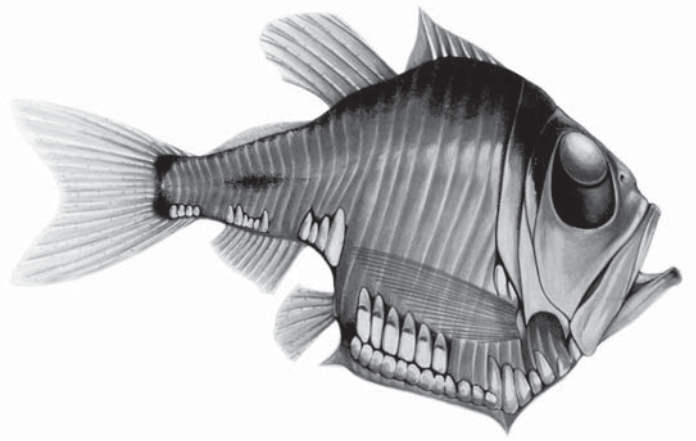


Fig. 41 (see color plate p. 84): *Argyropelecus hemigymnus*.

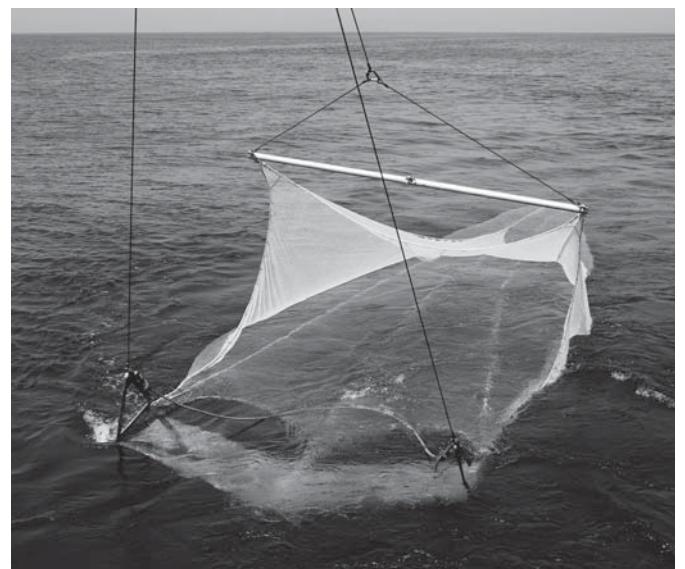


Fig. 42 (see color plate p. 84): An Isaacs-Kidd Mid-water Trawl (IKMT) hauling on board after a mesopelagic tow. Photo: Laure Mousseau, Enseignement UPMC-OOV.

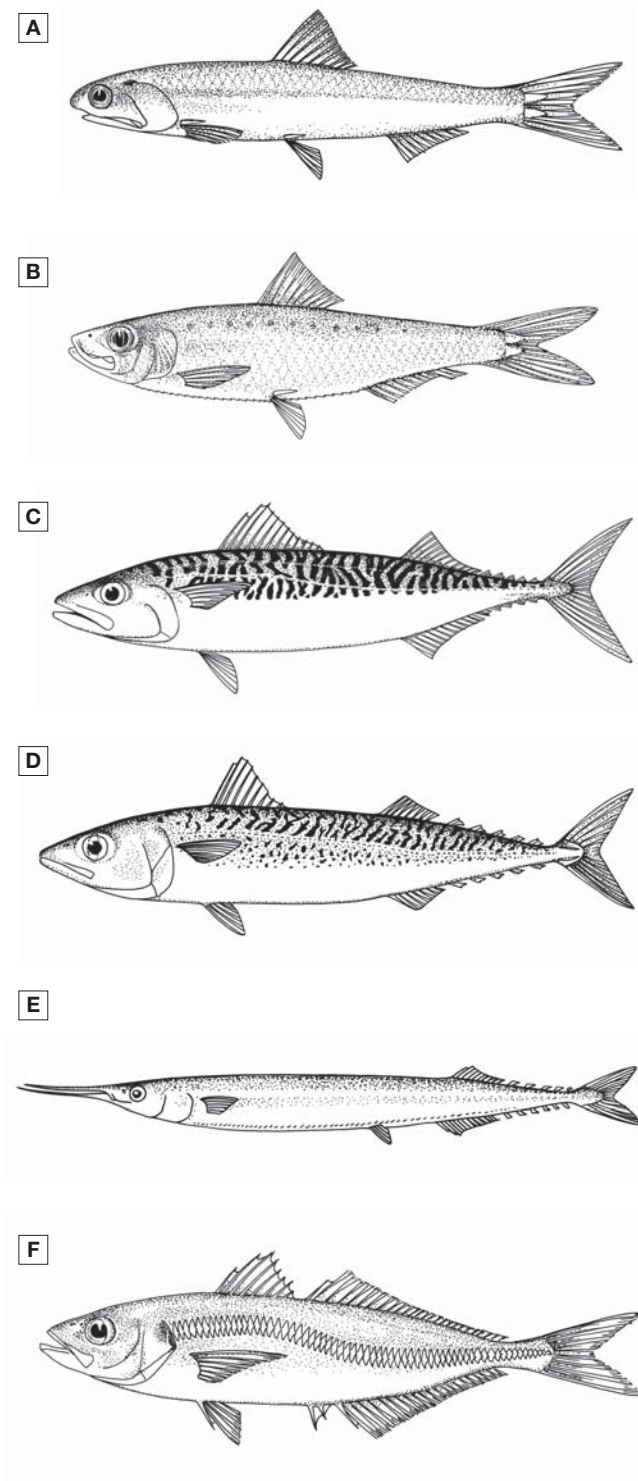


Fig. 43: Small pelagic species:

- A) Anchovy, *Engraulis encrasicolus*, size: common 15 cm;
- B) Pilchard, *Sardina pilchardus*, size: common 20 cm;
- C) Mackerel, *Scomber scombrus*, size: common 30 cm;
- D) Chub mackerel, *Scomber japonicus*, size: common 30 cm;
- E) Saury, *Scomberesox saurus*, size: common 40 cm;
- F) Horse mackerel, *Trachurus* sp., size: common 50 cm.

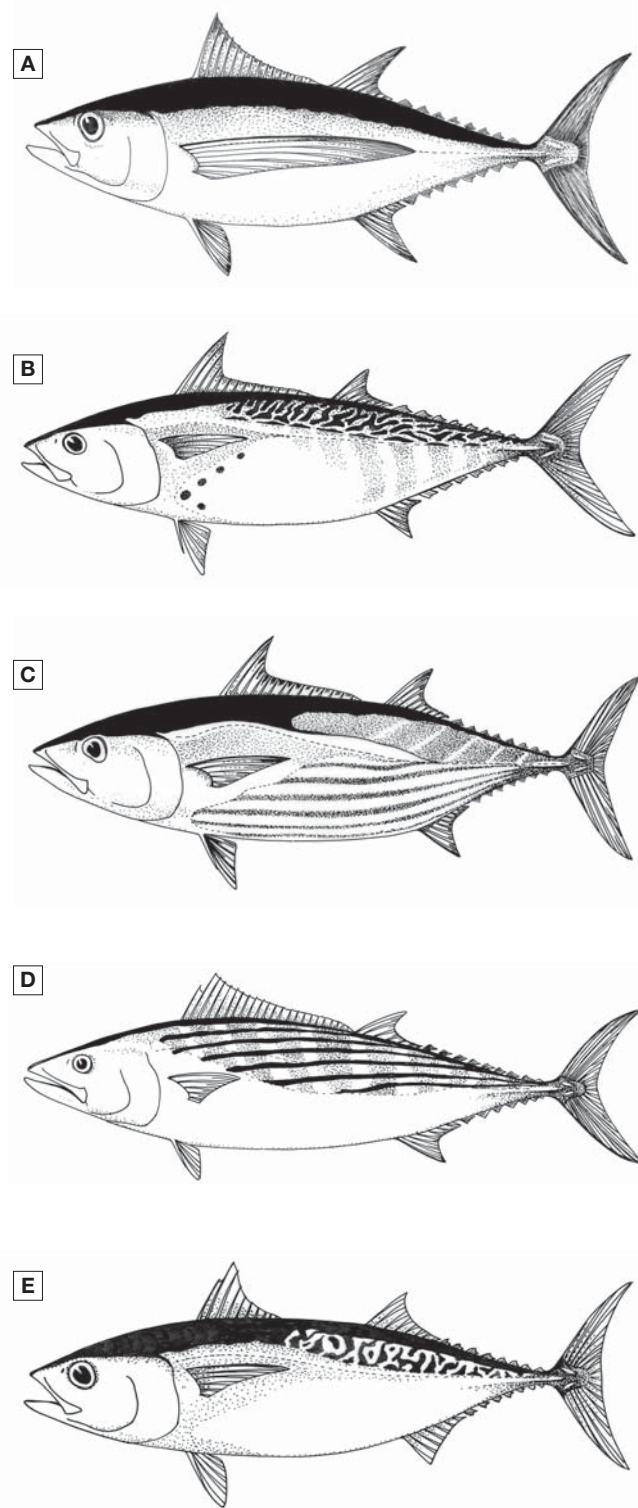
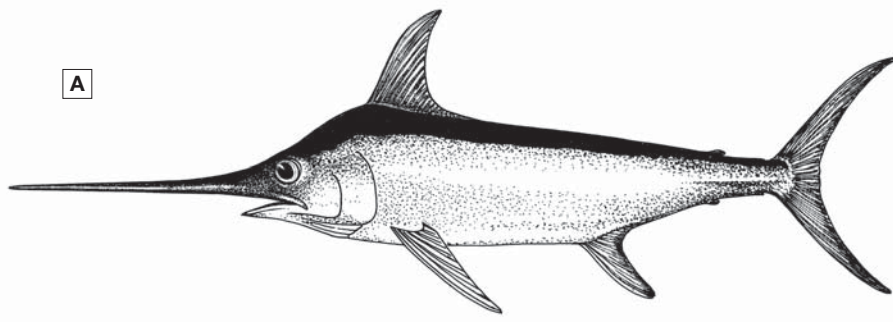
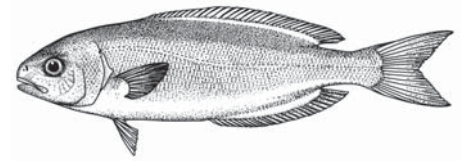


Fig. 44: Tuna-like fish species:

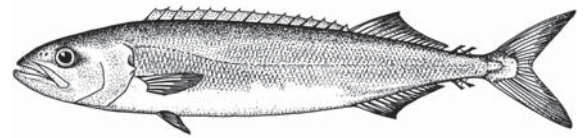
- A) Albacore, *Thunnus alalunga*, size: common 80 cm;
- B) Little tunny, *Euthynnus alletteratus*, size: common 80 cm;
- C) Skipjack tuna, *Katsuwonus pelamis*, size: common 60 cm;
- D) Atlantic bonito, *Sarda sarda*, size: common 65 cm;
- E) Bullet tuna, *Auxis rochei*, size: common 45 cm.



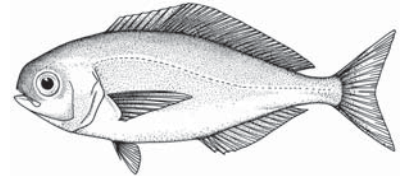
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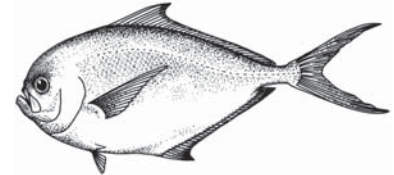
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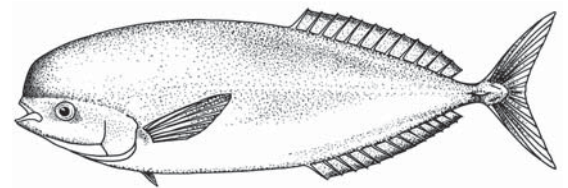
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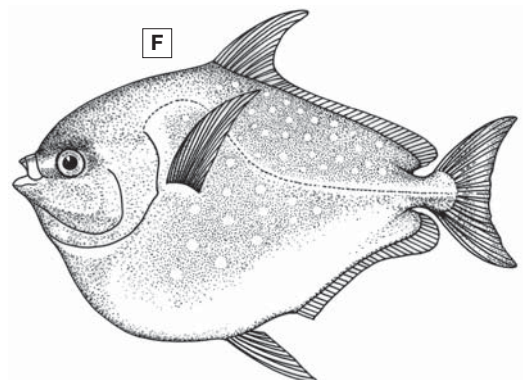


Fig. 45: Broadbill swordfish (Xiphiidae) and billfishes (Istiophoridae).

A) Swordfish, *Xiphias gladius*, size: common 250 cm;

B) Mediterranean spearfish, *Tetrapturus belone*, size: common 150 cm;

C) White marlin, *Tetrapturus albidus*, size: common 250 cm.

Fig. 46: Pelagic and bathypelagic bony fishes.

A) Blackfish, *Centrolophus niger*, size: common 90 cm;

B) Oilfish, *Ruvettus pretiosus*, size: common 150 cm;

C) Imperial blackfish, *Schedophilus ovalis*, size: common 60 cm;

D) Atlantic pomfret, *Brama brama*, size: common 60 cm;

E) Luvar, *Luvarus imperialis*, size: common 150 cm;

F) Opah, *Lampris guttatus*, size: common 120 cm.

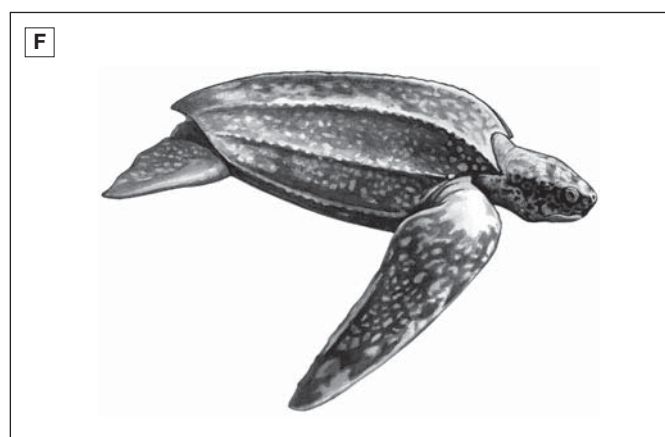
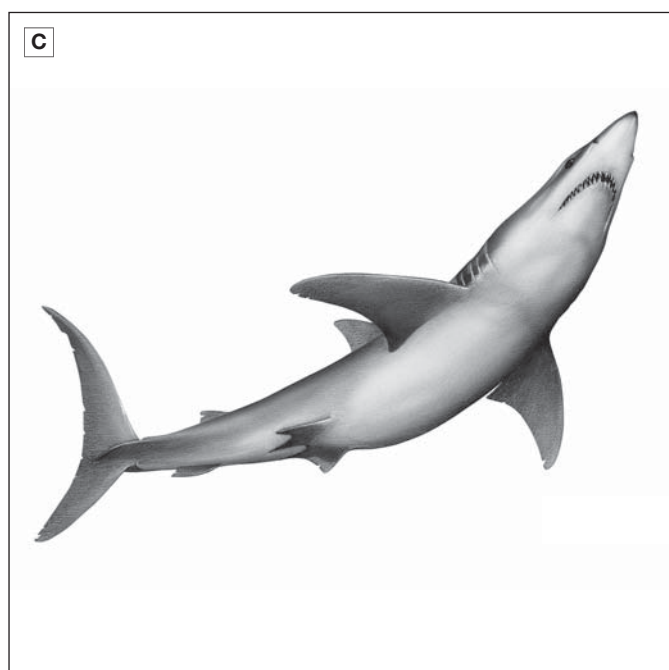
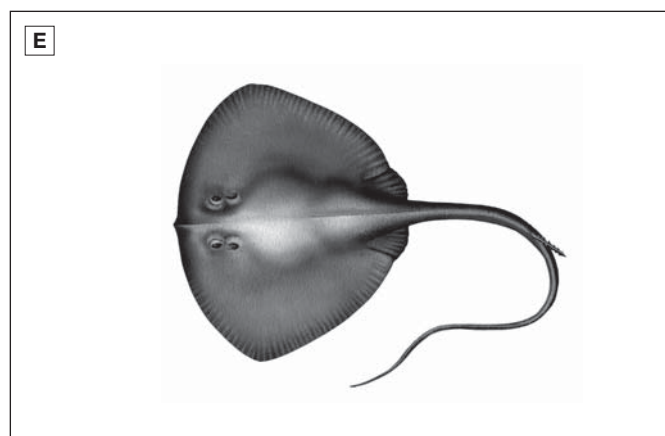
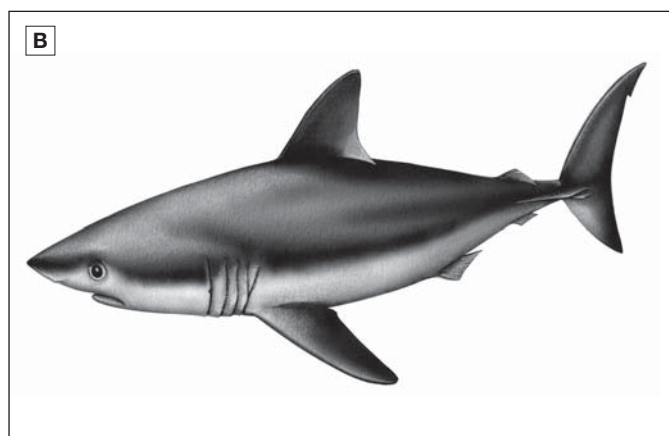
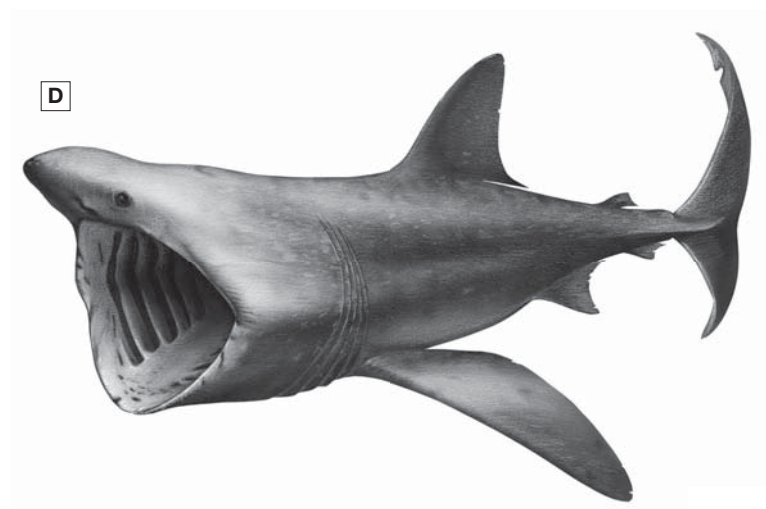
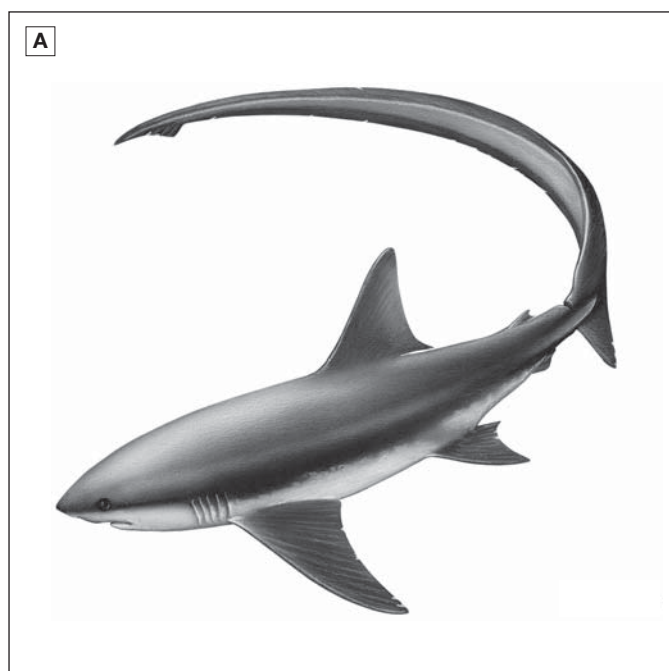


Fig. 47: Pelagic sharks, rays and turtles
(see color plate p. 85):

- A) *Alopias vulpinus*, size: common 400 cm;
 B) *Lamna nasus*, size: common 250 cm;
 C) *Isurus oxyrinchus*, size: common 250 cm;
 D) *Cetorhinus maximus*, size: common 500 cm;
 E) *Pteroplatytrygon violacea*, size: common 150 cm.
 F) *Dermochelys coriacea*, size: common 140 cm.

7. Pelagic food web

7.1. CLASSIC VIEW AND NEW PARADIGM

All life-forms need a supply of energy and nutrients to grow and reproduce. In the ecosystem, the autotrophs are *primary producers*, providing all original energy and organic material at the disposal of heterotrophs (*consumers*). Thus, autotrophs form the base of a *food web*, in which they are grazed by herbivores that are in turn consumed by carnivores. Food webs are divided into *trophic levels*, with primary producers at the first level, herbivores at the second, carnivores at the third, carnivores that eat carnivores at the next, and so on.

Until a few decades ago, marine pelagic food webs were described with only 3 major groups of organisms: algal cells as primary producers, herbivorous mesozooplankton (0.2–20 mm in size) at the second level and fish at the third level. This model is called the *classic food web* or the *herbivorous food web*.

However, this model of marine pelagic food web has been challenged by scientists (Pomeroy, 2001), who demonstrate that there is an alternative carbon flow pathway, from bacteria to protozoa to metazoa. Bacteria use dissolved organic matter (DOM) as substrate, which can enter the pelagic environment from a variety of sources: excretion of dissolved organic carbon (DOC) by algal cells, algal cell lyses, “messy eating” by mesozooplankton or diffusion from faecal pellets. This new food web paradigm has been called the *microbial loop* and, in its original definition, did not contain autotrophs.

Recent models of pelagic food webs link the classic food web to microbial food webs, including nanoplankton and picoplankton.

Today, microbial food webs are accepted as the primary oceanic food webs (Pomeroy, 2001) and in oligotrophic environments (such as the Mediterranean Sea) bacterioplankton can constitute 70–80 % of the total biomass. Hence, bacterial production and respiration are the dominating processes in the ocean waters. The earlier assumptions of a 10% ecological efficiency of each trophic level has been shown to be a poor generalization (Pomeroy, 2001). In certain cases, such as detritus food webs, the passage of material through bacteria can be very inefficient.

However, if the main primary producers are a mixture of microflagellates and autotrophic bacteria, as in the oligotrophic waters, the trophic efficiency of the microbial food web can be significantly higher. The connection between the microbial chain and the metazoan chain is an integral part of a coherent food web which is the principal support of larger metazoans (Rivkin and Legendre, 2002).

Similar processes to those described above seem to drive the energy flux in the Mediterranean Sea, particularly where primary production is minimal due to seasonal fluctuations or water mass characteristics. Carnivorous and herbivorous jelly macroplankton have been found to play an important role directly as trophic links between nanoplankton and larger predators. Picoplankton bacteria and cyanobacteria are eaten by nanoplankton, which are eaten by microplankton as well as meso and macrozooplankton jellyfish (Jacques, 1989).

7.2. FUNCTIONING OF THE PELAGIC TROPHIC WEB

Different types of energy flows can occur in marine ecosystems: *bottom-up control*, where the primary producers control the larger predator, *top-down control*, where predators regulate their prey populations, and *wasp-waist control* exerted by dominant species in both bottom-up and top-down controlled food chains.

Bottom-up control predominates in the oceans, where primary production may act as a large-scale factor that determines the ecosystems' productivity.

As suggested by Ursin (1973): “[fish] stomach contents are a simple function of local prey availability and suitability, this latter often simply being a function of size”. The feeding process in marine food webs can be considered as opportunistic and almost exclusively dependent on prey size. This feeding behaviour implies that predator diets comprise large prey diversity. For instance, fish larvae generally feed at the base of the food web, while as adults, occupying higher trophic levels, they feed at one or several trophic levels below their own.

Hence, considering the number of potential interactions between the different species, trophic levels or age groups, marine food webs appear to have complex and evolving dynamics, operating through multiple and weak trophic interactions between species. This situation has been theoretically proved to favour stability.

It is recognized that certain species play a more important role than others in structuring ecosystems. The most widely-used definition for a keystone species is: one “whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance” (Power *et al.*, 1996). Hence, keystone species affect processes at the community or ecosystem level to a greater extent than would be expected based upon their relative abundance alone (Bond, 1993).

Keystone species are likely to be found near the top of the food chain, although they are not necessarily at the highest trophic levels (Power *et al.*, 1996). Moreover, they are by definition not abundant. They have an impact on other species by means of consumption, competition, etc., as well as by physically modifying habitat characteristics (ecosystem engineering). Ecologists devoted a lot of attention to identifying keystone species in different ecosystems, as it was suggested that the future of conservation management might lie in maintaining keystone species rather than attempting to protect and manage all species (Power *et al.*, 1996, Cury *et al.* 2003).

Although keystone species are not frequently identified in marine ecosystems, they may, in addition to other changes in dominant species, cause major changes to ecosystem structure and functioning through trophic cascades down the marine food web.

Trophic cascades are defined as reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web (Pace *et al.*, 1999). True trophic cascades imply keystone species (Paine, 1980). Trophic cascades result in inverse patterns in abundance or biomass across trophic links in a food web. In pelagic marine ecosystems, alterations of consumer abundance can cascade down food webs to affect the phytoplankton biomass.

In many of the world's productive ecosystems, and particularly in upwelling ecosystems, there is an intermediate trophic level occupied by a limited number of species of small, plankton-feeding pelagic fish, comprising massive populations that are intensively exploited and vary radically in abundance (Cury *et al.*, 2000).

Small mesopelagic fish seem to exert a major control on energy flows, and this has been called *waspy-waist control*. Top-down control of sardine or anchovy on zooplankton is well known, whereas bottom-up control of them on their predator has been noticed. In fact, predatory fishes (such as tuna-like species) suffer from the collapse of their prey (Cury *et al.*, 2000). Once food becomes abundant again, recovery of the depleted predator biomass may be immediate or delayed by short or long periods, highlighting the complex response of the ecosystem towards change.

7.3. SPECIES COMPOSITION AND ABUNDANCE WITHIN THE WATER COLUMN, AS SEEN THROUGH PREDATOR STOMACH CONTENT ANALYSES

A particularly important aspect of gut content analyses is that the results give information on distribution and abundance of pelagic prey species (according to diet specialization and diving performances of the predators) that generally escape every sampling attempt, due to swimming ability, difficulties to attract with bait or catch by means of other fishing techniques. A summary of the result of feeding ecology studies available for the Mediterranean pelagic species shows that prey species composition in gut content analyses adds useful information about pelagic fauna. Clarke (1977) has shown the importance of both qualitative and quantitative differences in the cephalopod species composition in net catches (scientific and commercial purposes), and in the stomach of *teutophagous* (cephalopod eating) cetaceans, respectively. There are also striking differences correlated to cephalopod mean size, as adult squids are poorly represented in net samples. As every predator species feeds differently, and thus samples differently, gut content, together with predator ecology, provides a different window into the pelagic deep-sea environment.

Various Authors have investigated the feeding ecology of large pelagic predators of the Mediterranean Sea. Stomach contents of stranded cetacean specimens have been analyzed by Astruc (2005), Blanco *et al.* (2001), Blanco *et al.* (2000, 2001, 2006), Bello (1992), Carlini *et al.* (1992a, b), Lefkaditou and Pouloupoulos (1998), Orsi Relini and Garibaldi (1992), Orsi Relini and Relini (1993), Öztürk *et al.* (2007), Podestà and Meotti (1991), Pulcini *et al.* (1992), Roberts (2003), Würtz and Marrale (1993) and Würtz *et al.* (1992). Tuna, tuna-like species and swordfish prey have been identified by Bello (1991), Orsi Relini *et al.* (1995), Peristeraki *et al.* (2005), Sarà and Sarà (2007), Sinopoli *et al.* (2004) from specimens obtained from commercial fishery catches. Pelagic shark (*Prionace glauca*) feeding behaviour has been studied by Politi (1991), while Tomas *et al.* (2001) carried out investigations on loggerhead turtle diet. An overall view of pelagic fauna which can be drawn from these studies is given in Fig. 48.

Deep diving predators such as Cuvier's beaked whale (*Ziphius cavirostris*) and sperm whale (*Physeter catodon*) are mostly or exclusively teuthophagous. They feed on deeper mesopelagic and bathypelagic species that live down to a depth of 2000 m. They can thus give us information about cephalopods living in the deeper water layers. Risso's dolphin (*Grampus griseus*), which is also teuthophagous, finds its prey in less deep layers (Fig. 49). Approximately 60 Mediterranean cephalopod species have been identified: among them, Histiotheuthids are the most represented (57,8%), followed by Ommastrephids (see box *Mesopelagic cephalopods*).

A rough estimate of biomass of pelagic cephalopods eaten by the three cetacean species *S. coeruleoalba*, *G. griseus* and *Globicephala melas* in the Ligurian Sea area has been published by Marrale and Würtz (1994), giving the total mass of 30.800 t for eight cephalopod species (*Ancistroteuthis lichtensteinii*,

A



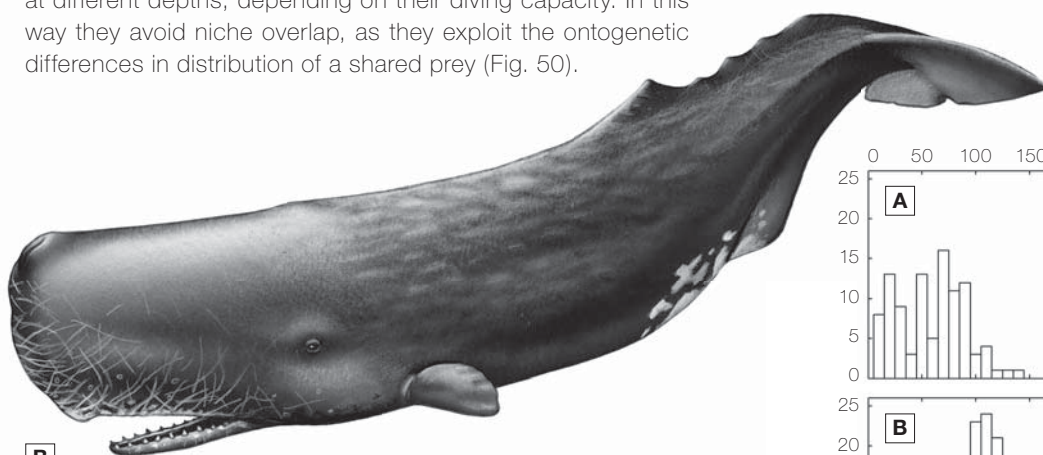
Histoteuthis reversa, *Histoteuthis bonnellii*, *Todarodes sagittatus*, *Illex coindetii*, *Todaropsis eblanae*, *Sepietta oweniana*, *Heteroteuthis dispar*.

Other predator species such as smaller odontocetes (e.g. *Stenella coeruleoalba*), tuna (*Thunnus thynnus*), swordfish (*Xyphias gladius*) and sharks (*Prionace glauca*, *Alopias vulpinus*, *Isurus oxyrinchus*) are omnivorous. It is likely that the diet of opportunistic predators will give a reliable idea of the composition of pelagic fauna in the relative abundance of the prey taxa, as well as their seasonal occurrence.

The presence of some top predators in a specific area is then the result of mesopelagic fauna abundance.

These predators frequently feed in the same oceanic area with favourable oceanographic conditions, but they search their prey at different depths, depending on their diving capacity. In this way they avoid niche overlap, as they exploit the ontogenetic differences in distribution of a shared prey (Fig. 50).

B



C

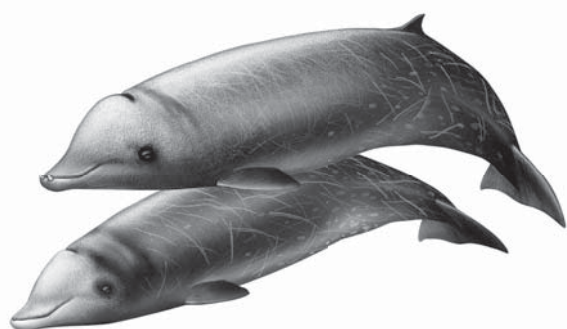


Fig. 49 (see color plate p. 86): Teuthophagous cetaceans:

- A) Risso's dolphin, *Grampus griseus*, size: maximum 4 m;
 B) Sperm whale, *Physeter catodon**, size: male maximum 18 m, female maximum 12 m;
 C) Cuvier's beaked whale, *Ziphius cavirostris*, size: maximum 7 m.

* *Physeter catodon* is the correct scientific name, according to the priority given by the *Code of Zoological Nomenclature* and the clear description by Linnaeus (*Physeter catodon* is described to have *fistula in rostro*, while *Physeter macrocephalus* carries *fistula in cervice*).

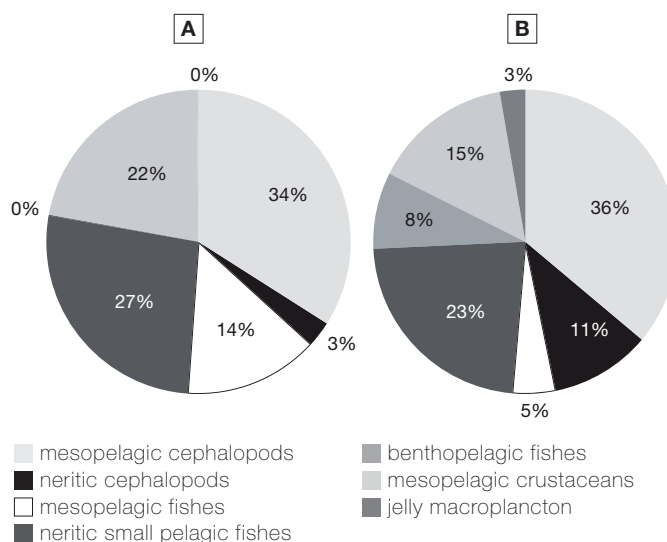


Fig. 48 (see color plate p. 86): Cumulative percentage of prey composition (A) and prey occurrence (B) as found in the stomachs of several top pelagic predators (Astruc, 2005; Orsi Relini *et al.*, 1992; Orsi Relini *et al.*, 1995; Pulcini *et al.*, 1992; Würtz *et al.*, 1992; Würtz and Marrale, 1993).

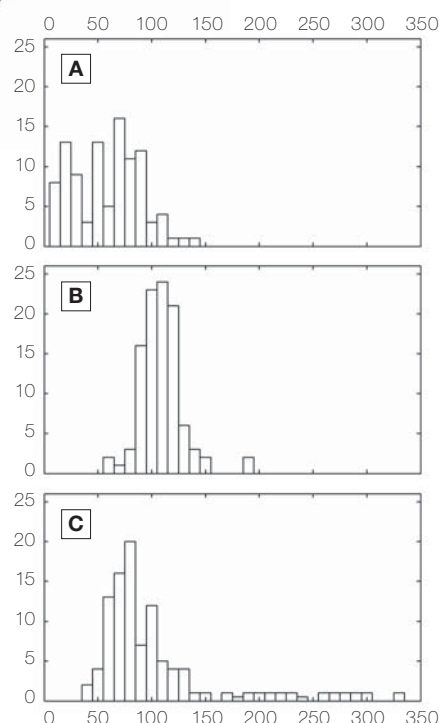


Fig. 50: Difference in prey sizes found in the stomach contents of three pelagic predators (A) *Stenella coeruleoalba*, (B) *Gampus griseus*, (C) *Ziphius cavirostris* occurring in the same feeding area of the Ligurian Sea. Dorsal mantle length (DML) frequency distributions of the prey *Histoteuthis reversa*.

8. Top predators

8.1. STRATEGIES FOR EARLY LIFE STAGES SURVIVAL

As previously explained, prey abundance tends to coincide with predator abundance (Bakun, 2006a). If plankton, on which fish larvae feed, can be concentrated in convergent frontal structures, so can planktonic predators which feed on these larvae (e.g. medusas, ctenophores and predatory larvae of other fishes). If frontal structures can attract adult fishes for feeding and spawning offspring within them, then predatory fishes can use the same attraction to position themselves to prey upon these offsprings. Consequently, the key for reproductive success is to allocate larvae in a situation where feeding conditions coincide with a density of predators low enough to permit significant survival, which can also be attained by means of rapid growth through the most dangerous early life stages.

Bakun (2006b) offers a simple model to summarize and demonstrate the basic dynamic effects of the above-described interactions. The *predator pit* function (Fig. 51) offers a refuge from predation when prey abundance is very low. In the first stage very destructive predation will occur, reducing prey density to a level which is insufficient to attract predator interest. On the other hand, if prey abundance is enough to satiate local predators, then specific predation mortality steadily decreases and prey density can increase beyond this satiation level.

If the prey production rate is then superimposed on the *predator pit* function (Fig. 51), the intersection indicates a critical point. Below this point, population density will decrease (collapse into the pit), while above it density will tend to increase. This point has been called *reproductive breakout*.

8.2. NORTH ATLANTIC BLUEFIN TUNA (*Thunnus thynnus*)

Atlantic bluefin tuna (*Thunnus thynnus*) grow more than 300 cm in length and attain weights of 680 kg (Block *et al.*, 2001). The age-length relationships have been calculated by various methods (otolith examination, modal analysis of length frequencies and

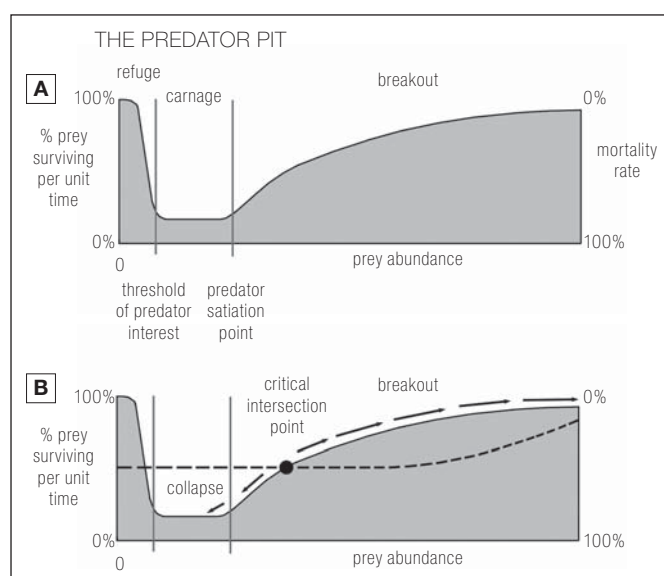


Fig. 51:

A) Diagram of the predator pit function. Survival rate (plotted on the left ordinate) which increases upwards, while the mortality rate (plotted on the right ordinate) increases downwards.

B) Production rate curve (biomass produced per unit biomass per unit time dashed curve) of the prey population superimposed on its predator pit function. A critical intersection point (circled), where the two curves intersect, marks the abundance level above which the rate of production exceeds the rate of predation mortality and the population increases, and below which the rate of predation mortality exceeds the rate of production (Bakun, 2006a).

tagging studies): growth slows down from about 200 cm in length, corresponding to 10 year-old specimens (Rooker *et al.*, 2007). The bluefin tuna's endothermic physiology allows it to exploit a wide range of pelagic environments, from warm tropical waters, up to 30°C, to subpolar waters as cold as 3°C in the Mediterranean Sea and North Atlantic Ocean.

Despite the fact that Atlantic bluefin tuna have been considered over-exploited since 1982, recent catches continue to exceed TAC levels (Total Allowable Catches). The catch quota are annually

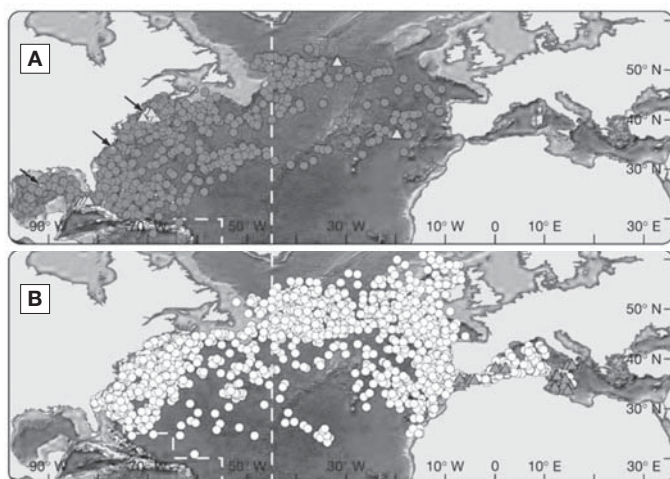


Fig. 52 (see color plate p. 86): Results of Atlantic Bluefin tuna electronic tagging campaigns (Block *et al.* 2005) show that eastern stock specimens do not reach the Mediterranean Sea spawning grounds (A) and western stock specimens do not reach the Gulf of Mexico spawning grounds (B).

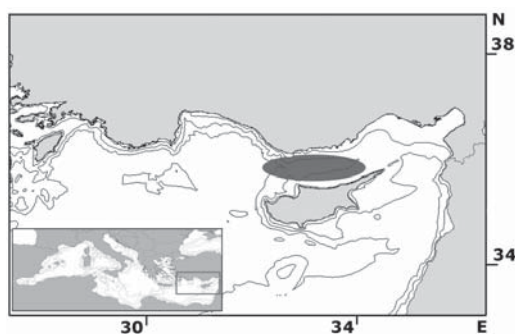


Fig. 53: Bluefin tuna spawning area in the Levantine Sea (dark grey area) (Karakulak *et al.*, 2004).

defined by the International Commission for the Conservation of Atlantic Tunas (ICCAT), which currently recognizes two management units conventionally separated by the 45°W meridian: western stock, breeding in the Gulf of Mexico, and east Atlantic stock, breeding in the Mediterranean Sea.

The existence of two *T. thynnus* stocks (Carlsson *et al.*, 2007) has been indicated by tagging data and genetic differentiation studies. This assumption has been questioned (Rooker *et al.*, 2007), as a great number of both western and eastern specimens cross the Atlantic to reach feeding grounds (Fig. 52, Block *et al.*, 2005), frequently coming back in the same year. This debate is of particular concern because of the relative dimension and the response to exploitation of the two stocks. In fact the western stock is smaller and far below the reference level, despite more than 20 years of fishing regulations, while the eastern stock is significantly larger and apparently more stable (Fromentin and Powers, 2005). On the other hand, recent assessments concluded that eastern stock is overfished and probably in a state of decline (Alemany, 2008).

In the Mediterranean Sea it was estimated that 50% of *T. thynnus* females were reproductively active at approximately 103 cm fork length (age 3), and 100% maturity was reached between

115 and 131 cm fork length (age 4 or age 5). Nevertheless, inferences drawn from tagging data suggest that some eastern bluefins may not initially spawn until they are considerably older. In fact, adolescents tagged in the western Atlantic and destined to return to the Mediterranean Sea for spawning did not re-enter the Mediterranean until they were larger than 205 cm fork length (ages 9 to 10) (Block *et al.*, 2005).

Bluefin tuna is oviparous, iteroparous and a multiple batch spawner due to its asynchronous oocyte development. Spawning frequency is estimated at 1-2 days in the Mediterranean (Medina *et al.*, 2002) and egg production appears to be age-(or size)-dependent. The conventional assumption is that adults spawn each year. However, tagging experiments suggest that individuals might spawn only once every two or three years (Alemany, 2008).

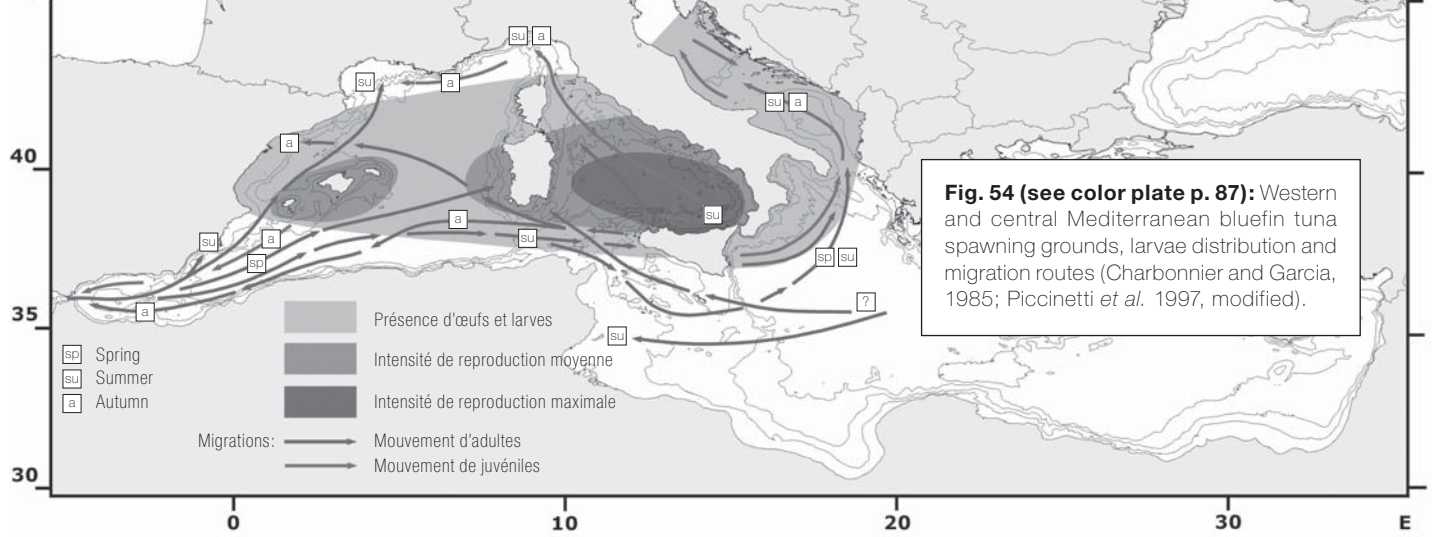
Tuna are known to spawn in SSTs above 24°C. In the Levantine Sea, SSTs values between 22.5 and 24.9 C are generally recorded from the second half of May, in fact in the eastern Mediterranean, the reproductive season of bluefin tuna starts almost 1 month earlier (mid-late May) than in other Mediterranean spawning grounds (June - early July). Several years of investigation on bluefin tuna larvae distribution, as well as studies on the presence of females with hydrated oocytes and post-ovulatory follicles, have not sufficed to complete the map of spawning areas in the Mediterranean. Large knowledge gaps mainly exist for the eastern basin, where an important spawning ground has been recently identified North of Cyprus (Karakulak *et al.*, 2004) (Fig. 53).

According to the results of larval campaigns, bluefin tuna spawn within a large portion of the pelagic Mediterranean environment (Piccinetti *et al.*, 1997; Nishida *et al.* 1998; Tsuji *et al.*, 1997). Remarkable concentration of eggs and larvae occurs south of the Balearic islands, around Malta, off the eastern coast of Sicily and in the South Tyrrhenian Sea, where hydrological features are more favourable for their survival (Charbonnier and Garcia, 1985) (Fig. 54).

As shown by tagging campaigns (De Metrio *et al.*, 2005), movement of *T. thynnus* within the Mediterranean Sea is often limited, particularly for individuals tagged in the eastern regions of the basin. It seems that movement of bluefin tuna tagged in the central and western Mediterranean Sea are more pronounced than in the east. Seasonal prey abundance (e.g. *E. encrasicolus*, *S. pilchardus*, *M. norvegica*, *S. scombrus*, *A. rochei*, etc.) drives the concentration of both young and adult specimens in Mediterranean areas not used for reproduction (e.g. Ligurian sea, north-central Adriatic). Larger individuals (>150 kg) move out of the Mediterranean: their movement patterns or displacement distance are linked to size, as previously hypothesized by Sarà (1964, 1973) and they are likely to be related to the exploitation of feeding grounds outside the Mediterranean (Stokesbury *et al.*, 2004) (Fig. 54).

8.2.1. Balearic spawning grounds

Observations from field surveys focusing on the spawning habitat of bluefins off the Balearic archipelago showed a tendency to prefer a temperature range of 23°-25°C as well as water masses



of Atlantic origin (García *et al.*, 2006). Bluefins use relatively oligotrophic regions for eggs and larvae habitat. Certain data have suggested that climatic variations that should act to decrease ocean primary productivity actually tend to improve tuna reproductive success. On the other hand, those that should act to increase local primary productivity have yielded particularly poor reproductive success (Bakun and Broad, 2003). This implies that the tuna spawning strategy may be largely directed to minimizing mortality at early stages due to predation by medusas and other pelagic predators.

The spawning grounds of tuna usually seem to be associated with warm waters (more than 24°C) and rather strong ocean current systems.

Large tunas can use their body size and swimming and migrating capabilities as a comparative advantage over other organisms feeding on, or competing with, tuna larvae (Bakun, 2006b; García *et al.*, 2006). Tuna spawning zones in general appear to be characteristically strongly patterned by surface frontal interfaces and mesoscale eddy structures. They may offer opportunities for exceptional population growth of species or populations particularly adapted to excel in such highly-productive/rapid-growth/high-mortality situations. Most of the larvae are found in anticyclonic eddy structures, where larval food organisms would tend to be concentrated in the convergent flow patterns.

From the hydrographic point of view, the Balearic region is characterised by the convergence of Atlantic water masses (AW) and Mediterranean water masses (MW). Spawning of bluefin tuna seems to take place mainly in mixed offshore waters, as suggested by their preference for waters with salinity between 36.9 and 37.7, located near frontal areas in the confluence of AW and MW. Larval distribution also suggests that spawners reach the Balearic Sea area associated with the inflowing AW (Alemany, 2008).

The greatest concentrations of bluefin tuna larvae, as well as the other tuna species, were found east of Ibiza in the Mallorca channel and in the area south of the island of Menorca. The distribution pattern of tuna larvae seems to describe an eastward path from the Mallorca channel towards the area south of Menorca. General circulation patterns could facilitate eastward transport of larvae from areas of major larval concentrations in the Mallorca channel to the southern region off Menorca. The greater proportion of larger tuna larvae located in this area could sustain this transport hypothesis (García *et al.*, 2002a, b, c).

Moreover, these major larval tuna concentrations are linked to the existence of anticyclonic eddies, such as the one observed east of Ibiza in the Mallorca channel, and even more in the eddy observed south of Menorca. Larvae reaching this anticyclonic eddy could maintain a constant relative position in the area, as the eddy acts as a retention mechanism, concentrating larvae from other areas (Fig. 55).

8.2.2. Nursery grounds. The effect of the environment, and particularly fronts, in structuring the distribution of juvenile bluefin tuna schools

Surface fronts can affect the spatial aggregation of bluefin tuna schools, at least at certain scales.

Fishing grounds, such as the Rhone plume's extension in the Gulf of Lion or the Liguro-Provençal current, have a clear frontal signature. Shelf-break fronts can be seen all around the basin and

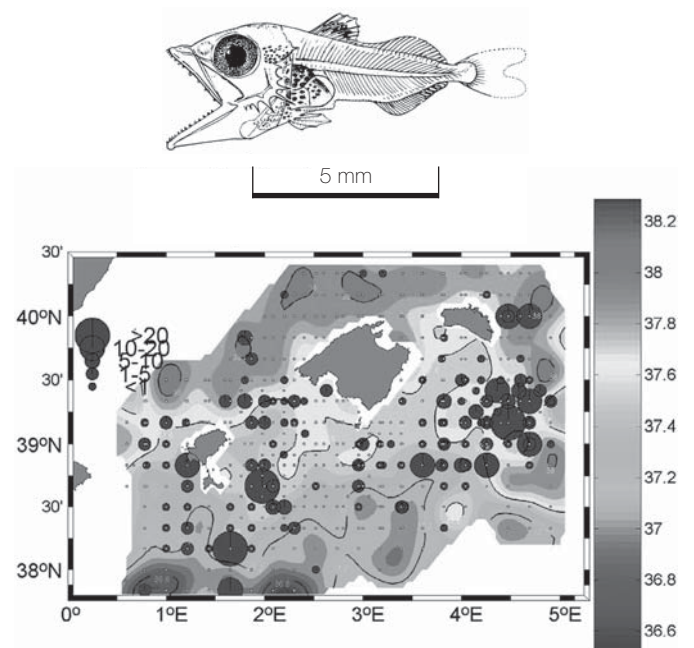


Fig. 55 (see color plate p. 86): Balearic spawning grounds of bluefin tuna. Larvae concentration related to salinity, according to the data from 2001-2005 TUNIBAL campaigns (García *et al.*, 2002a, b, c; Alemany, 2008). Drawing of *T. thynnus* larval stage from Padoa (1956).

very close to the shore, where the continental shelf is narrow (see the west coast of Corsica or the Algerian coast). Coastal fronts are also visible along the southern Sicilian coast. Circulation in the Tyrrhenian Sea apparently produces an important signal in the vicinity of Corsica, which is an area of sport fishing for bluefin tuna (Royer *et al.*, 2005).

The Alboran Sea, the Gulf of Lion and the central Tyrrhenian Sea all display a strong increase in frontal probability during May or June, with a relatively flat plateau until December. Such a signal may be linked to enhanced Eddy Kinetic Energy which displays comparable seasonal fluctuations. The Gulf of Gabes in Tunisia shows a decline in frontal density during September, possibly linked to tidal phenomena. The association between the distribution of juvenile bluefin tuna schools and thermal fronts was found valid only over a limited range of spatial scales (10-40 km). This indicates that other processes occur on small scales (over-aggregation due to unseen prey clusters or other behavioural processes) and larger scales (in and out movement at the border of the studied area).

The relationship between tuna aggregates and frontal meanders is most probably indirect and trophic-related. Advected material at fronts can provide favourable feeding grounds for small clupeids, which are in turn sought by bluefin tuna. Interannual and seasonal variations in frontal density in the Mediterranean Sea may not have a direct influence on the basin's global carrying capacity. However, it may have an important impact on the local aggregation of nutrients, phytoplankton and zooplankton species, and eventually on fish schools, thus leading to possible changes in density-dependent responses in marine populations. Transient surface fronts are particularly difficult to observe and assess (Royer *et al.*, 2005) (Fig. 54).

8.3. SWORDFISH (*Xiphias gladius*)

The swordfish is an epi- and meso-pelagic species, usually found in surface waters warmer than 13° C. It can reach the size of 455 cm fork length (weight 650 kg). It is an opportunistic feeder and forages over a wide depth range (0–800 m), feeding mainly on smaller fish and squid as well as on crustaceans (Orsi Relini *et al.*, 1995; Peristeraki *et al.*, 2005; Bello, 1991).

ICCAT considers the North Atlantic and Mediterranean swordfish populations as two separate fish stocks. Recent genetic analyses have confirmed genetic differentiation between the North Atlantic and the Mediterranean (Pujolar *et al.*, 2002). However, a phylogeographic signal, distinctive of the Mediterranean population, has also been identified in a reduced part of the northeast Atlantic limited to about 10° west. This indicates that the limit of Mediterranean populations exceeds the Strait of Gibraltar, enclosing this northeast Atlantic region where mixed stock can be found (Viñas *et al.*, 2006).

Swordfish is known to exhibit rapid growth in their first year, reaching up to 90 cm of LJFL (lower jaw-fork length) (~15 kg) after 1 year (Ward *et al.*, 2000). Growth parameters for Mediterranean

specimens have been calculated by Tserpes and Tsimenides (1995) as follows:

$L_{inf} = 238.60 (1 - e^{-0.185 (t + 1.404)})$ for sexes combined

$L_{inf} = 203.08 (1 - e^{-0.241 (t + 1.205)})$ for males

$L_{inf} = 226.53 (1 - e^{-0.210 (t + 1.165)})$ for females.

Valerias *et al.* (2008) found different growth rates in swordfish present in the western Mediterranean, in an area where mixing between Atlantic stock and Mediterranean stock is possible. According to this paper, the growth rate is lower compared to previous studies, particularly at young ages.

The first maturity (50%) occurs from 140 to 160 cm. Females smaller than 125 cm LJFL are all sexually immature. The spawning season occurs mainly in spring-summer, with a peak in July-August, although variations in timing occur possibly due to environmental and oceanographic variability (Di Natale *et al.*, 2002; Deflorio *et al.*, 2005). Eggs of this species are found from June to September, and young swordfish up to 5 kg have been recorded from October to December. Juveniles are found throughout the Mediterranean from November to March. They often tend to concentrate close to the coast and in areas of favourable trophic and oceanographic conditions. Female gonads contain 2 to 5 million eggs.

Known areas where spawning is concentrated are in the Balearic Islands (de la Serna *et al.*, 2008), the Strait of Messina, the southern Tyrrhenian and Ionian Seas. Other spawning areas may exist, but further research is needed to locate them. As an example, the presence of pre-spawning, spawning and recent post-spawning mature females, during the June-August period, supports the existence of a reproductive area in the South Western Spanish Mediterranean (Macias *et al.*, 2005) (Fig. 56).

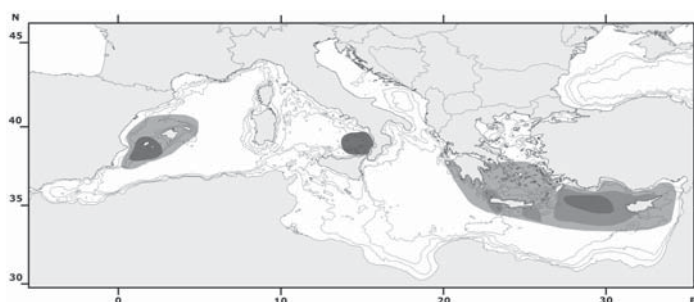
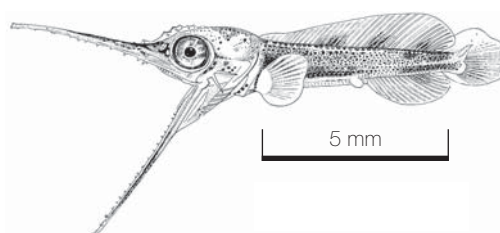


Fig. 56: Mediterranean swordfish breeding and spawning areas. Grey intensity is proportional to the importance of the area for swordfish reproduction (from Romeo *et al.*, 2008, Tserpes *et al.*, 2008, de la Serna *et al.*, 2008, modified). Drawing of *X. gladius* larval stage from Padoa (1956).



It is likely that the best-known spawning grounds of swordfish are located off the southern part of the Italian Peninsula and Sicily. The main concentrations occur in the Straits of Messina, where adults are present in all months except January and February. Reproduction activity is most intensive from the end of June to August, when males are often observed pursuing females and showing well-defined patterns of courtship behaviour (Romeo *et al.*, 2008).

In the eastern Mediterranean, during the spawning season, swordfish concentrate near the Anaximander seamounts, in an area between the Anaximander eddy, the Antalya eddy and the Rhodes Gyre. During the rest of the year, swordfish spatial distribution is much broader with relatively higher concentrations occurring in areas with high prey potential (Tserpes *et al.*, 2008).

Swordfish are very sensitive to specific environmental parameters and tend to congregate near converging oceanic fronts, strong thermoclines or underwater features such as seamounts and shelving banks (Ward *et al.*, 2000). High swordfish density values in the feeding period are found in areas surrounding eddies (Bakun, 2006a; Damalas *et al.*, 2007). Swordfish abundance seems also inversely related to the winter North Atlantic Oscillation index. However fish aged 1 year (recruits) do not appear to be related to large-scale environmental factors (Orsi Relini *et al.*, 2008).

Swordfish show a daily migratory pattern. During the daylight hours they swim at depths between 250m and 650m with a marked preference for water masses with temperatures between 14 and 15 °C. Sometimes animals perform fast surfacing from elevated depths to the surface, where they stay for about an hour, after which they dive to regain deep waters. During night-time, swordfish stay in the superficial layer between 0 m and 10 m (Canese *et al.*, 2008).

Swordfish fisheries operate throughout the Mediterranean. In the last decades, average annual catches amount to more than 14,000 t. Mediterranean catches contain a large number of small sized swordfish, less than 3 years old, many of which have probably never spawned. FAO-GFCM endorsed the recommendation recently adopted by the International Commission for the Conservation of Atlantic Tunas (ICCAT), which called for a complete ban on fishing for this species from October 15 to November 15, 2008. According to FAO stock assessments, the status of swordfish in the Mediterranean ranges from fully exploited to over-exploited, which means that the stock is being harvested beyond sustainable levels (Tserpes, 2008) (Fig. 57).

8.4. SHARKS

The distribution of pelagic sharks in the Mediterranean Sea is mainly known through swordfish fishery and bluefin tuna traps as well as by catching using other pelagic fishing methods. IUCN classifies as "vulnerable" blue shark (*Prionace glauca*), basking shark (*Cetorhinus maximus*), white shark (*Carcharodon carcharias*) and porbeagle (*Lamna nasus*), as "near threatened" the shortfin mako (*Isurus oxyrinchus*) and as "data deficient" the common thresher shark (*Alopias vulpinus*). These species can be considered as the most representative of the Mediterranean pelagic environment for their role in trophic webs, and also as scavengers. Nevertheless, knowledge about their ecology and migratory behaviour is poor.

According to fishery data, it is possible to obtain rough maps of distribution and relative abundance for some of the species mentioned above. Megalofonou *et al.* (2005) estimated incidental catches from swordfish and tuna fisheries throughout the Mediterranean Sea : twelve shark species were documented as bycatch; blue shark were most abundant in all gears and areas studied, while shortfin mako and common thresher shark were the next most frequent species. Sharks represented 34.3% in weight of total catches sampled in the Alboran Sea, where the mean catch rate was 3.8 sharks/1000 hooks. The longline swordfish fishery has given higher shark by-catches. There was a significant variation in size distribution of sharks by fishing gear, albacore longline fished mainly juveniles, while larger specimens were more frequent in the swordfish longline and driftnet fishery (Fig. 58).

The basking shark (*C. maximus*) can be considered frequent, especially during spring. In the northwestern Mediterranean, the main source of information on this species comes from specimens incidentally entangled in trammel nets. This species is widely distributed in temperate waters, but a large number of specimens tend to be concentrated in favoured coastal areas near the surface for feeding and, possibly, for breeding. Basking sharks locate and remain within productivity "hot-spots" occurring seasonally along large-scale frontal features. They forage selectively on specific zooplankton assemblages (Sims *et al.*, 2003). Some specimens seems to be philopatric, showing the tendency to return every year to the same summer feeding locations. In the Mediterranean, basking shark distribution could be related to surface water temperature, wind speed, surface currents and average chlorophyll concentration data. It seems that a potential aggregation site corresponds to the Cetacean Sanctuary in the Ligurian Sea (Northern Tyrrhenian) and in the Balearic region. The return of basking sharks to these waters in the spring is probably associated with periods of high biological production and particularly northern krill (*M. norvegica*) swarms (Fig. 59).

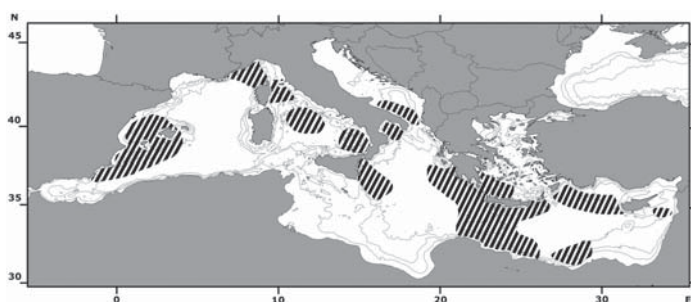


Fig. 57: Main Mediterranean fishing area for swordfish longliners (Dalmas *et al.*, 2007; Deflorio *et al.*, 2005; Orsi Relini *et al.*, 2008; de la Serna *et al.*, 2008).

The white shark (*C. carcharias*) is a cosmopolitan generalist predator and scavenger, feeding on a wide spectrum of vertebrate and invertebrate taxa. In the Mediterranean Sea, this species is recognized as resident. Parturition occurs from spring to late summer in temperate shelf waters of the Southern-Central Mediterranean Sea, especially those between Western Sicily and the Tunisia Areas. Here large adults of both sexes and neonates are found together, indicating the presence of nursery-grounds. Young white sharks a year-old or less have also been caught elsewhere in the Mediterranean - off Algeria, France and in the North Aegean (Fig. 60). The majority, however, originate from the Sicilian Channel during high summer, when Sicilian-based trawlers can net the young sharks at depths of about 200 m or more (Fergusson and Compagno, 1996). On the other hand, records of this species in Italian waters are more numerous than previously reported. In the Mediterranean Sea, large juvenile and adult white sharks feed upon odontocetes or large pelagic fish, as well as upon chelonians (Morey *et al.*, 2003).

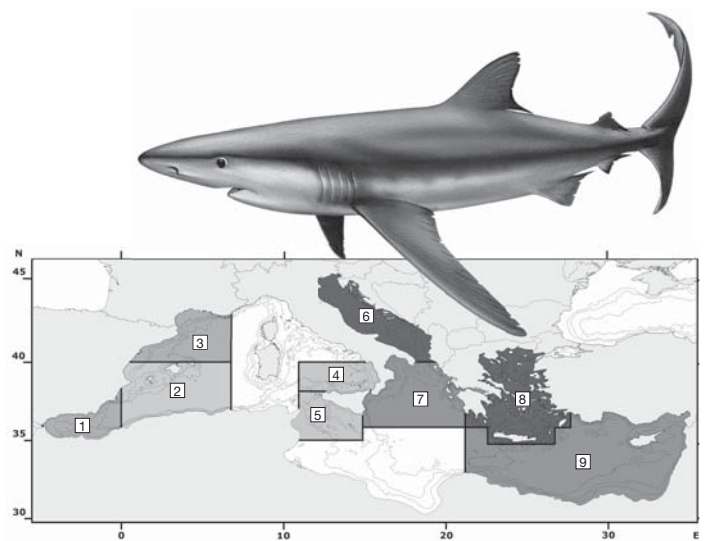


Fig. 58 (see color plate p. 87): Map of relative shark abundance in nine areas of the Mediterranean Sea according to the study on shark bycatch in swordfish fisheries during the period 1998–2000 (Megalofonou *et al.*, 2005, modified). Main species represented in the catches was *Prionace glauca*. 1) Alboran Sea, 2) Balearic Islands area, 3) Catalanian Sea, 4) Tyrrhenian Sea, 5) Straits of Sicily, 6) Adriatic Sea, 7) Ionian Sea, 8) Aegean Sea, and 9) Levantine basin.

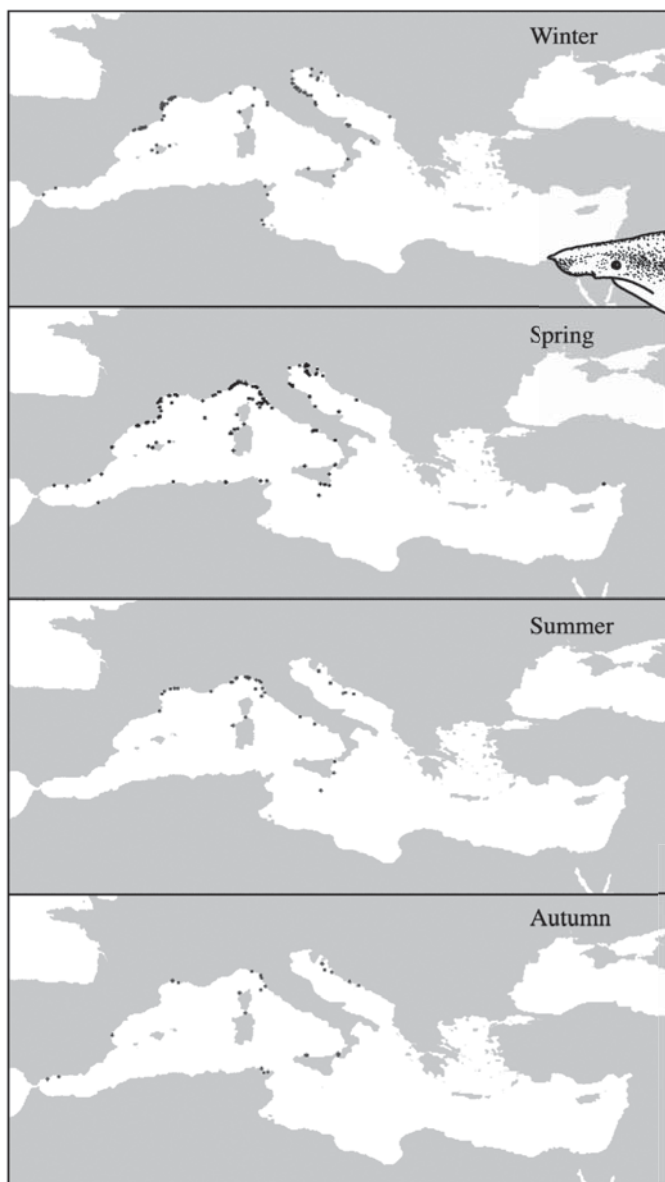


Fig. 59: Seasonal and geographic distribution of basking shark records (sightings, incidental catches, etc.) along the Mediterranean coast. (Mancusi *et al.*, 2005).

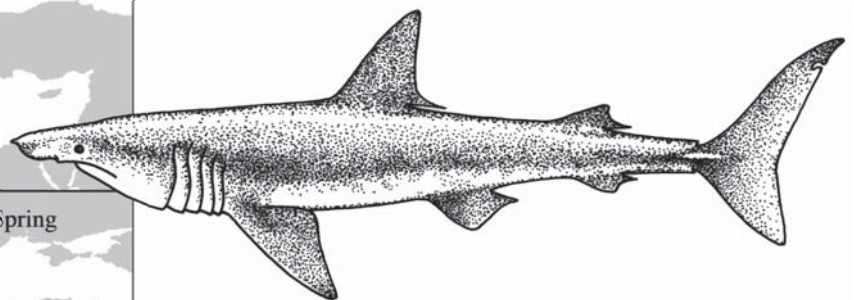
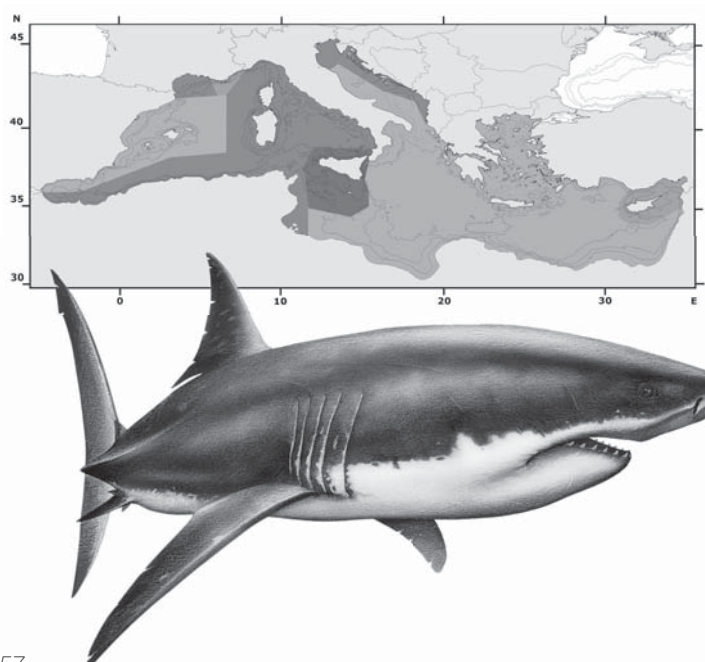


Fig. 60 (see color plate p. 87): White shark (*Carcharodon carcharias*) distribution in the Mediterranean sea, according to Fergusson and Compagno (1996). Grey intensity is proportional to the relative shark abundance.



8.5. SEA TURTLES

The Mediterranean region is an important breeding area for the loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*). The leatherback (*Dermochelys coriacea*) is distributed across the whole region, although no regular reproduction has been observed. Hawksbill (*Eretmochelys imbricata*) and Kemp's ridley (*Lepidochelys kempii*) have also been occasionally recorded. *C. caretta* (Fig. 30) is the most abundant sea turtle in Mediterranean waters and its distribution extends from the eastern to the western basins, including the Black Sea. On the other hand, green turtles are restricted to the eastern Mediterranean and are regarded as critically endangered.

The Ionian Sea constitutes the major breeding ground for turtles. Up to now, nesting beaches have been identified in ten countries (Cyprus, Egypt, Greece, Israel, Italy, Lebanon, the Libyan Arab Jamahiriya, the Syrian Arab Republic, Turkey and Tunisia). Sporadic cases have been reported in Croatia, on the Italian Adriatic coast and in southern Spain. One of the highest densities of nests in the world is located in the Gulf of Laganas (island of Zakynthos, Ionian Sea). The beaches of the island of Kefallonia, other Ionian islands and the west coast of the Peloponnisos are also important nesting sites.

Demographically independent nesting colonies have been identified in the Mediterranean breeding loggerheads, providing the evidence of subpopulations. Some genetic divergences also exist between specimens nesting in the western Atlantic as result of reduced gene flow. This genetic isolation is more evident in the case of colonies nesting in Turkey, which have been defined as a demographic unit. It was estimated that 53-55 % of pelagic loggerheads in both the western and eastern basins come from Mediterranean nests and the rest derive from western Atlantic stocks.

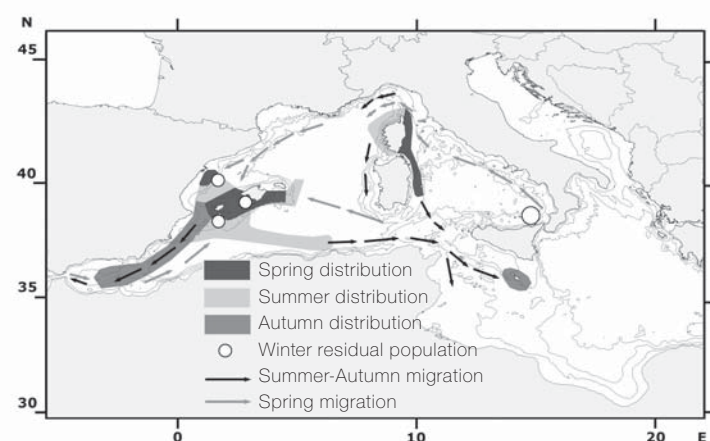


Fig. 61 (see colour plate p. 87): Loggerhead turtle (*Caretta caretta*) migration routes and distribution in the western and central Mediterranean Sea. From Camiñas (2004), modified.



Loggerhead turtle specimens from the Atlantic Ocean are known to migrate into the Mediterranean Sea during the first half of the year. Together with those from the Mediterranean, they congregate annually for feeding in a broad area around the Balearic Islands. Aggregations also occur from spring to late summer around Corsica Island, off the eastern Sardinia and Algeria coasts, with a period of migration from the Atlantic to the western Mediterranean and vice versa (Camiñas, 2004) (Fig. 61).

8.6. COMBINED EFFECTS OF BOTTOM MORPHOLOGY AND CIRCULATION ON CETACEAN DISTRIBUTION

8.6.1. Overall cetacean distribution within the Mediterranean Sea

Almost 26 cetacean species have been recorded in the Mediterranean, nevertheless only eight have resident populations with various degrees of genetic isolation from the Atlantic: fin whale (*Balaenoptera physalus*), striped dolphin (*Stenella coeruleoalba*), common dolphin (*Delphinus delphis*), bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), long fin pilot whale (*Globicephala melas*), Cuvier's beaked whale (*Ziphius cavirostris*) and sperm whale (*Physeter catodon*).

It is likely that the effects of physiographic features on cetacean distribution have been much more extensively investigated within the international "Pelagos" Sanctuary than in other sectors of the Mediterranean Sea. "Pelagos" is the first large pelagic protected area in the Mediterranean, encompassing heterogeneous water masses over a surface of about 100,000 km² of the Ligurian, Higher Tyrrhenian and Corsica Seas. Cetacean distribution related to variable oceanographic conditions has been also investigated in the Alboran Sea, Spanish Mediterranean (Cañadas *et al.*, 2002), Gulf of Lion (David, 2000), Ionian and Aegean Sea (Frantzis *et al.*, 1999).

IFAW has carried out a basin-wide survey mainly focused on the sperm whale; nevertheless data on overall distribution of all species are still scarce or non-existent for the far-eastern and southern part of the Mediterranean basin.

In general, cetacean abundance is strongly dependent on prey distribution and the diversity of cetacean feeding strategies is reflected in the significant differences in their habitats. Studies have suggested that odontocetes, for example sperm whales, feeding mainly on deep-squids, are commonly associated with topographic structures such as canyons and submarine mountains (David, 2000), while mysticetes, e.g. fin whales feeding on plankton, aggregate on thermal fronts or convergent structures rich in zooplankton.

Given the lack of detailed information on prey concentration, other parameters have had to be used for estimating cetacean distribution (Moulins *et al.*, 2005).

The distributions of two commonly encountered cetacean species, the fin whale and striped dolphin, seems to be correlated to bathymetry, bottom slope and daily-SST. In fact, these parameters



Fig. 62 (see color plate p. 86): Fin whale (*Balaenoptera physalus*) distribution patterns in the western and central Mediterranean Sea related to depth and to circulation (Aissi *et al.*, 2008; Canese *et al.*, 2006).

affect prey concentration, as the fin whale feeds mainly on krill and the striped dolphin feeds on both squids and fishes. Fin whales are frequently found in deep offshore waters, seldom descending deeper than 2,000 m, (Notarbartolo di Sciara *et al.*, 2003). However, if depth would appear to be the most important physiographic parameter used to describe the distribution of this large mysticete, it must be taken into account that the variability of pelagic habitats does not permit easy generalizations for the entire Mediterranean. The habitat choice of fin whales, when they are in their feeding grounds, mostly depends upon the distribution of their prey, and this last is highly time-space heterogeneous in its correlation with ocean dynamics (Moulins *et al.*, 2005).

In the Ligurian Sea, known offshore preferences of fin whales coincide with the winter-spring presence of high levels of nutrients and upwelling currents in the centre of the basin, likely reflecting the distribution of Northern krill, *Meganctyphanes norvegica* (Relini *et al.*, 1994; Orsi Relini *et al.*, 1992). Nevertheless, inter-annual as well as seasonal differences in prey biomass may be related to whale presence and aggregation behaviour in various areas. In the Gulf of Lion, the Ligurian Sea and Tyrrhenian Sea, fin whales can occasionally be sighted close to the coast (less than 2 km from shore, and often entering small bays and harbours), possibly as a consequence of prey aggregation due to a change in circulation patterns. On the other hand, each year several fin

whale specimens follow a less variable seasonal pattern, from January to the end of March, to exploit annual concentration of *Nictyphanes couchi* in the Sicily Channel shelf, around Lampedusa island (Aissi *et al.*, 2008; Canese *et al.*, 2006) (Fig. 62).

8.6.2. Sperm whale (*Physeter catodon*)

The sperm whale is the largest odontocete and, excluding filter feeding baleen whales, it is the largest predator in world oceans. The daily rate of food consumption for this species has been estimated at 0.15-0.3 t (Clarke, 1977) and 0.66-0.86 t (Santos, 1999). Thus, even if the more conservative rate is considered, it is clear that the presence of sperm whales in a given pelagic area means a large amount of prey, making this species a reliable indicator of ocean productivity. Moreover, taking into account that it is mostly a teutophagous cetacean and that mesopelagic squid are high-level predators, the mechanisms acting on their prey (both of sperm whale and squids) must be very effective. These mechanisms must concentrate favourable conditions and speed up energy turnover in specific pelagic habitats, such as certain submarine canyons in the central-western Mediterranean basin, along the Hellenic trench and in waters off southwestern

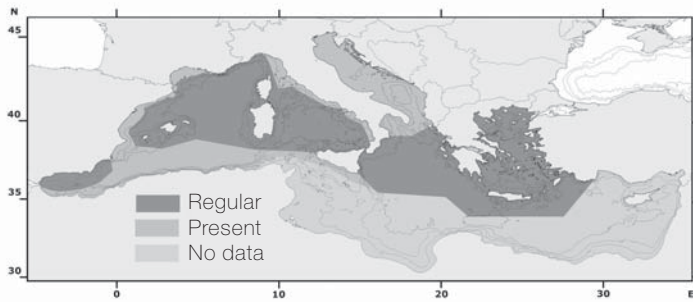


Fig. 63: Sperm whale (*Physeter catodon*) distribution in the Mediterranean Sea. From Reeves and Notarbartolo di Sciara (2006); IFAW (2006), modified.

Crete. In fact, in these areas sperm whales are present all year around.

The overall distribution of sperm whale in the Mediterranean Sea has been investigated in several campaigns by IFAW (2006) and Gannier *et al.* (2002). Studies in specific sectors of both the western and eastern basins have been carried out by Frantzis *et al.* (1999) and Fernandez-Casado (2001). The resulting overall distribution map is shown in figure 63.

According to genetic studies (Drouot *et al.*, 2004), a separate population of sperm whale may exist in the Mediterranean Sea. On the other hand, the presence of mature male groups in the Strait of Gibraltar area could indicate a lower level of philopatry among the latter than in females. The hypothesis of a certain level of isolation is also consistent with the presence of newborns and calves. Gannier *et al.* (2002) have suggested 41° parallel as the northern limit of Mediterranean sperm whales' breeding schools, nevertheless a group of females followed by very young calves has been observed in December, in the northwestern sector of the Liguria sea (Moulins and Würtz, 2005).

Whether Mediterranean sperm whales have regular movements or not is still unclear, even if a migration scheme has been proposed by Bolognari (1949). Feeding and breeding grounds do not seem to be differentiated. Both solitary males and groups of females may feed, and short reproductive association have been observed, along their distribution range (Reeves and Notarbartolo di Sciara, 2006).

8.6.3. Ligurian sea Cuvier's beaked whale (*Ziphius cavirostris*) hotspot

Cuvier's beaked whale is a deep-water pelagic cetacean, widely distributed throughout the Mediterranean. Its preferred habitats are correlated to canyons, seamounts as well as troughs influenced by prevailing cyclonic hydrodynamics. This large cetacean, essentially teutophagous, seems to be concentrated into specific areas: western Alboran off Almeria, eastern Ionian Sea off the Greek islands, off southwestern Crete and within the *Pelagos* Sanctuary. In the Mediterranean Sea, this species has been sighted between 500 and 2500 m, but the modal frequency of sightings is recorded at a mean depth of 1500m. Cuvier's beaked whales may be found close to the coast where there are submarine canyons and, indeed, the species can be more frequent where bathymetric anomaly is positive, i.e. where water is deeper than expected. Nevertheless, considering the modal

frequency of bathymetric gradient, the bottom slope at animal positions is not so steep (60 m/km), while the typical gradient of canyon walls in this area reaches values of 150 to 190 m/km (Moulins *et al.*, 2007). Considering the bathymetry pattern, in the Mediterranean Sea the highest number of observations of Cuvier's beaked whale has been recorded in the trough linked with Genoa Canyons with an edge limited by 1000 m-isobaths (Fig. 64).

This edge constitutes a topographical southward barrier to the cyclonic Liguro-Provençal current, running parallel to the coast. As Nesis (1993) proposes, topographic features associated with a perpendicular current may participate in enriching cephalopod productivity. In consistence with this hypothesis, all collected floating squids are found in this area. Moreover, the squids mainly found here belong to only two species, *Histioteuthis bonnellii* and *Histioteuthis reversa*, which are well-known as the main prey of beaked whales in the Mediterranean Sea (Podestà and Meotti, 1991; Carlini *et al.*, 1992a; Frantzis and Cebrian, 1998). Hence, these results demonstrate evident relationships between Cuvier's beaked whale and a topographic situation (Moulins *et al.*, 2007).

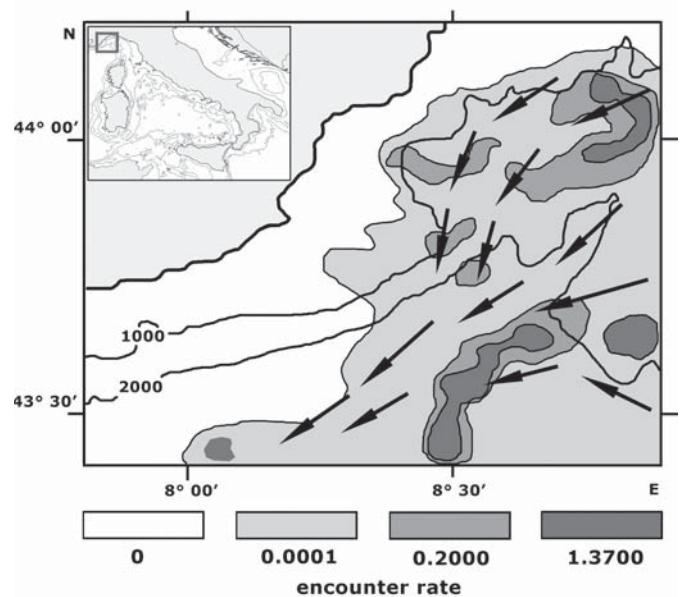


Fig. 64: Cuvier's beaked whale (*Ziphius cavirostris*) encounter rates (number of sightings divided by number of kilometres surveyed) in the trough between Genoa and Imperia, western Ligurian Sea (central Mediterranean Sea). Arrows indicate the direction of the main cyclonic current flowing in that area (Moulins *et al.*, 2007, modified).

9. Small coastal pelagic species

In the Mediterranean Sea, summer has been found to be the only season of the year not characterized by very high rates of mechanical energy added to the water column by the wind. Hence, during the rest of the year, turbulent mixing intensities are high in areas exhibiting linked enrichment and concentration processes, and appear to preclude conditions that may characterize favourable reproductive habitats. Other areas, however, have been found representing apparent large-scale *ocean triads* during the summer season (Fig. 15). They can then be considered as potentially very favourable reproductive habitats, considering the arrangement of physical mechanisms. The areas found by Agostini and Bakun (2002) were located in the Aegean Sea, off the Catalan coast, in the Alboran Sea, Adriatic Sea and Straits of Sicily. In the Mediterranean Sea, *ocean triads* appear to be associated particularly with summer conditions, and interestingly, summer is also the seasonal spawning period for anchovies and sardines, as well as other important pelagic fish (Agostini and Bakun, 2002, Iglesias *et al.*, 2003).

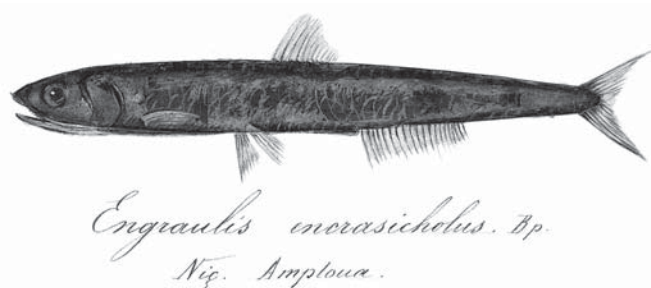


Fig. 65 (see color plate p. 88): Anchovy, *Engraulis encrasicolus*, by V. Fossat, 1842. Coll. Muséum d'Histoire naturelle de Nice.

9.1. AEGEAN SEA

The Aegean Sea is apparently an important spawning area for various fish species, especially small pelagic fish (Stergiou and Christou, 1996). 90% of the annual anchovy catch in the Aegean Sea usually comes from the northern and north-western parts of the sea (Stergiou, 1992). Anchovy spawning occurs from May

to September with a peak in July (Stergiou *et al.*, 1997b). This is associated with inshore migrations beginning in early spring and leading to a peak in abundances in near-coastal waters during the spawning season (Stergiou, 1992; Stergiou *et al.*, 1997a). Egg and larval abundances seem to be highest along the northern rim of the Aegean Sea, but also around the Limnos island (Iglesias *et al.*, 2003).

9.2. THE GULF OF LION AND THE CATALAN SEA

Anchovy fishery in the Catalanian Sea is concentrated particularly in the area between Cape Creus and the Ebro river delta: catches in this area are reported to be the highest in the entire Mediterranean. Peak anchovy spawning occurs during June–July along the Catalan Coast (Palomera *et al.*, 1995, Garcia and Palomera, 1996), with apparent peaks near Cape Creus and the Ebro River outflow (Palomera *et al.*, 1995), while very low densities of anchovy larvae are found further north, in the inner Gulf of Lion. There is also an important local spawning ground associated with the Rhone river outflow (Palomera, 1991), apparently located east of the offshore-directed wind jet system.

Due to its special oceanographic characteristics, the Ebro Delta is the main area in which anchovy schools have been found. The input of the Ebro River, together with coastal wind-induced upwelling, causes high nutrient concentrations. This phenomenon is reinforced by a permanent upwelling originating from the intrusion of water from the open sea towards the shelf at the mouth of the Ebro. The combination of these two factors makes the Ebro Delta a highly productive area in terms of phytoplankton and zooplankton, and hence of great trophic importance to the major pelagic species. The freshwater runoff flowing into the Mediterranean Sea also appears to favour spawning of the sardine and anchovy.

Surveys carried by Alemany *et al.* (2006) out in the pelagic waters around the Balearic Islands showed the influence of physical environmental factors on the horizontal distribution of larval fish assemblages, focusing on larvae of large migratory pelagic fish species. In June, patterns of horizontal distribution of fish larvae



Fig. 66 (see color plate p. 88): *Sardina*, *Sardina pilchardus*, by V. Fossat, 1877. Coll. Muséum d'Histoire naturelle de Nice.

appeared to be mainly conditioned by depth and the distribution of two surface water masses: the Atlantic Waters (AW), of recent Atlantic origin, and the older Mediterranean Waters (MW). In August, however, patterns of horizontal fish larvae distribution were significantly correlated with the surface salinity gradient resulting from successive AW inflows. Depth did not show any significant effect, probably due to bottom topography and a very narrow shelf area. The data from this study highlights the Balearic Islands as an important spawning ground for most of the large pelagic fishes inhabiting Mediterranean waters, both highly migratory and resident species (Alemany *et al.*, 2006).

generated by subsurface upwelling produced by the effect of cyclonic gyres released from the Atlantic mainstream, within the Bay of Malaga during the 2000-2001 anchovy spawning seasons. This hydrographic feature enhances primary production which, in turn, causes an increase of the mesozooplankton biomass in the inshore nursery grounds.

9.3 ALBORAN SEA

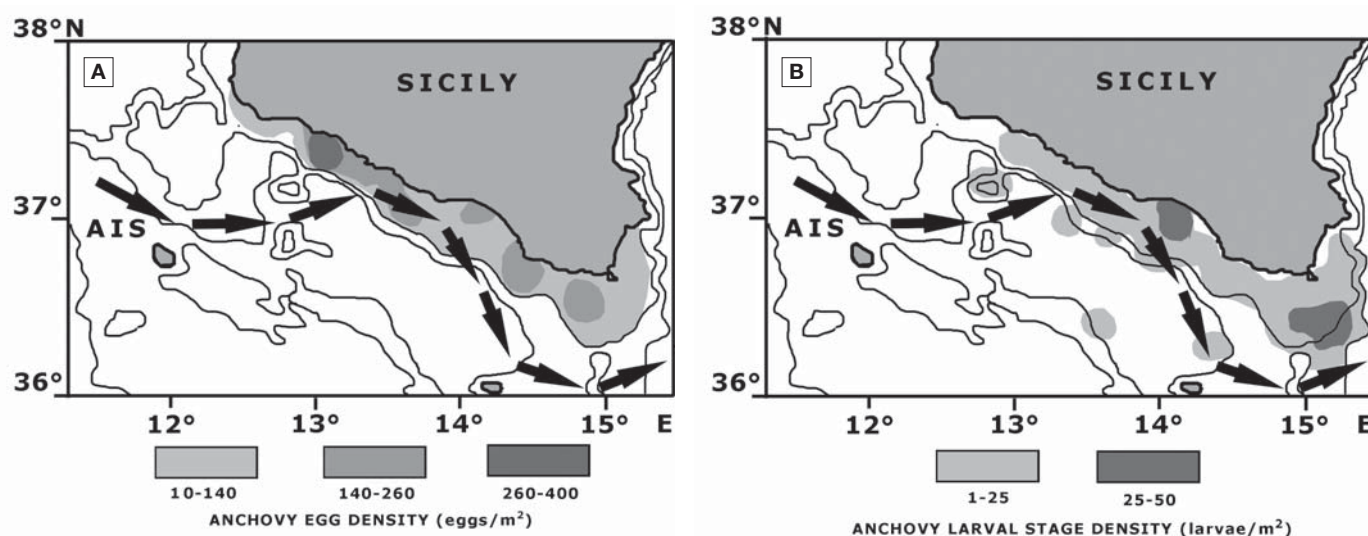
The Alboran Sea is one of the main areas of anchovy abundance and fishing in the Western Mediterranean Sea (Garcia and Palomera, 1996). The spawning peak occurs in July (Giraldez and Abad, 1995; Rubin, 1997), as in the other areas discussed here, and the highest concentrations of both eggs and larvae are found in the southern Alboran Sea off Alhucemas Bay and near the Chafarinas Islands. Anchovies spawning in an area of very high mixing intensity, near the Chafarinas, can be considered an anomaly, but possibly there are areas sufficiently sheltered, among the islands, and between the islands and the coast, to allow successful early larval feeding. Rubin (1997) reports both anchovy and sardine nursery grounds within the Bay of Malaga, which has a shape providing shelter from the large scale westerly wind flow. The density of surface waters is relatively higher near the northern coast of the Alboran, thanks to the cooler Atlantic surface water input and coastal upwelling. This should induce an eastward geostrophic flow along the coast, which would transport nutrient-enriched conditions (favoured by both processes), together with larvae spawned in the west, to the vicinity of the Bay of Malaga. (Garcia *et al.*, 2002c) discuss retention and conditions favourable for larval feeding and growth

9.4. THE ADRIATIC SEA

Anchovies are an important resource for the Adriatic Sea. During the period between 1962 and 1973, anchovy catches were 47% of the mean annual catch of pelagic fish (Regner, 1996), although a decrease in the catch has been observed since 1978 (anchovies comprise 29% of pelagic fish landings for the period 1977–89). Despite the fact that anchovy remains the most intensely studied fish species in the Adriatic, there are no available detailed studies of the influence of Adriatic circulation on the transport and survival of its larval stages. (Agostini and Bakun, 2002).

Positive correlations have been identified between the quantities of anchovy eggs and larvae and the concentration of phytoplankton in the Adriatic (Regner, 1996). Anchovy spawning is more intense along the western side of the Adriatic where primary production appears to be higher. Giovanardi (1998) identified the area close to the outflow region of the river Po as a particularly important spawning and nursery area for anchovy in the Adriatic. In the eastern Adriatic, on the other hand, anchovy egg production is concentrated near local upwelling sites (Regner, 1996). From these sites, larvae are likely to be rapidly *advected* (transported horizontally by a mass of fluid). Otherwise, they are entrained in

Fig. 67: Anchovy egg (A) and larvae (B) distribution along the southern coast of Sicily. The map (B) shows the effect of Atlantic Ionian Stream flow (AIS) on the larvae concentration off Capo Passero (Garcia-Lafuente *et al.*, 2002. Modified).



relatively enriched waters probably benefitting from fine-scale convergence zones formed between water patches of slightly differing densities, related to differing degrees of upwelling conditions, across to nursery grounds on the opposite coast.

9.5. THE STRAITS OF SICILY

It has been difficult to locate much of the information published on anchovy reproduction off Tunisia. Anchovy eggs were found and reported in a survey conducted in 1972 (Ktari-Chakroun, 1979), but in spite of their comparatively high values, anchovies, even during that period, never attained more than 9% of the pelagic landings in the area.

Anchovy spawns along the narrow shelf off the southern Sicilian coast, from Sciacca to Gela (Garcia-Lafuente *et al.*, 2002). The most important spawning ground is located off Sciacca, where a branch of the Atlantic Ionian Stream (AIS) impinges the coast. Other places can provide similar favourable spawning conditions, such as the region off Cape Passero. East of Cape Passero, the continental shelf drops sharply and by lateral friction with the coastline to the left side of the jet, it makes a northward bending with a cyclonic circulation cell of the AIS, flowing into the deep Eastern Mediterranean Basin (Fig. 67A). This area could act as a retention area with low current velocities. A second area of low flow velocities is the southeast end of the Gulf of Gela, off Sicily, due to the detachment of the AIS from the shore, as observed from the general circulation pattern.

Larval distribution shows the role played by advection. Larval abundance and larval size increase towards the southeast (Fig. 67B), and Cape Passero not only registers maximum larval densities but also larger individuals. On the other hand, the locally unbalanced ratio anchovy eggs/anchovy larvae in this zone indicates that the larvae did not hatch there, but were advected from other areas.

High larval concentration observed by Garcia Lafuente *et al.* (2002) off Cape Passero raises the question of whether there are physical reasons for defining it as a retention area. As shown in Figure 14, the general surface circulation of the AIS generates vortices. These result in the formation of a series of anticyclonic and cyclonic vortex off the southern coast of Sicily and Malta. The maintenance of cyclonic vortex implies the existence of upwelling at its centre to counterbalance the effects of friction. This is a suitable condition for sustaining high rates of primary production. Convergence generated by anticyclonic eddies southeast of Cape Passero allows the larvae to maintain their relative position in an area where retention also provides favourable conditions for larval feeding and growth.

10. Climate change

10.1. GENERAL OVERVIEW

In the last 420,000 years, Earth experienced more than four climatic cycles. The latest glacial period started 120,000 years ago and ended just 16,000 years ago, followed by a warm period up to the present. The strong relationship between greenhouse gases of natural origin, such as carbon dioxide (CO₂) and methane (CH₄), and the Antarctic climate documented over the last climatic cycle, has been remarkably confirmed over the four climatic cycles, spanning 420,000 years. With the industrial revolution of the 18th century, man caused a rapid increase of the two greenhouse gases mentioned, continuing up until the unprecedented present-days levels. This increase is associated with a corresponding rise of global surface temperatures of between 0.4°C and 0.8°C since 1860. 20th-century warming appears to have a naturally forced component, however the rate seems too large to be explained by natural influences alone. In particular, summer temperatures in the Northern Hemisphere during recent decades are the warmest in at least six centuries. Land surface precipitation has increased in much of the Northern Hemisphere at mid and high latitudes, while much of the tropical areas have become drier. According to the scenarios produced by the Intergovernmental Panel of Climate Change (IPCC), the remarkable rise in greenhouse gases will lead to an increase in the global surface temperature of 1.7-4.0°C before 2100 and to a mean sea-level rise of 22-75 cm, while temporal and spatial features of precipitation will be altered. Hence, as the global climate appears to be changing, we would expect the Mediterranean climate to follow the same pattern.

10.2. FUTURE CHANGES OF CLIMATIC PARAMETERS IN MEDITERRANEAN

The hypothesis of a current warming of the Mediterranean water was advanced for the first time, backed up by proof by Bethoux *et al.* (1990), with an increase of the temperature of the deeper water of 0.12°C in 30 years. Since 1990, the rising of temperature has continued in an almost linear manner (Bethoux and Gentili, 1999; Bethoux *et al.*, 1999).

All model simulations share one feature: the temperature will increase considerably during the next decades.

Temperatures over the Mediterranean may increase by as much as 3.5°C before the year 2050, assuming a doubling of CO₂ concentration. The estimation of the warming range over the Mediterranean presents a considerably high variation (2.0-6.0°C by the year 2100). A lower temperature increase is expected over the sea and coastal regions, compared to inland Mediterranean areas, and the regions presenting the maximum temperature increase and sensibility are situated in the southern part of the Mediterranean.

Most projections point to significantly less precipitation in summer over the region as a whole. On the other hand, several models suggest an overall increase in winter precipitation mainly over the northern part of the Mediterranean region, a smaller increase however than over northern Europe. In general, prospects for precipitation over the Mediterranean region in a warmer world are still highly uncertain, as general circulation models for predicting regional precipitation are still weak.

Despite these uncertainties regarding the exact extent to which climate variability and extremes will change in the Mediterranean region, the overall picture suggests an increase in the frequency of extreme events and, in particular, of droughts in the western Mediterranean. In general, warmer conditions over the Mediterranean region should lead to an increase in the occurrence of extremely high temperatures and a decrease in extremely low temperature events. In areas experiencing a general decrease in precipitation, droughts are likely to become more frequent as the probability of dry days and the length of dry spells increases.

Mean sea level in the Mediterranean is expected to rise at the rate of 5 cm/decade: the Nile Delta, Venice and Thessaloniki appear to be the more sensitive areas in Mediterranean.

(From: www.climate.noa.gr/Reports/Executive_summary_Eng.PDF).

Jellyfish blooms

Because of the pulsed nature of their life-cycles, gelatinous zooplankton come and go seasonally, giving rise in even the most undisturbed circumstances to summer blooms. Holoplanktonic species like ctenophores also increase in number in the spring or summer, when planktonic food is available in greater abundance. Beyond this basic, lifecycle-driven, seasonal change in numbers, several other kinds of events appear to be raising the number of jellyfish present in some ecosystems. Over recent decades, man's expanding influence on the oceans has begun to cause real change. There is reason to think that in some regions, new blooms of jellyfish are occurring in response to some of the cumulative effects of these anthropic impacts. The issue is not simple and in most cases there is little data to support our perceptions. Some blooms appear to be long-term increases in native jellyfish populations. Jellyfish, whose populations regularly fluctuate, apparently with the climate, thereby causing periodic blooms, demonstrate a different phenomenon. Perhaps the most damaging type of increasing numbers of jellyfish has been caused in recent decades by populations of new, non-indigenous species gradually expanding to attain "bloom" levels in some regions. There are also examples of jellyfish populations decreasing in heavily impacted coastal areas. Some jellyfish will undoubtedly fall subject to on-going species elimination processes that already portend a vast global loss of biodiversity. Knowledge about the ecology of both the medusa and the polyp phases of each life-cycle is necessary if we are to understand the true causes of these increases and decreases, but in most cases where changes in medusa populations have been recognized, our knowledge about the field ecology of polyps is very poor (Mills, 2001; Boero *et al.*, 2008).



10.2.1. Possible effects of anomalous weather conditions on Mediterranean circulation

The seasonal cycle drives the variability of sea surface parameters in all temperate regions, including the Mediterranean Sea. Variations produced in Sea Surface Temperatures (SST), and current intensity and direction, can directly influence either the physical variables or different biological processes. The effects of climate change on the Mediterranean biodiversity has been reviewed by Perez (2008), these effects include various aspect of top pelagic predators and small-pelagic species biology such as metabolic functions, genetic modifications, growth, concentration and retention of early life stages, recruitment, reproductive strategies and overall distribution. Furthermore, seasonal water stratification characterising the seas of temperate regions in the summer period determines a reduction in mixing from deep to surface that can strongly influence nutrients and phytoplankton dynamics (Olita *et al.*, 2006).

Changes in upwelling can have a profound effect on a variety of ecosystems, and variations in upwelling may result in significant changes in productivity. Changes in ocean temperature have already been linked to changes in marine ecosystems. If the hypothesis that increased greenhouse gas forcing will lead to intensified upwelling is correct, it is not yet clear what might be the future of these systems and their effect on ocean productivity (Snyder *et al.*, 2003)

Fig. 68: "Medusen I", plate by C. Mercuriano in *Meyers Großes Konversations-Lexikon*, Auflage 6, Bibliographisches Institut, Leipzig, 1902-08.

11. Mediterranean pelagic ecosystem protection

There is growing interest in the protection of the pelagic realm at world level and various approaches have been proposed. In the Mediterranean pelagic ecosystem, the high variability and heterogeneity of habitats, which evolve within a four-dimensional (time-volume) environment, create a very complex network of interactions among the organisms living there.

Even if evidence of some regularly recurring patterns does exist, the descriptive and provisional power of the models is still poor, making it very difficult to set appropriate solutions for the protection of “*ephemeral habitats*” with conditions favourable to high biodiversity. The life of these habitats can span from a few hours up to several months over very small-scale to mesoscale levels, nevertheless fundamental for the general functioning of the system.

Concerning protection issues, the complexity of maritime jurisdiction must be added to the complexity of the natural habitats. In the Mediterranean Sea, the number of coastal countries and the level of political and economic interests make complexity higher than in other sectors of the world seas (Fig. 1) and contribute to make conservation tasks very difficult.

Awareness of these difficulties leads to different approaches among the people involved in protection issues. A “*pragmatic approach*” mainly focuses its attention on overcoming initial political and social resistances by proposing solutions that recall well-tested experiences. Up to now, coastal MPAs are the only effective models we dispose of for inspiration, so the same application scheme recurs in various MPA proposals for the Mediterranean Sea (Fig. 4). For the same reasons, it is not surprising that the same scheme has also been applied for the only large pelagic MPA existing in the Mediterranean, the *Pelagos* Sanctuary.

Once a pelagic MPA becomes a realistic idea, the major problem is represented by the setting of boundaries. This always represents a compromise between identified protection needs and other interests (public and private), but never encompasses the system's variability. Fixed boundaries can be understood and accepted

by the maritime jurisdiction in force, but cannot be respected by highly mobile pelagic organisms. Larger protected pelagic areas could be established in order to include the known variability of those oceanographic structures determining biodiversity hotspots. Nevertheless, wider MPA extension corresponds to higher costs and more difficulties regarding effective surveillance and monitoring.

In respect of this last aspect, it could be useful to identify a number of critical habitats within a larger pelagic MPA or even create a network of smaller MPAs. In this way it would be possible to carry out improved protection of more sensitive areas, e.g. “stepping stones”, such as identified breeding, spawning and feeding grounds for vulnerable species. This may be more effective if the MPAs are set to cover the entire distribution ranges of a particular species.

A MPA network could also be designed to protect a number of representative habitats, in order to assure protection for enough biodiversity hotspots. Static MPA boundaries could be effectively defined in order to protect static pelagic habitats such as seamounts and submarine canyons (Fig. 17, Fig. 19).

Many Mediterranean pelagic species undertake very wide migrations, inside and outside the Strait of Gibraltar. An MPA network must take into account this aspect of the species' biology. If a migration route is interrupted by natural events or causes of anthropic origin, the migrating species can change its conservative behaviour, leaving the migration routes forever. The more obvious consequence is that one or more MPA areas within the network could be abandoned. For many species moving throughout the entire Mediterranean Sea (i.e. bluefin tuna, swordfish, turtles, sharks and cetaceans), protection of migratory corridors could be as essential as protecting their feeding and spawning areas.

Protecting an area by means of fixed boundaries can be useful to mitigate and even solve certain problems deriving from human activities (as long as there are no changes in the system, which could drive protected species far from the protected area).

By establishing protection zones, it is possible to reduce and even eliminate the impacts of those activities directly affecting the individuals, e.g. fishing by catch, collisions, noise pollution, stress by high boating concentration, etc.

Pollutants concentrate in the top predator tissues through food webs, driving a series of negative effects such as immunodeficiency, reduction of reproductive potential, epidemic viruses, etc. In all ecosystems a great part of these threats are mediated by physical-chemical and biological processes, frequently originating far from the area in which they occur. Because of pelagic ecosystem dynamics, it is not surprising that a more effective approach can be to shift attention towards something else and somewhere else, for realistic protection of a given species or a given habitat.

This last consideration turns us to the ecosystem approach, which means confronting protection issues in their entirety, considering interactions among all the various elements (natural or anthropic) acting within the ecosystem. Representing a coherent application of the ecosystem approach, strongly limited by political, economical, cultural, technical and scientific gaps, the proposal of an MPA network seems to be the more realistic approach for the Mediterranean Sea, at least so far.

An MPA network, if it is designed on a static basis, could not properly correspond to ecosystem approach principles. Considering it impossible to protect the entire Mediterranean Sea area, since the main characteristic of its pelagic environment is high variability, the instruments for its protection must also be flexible enough to adapt quickly to a new situation. Moreover, protection carried out by area is limited to the evidence on the surface of the sea. Frequently what is visible is the result of processes linked to water masses, which may not be restricted to the water column exactly below the protected area. In the Mediterranean Sea, cyclonic circulation affects the productivity of the two basins and upwelling areas in their northern parts are strictly linked to convergence in the south. What is done in the north returns to the north with a contribution from the southern coast, through west-east and south-north cycles (Figs. 12, 13, 14).

For these reasons, the aspect related to water mass protection seems to be crucial for future application of the ecosystem approach to pelagic habitat conservation, even if it is not yet considered as a priority.

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Color plates



Fig. 1 (p. 9):
Strait of Gibraltar and Western Alboran Sea. Atlantic water (AW) generates strong eddies as it passes through the Strait of Gibraltar. AW undergoes intense mixing causing a loss in heat before it reaches the Alboran Sea. Here upwellings are set mainly on the Spanish side, while clockwise (anticyclonic) eddies generate convergence (downwelling) off the African coast. Image SeaWiFS (S1997361123941.png) <http://visibleearth.nasa.gov>

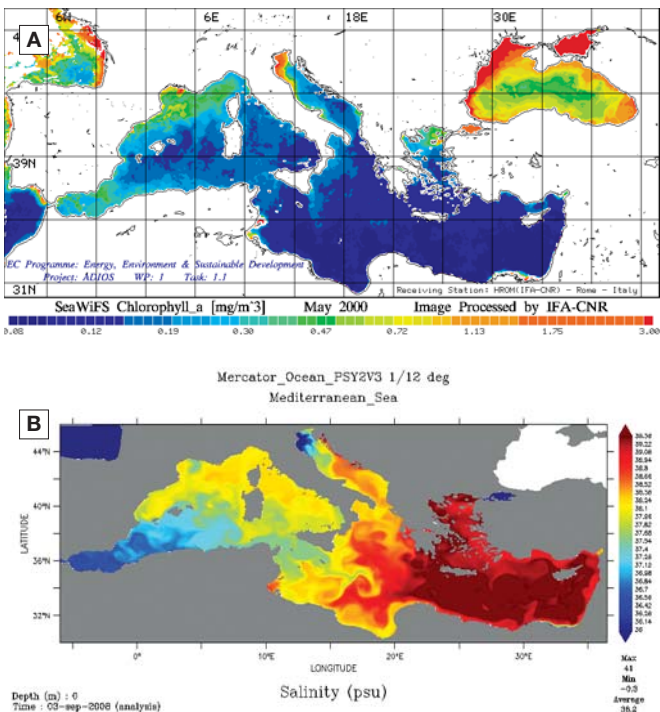


Fig. 2 (p. 11):
A) The west-to-east decreasing gradient of nutrients results in a gradual west-to-east reduction in productivity. The satellite image shows the eastern Mediterranean waters poor in pigment and the west-east gradient. Primary production in the northwestern basin of the Mediterranean is on average 3 times higher than that in the eastern basin.
B) Higher salinity increases water density, as in water leaving the Mediterranean. In the eastern basin, denser water flows down and westward at intermediate level, below the lighter incoming Atlantic water (AW).

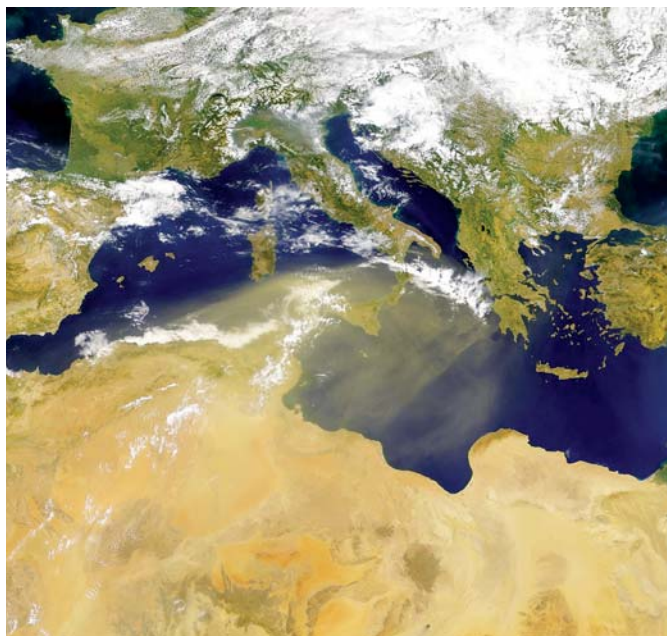


Fig. 3 (p. 12):

The desert meets the southern coast of the Mediterranean, while the northern coasts are mainly constituted of more productive lands. Dust inputs from the southern coast via atmosphere dynamics, is important to the functioning of the Mediterranean pelagic ecosystem (e.g. nutrient input). Provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE.

Fig. 8 (p. 18):

Floating objects can be attractive for young pelagic stages of off-shore benthic species such as *Polyprion americanus* as well as for larger predators (e.g. dolphin fish, billfishes, bluefin tuna, tuna-like species, etc.)..

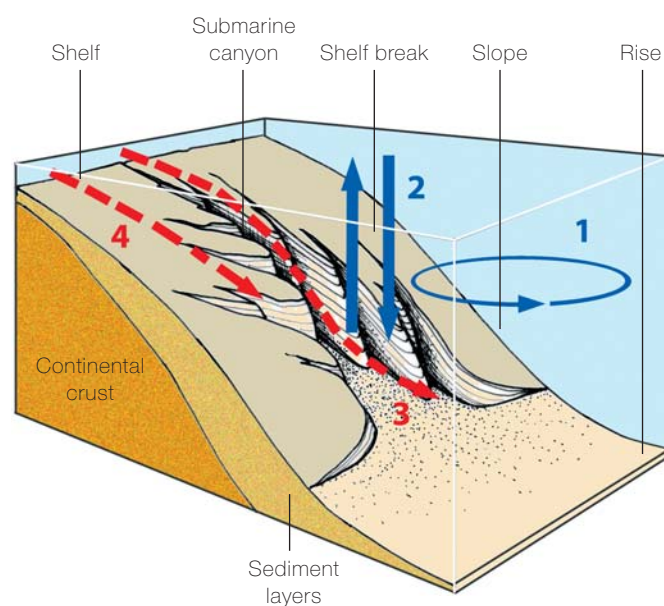


Fig. 18 (p. 26): Submarine canyon processes scheme. 1) Eddy formation; 2) Up- and down-welling; 3) Slumps, turbidity currents; 4) Off-shelf currents.

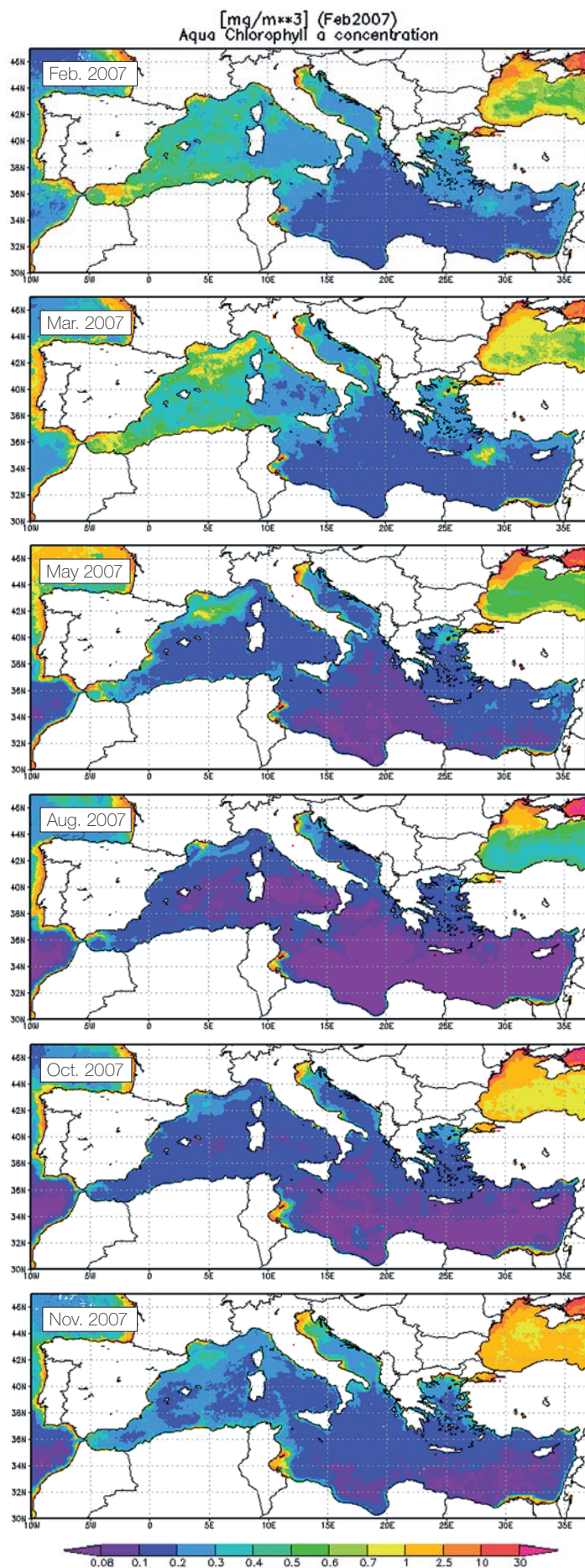


Fig. 12 (p. 22): Chlorophyll concentrations during the year 2007 (from NASA Giovanni).

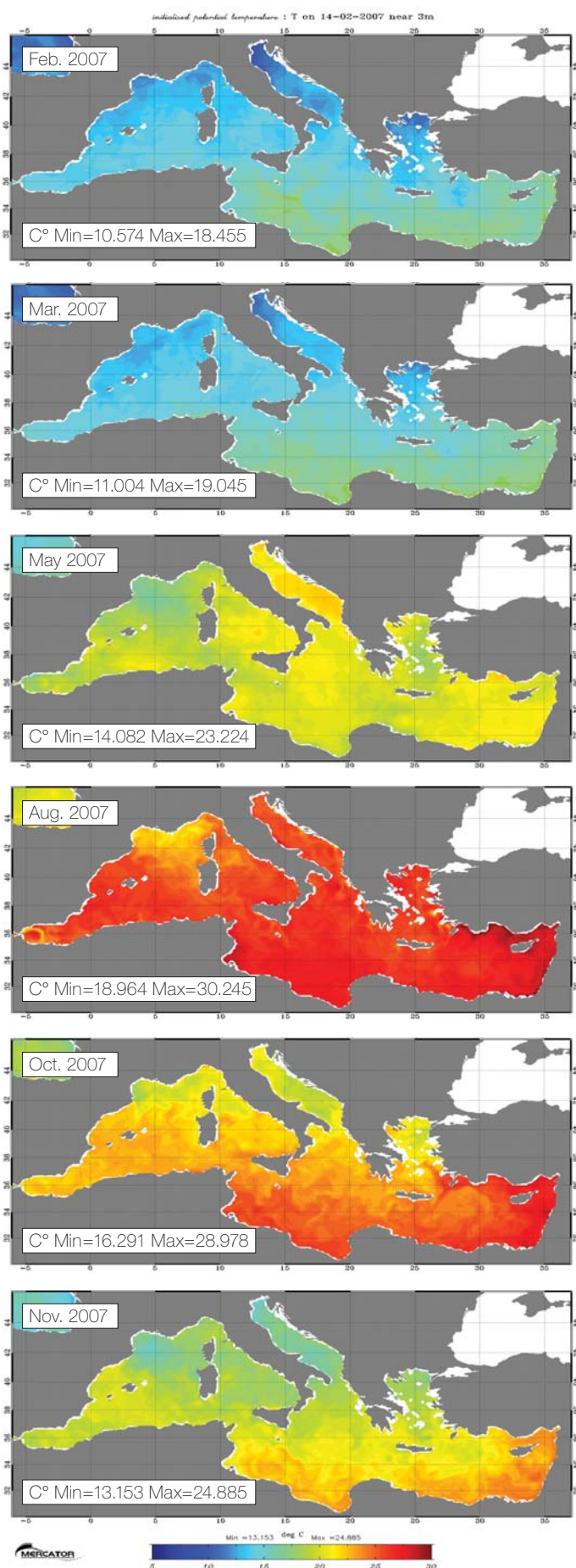


Fig. 13 (p. 22): Sea surface temperature (SST), year 2007 (from Mercator-Ocean).

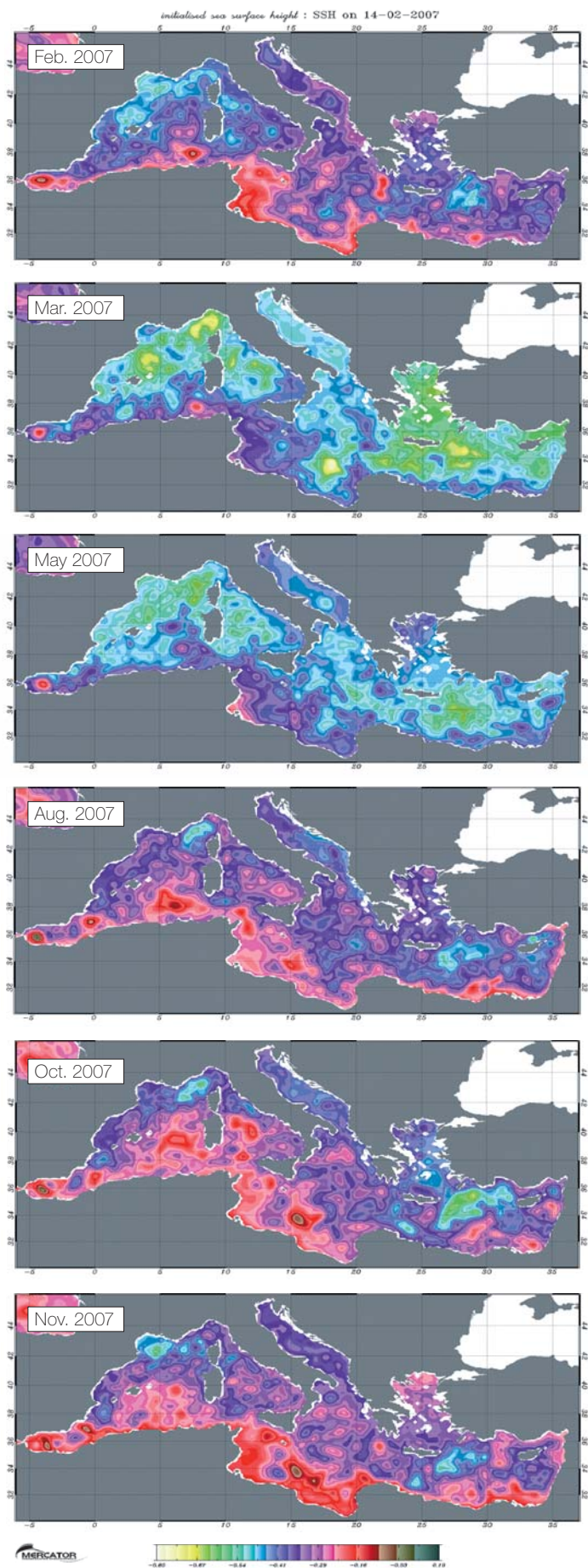


Fig. 14 (p. 23): Sea Level Height (SSH), year 2007 (from Mercator-Ocean).

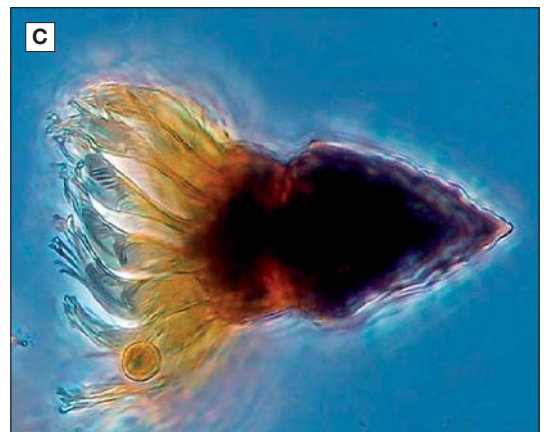


Fig. 22 (p. 31): Protozoans:

B) Foraminifera: *Challengeron willemoesii*.

C) Ciliates: a swimming oligotrich ciliate with its prey.
Photos: John Dolan, Station zoologique de Villefranche-sur-Mer, <http://www.obs-vlfr.fr/LOV/aquaparadox>

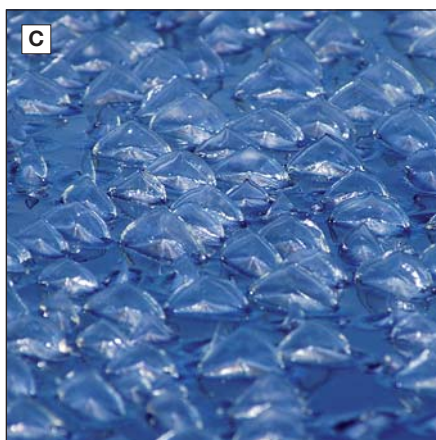
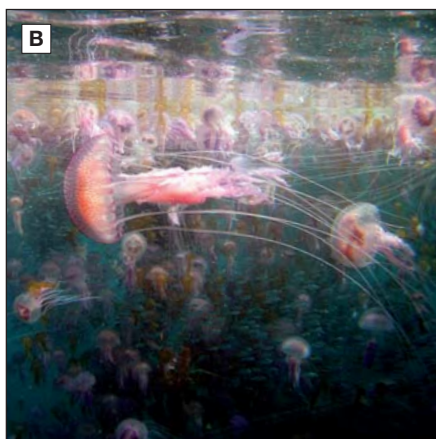
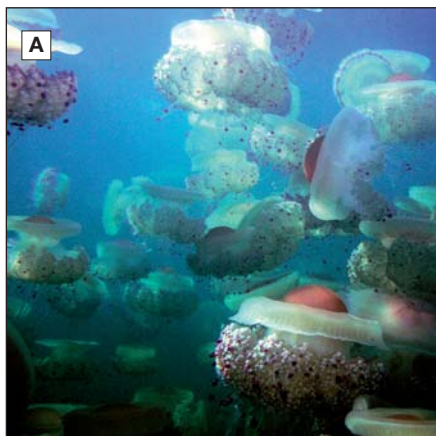


Fig. 23 (p. 32): Cnidaria.

- A) *Cotylorhiza tuberculata*.
Photo: Ignacio Franco,
Centro Oceanográfico de Murcia.
- B) *Pelagia noctiluca*.
Photo: Sandrine Ruitton.
- C) *Veella veella*.
Photo: M. Rosso, DIBIO, Unige.

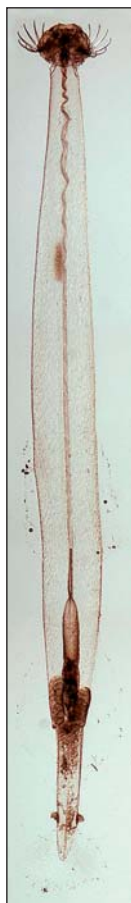


Fig. 25 (p. 32):

Chaetognatha, *Flaccisagitta enflata*. Size: 2 cm.
Photo: Yvan Perez,
Institut Méditerranéen d'Écologie et de Paléoécologie.

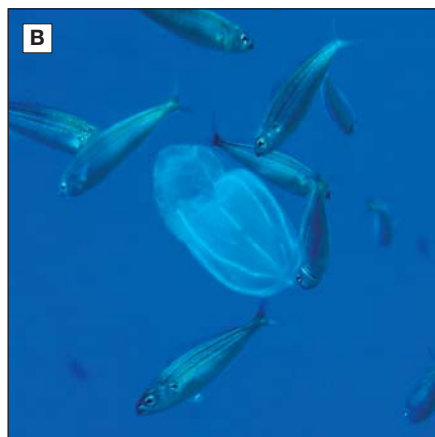
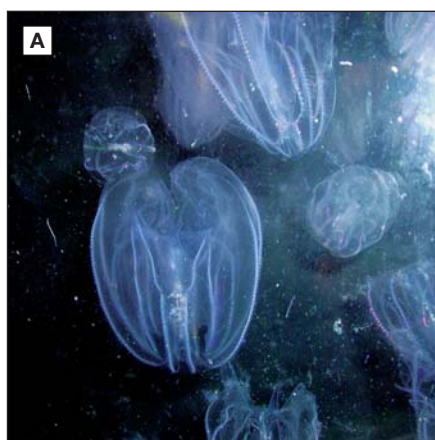


Fig. 24 (p. 32):

Ctenophora.

- A) *Mnemiopsis leidyi*. In the Eighties, it has been introduced into the Black Sea through tanker ballast waters, now is proliferating in the Mediterranean with a strong impact on fish eggs and larvae. Photo: Prof. Hans Ulrik Riiisgård, Marine Biological Research Centre (University of Southern Denmark).
- B) *Beroe* sp. Photo: Olivier Le Corre, <http://www.olivierlecorre.com/>

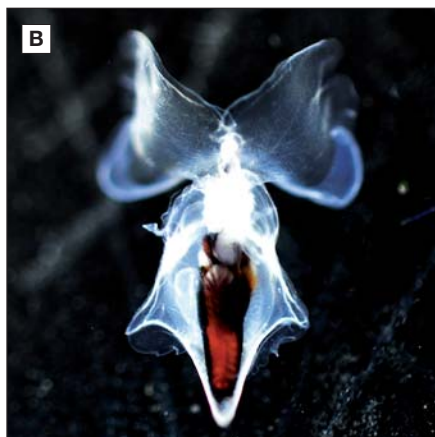


Fig. 27 (p. 33):

A) Heteropods Molluscs, *Pterotrachea* sp.
Photo: Olivier Le Corre.

B) Pteropods Molluscs: Adult of *Cavolinia inflexa* collected in the Villefranche-sur-Mer bay. Photo: S. Comeau, Observatoire Océanologique de Villefranche.

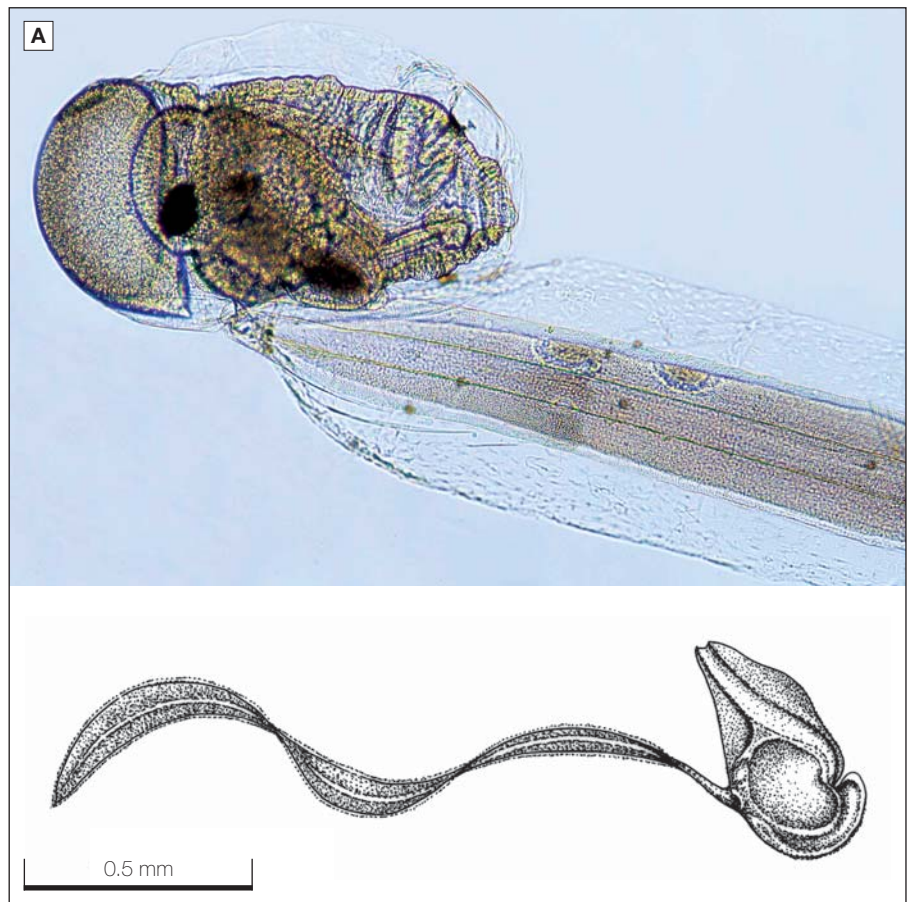
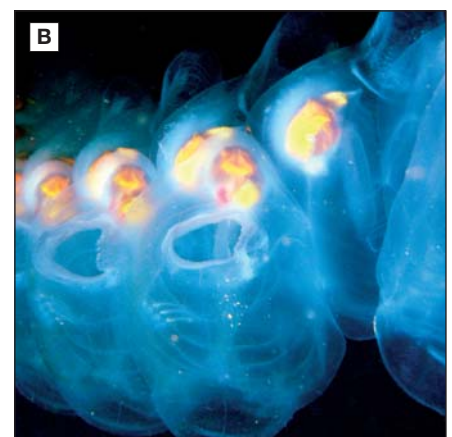


Fig. 28 (p. 33):

Urochordata.

A) Appendicularians: *Oikopleura dioica*. Photo: Maurice Loir,
<http://www.diatomloir.eu/Siteplancton/Tunicier.html>

B) Salps, Photo: Olivier Le Corre.



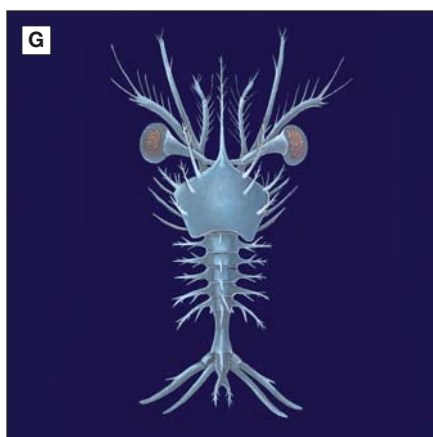
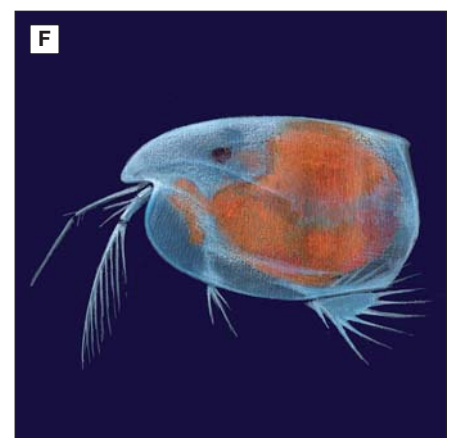
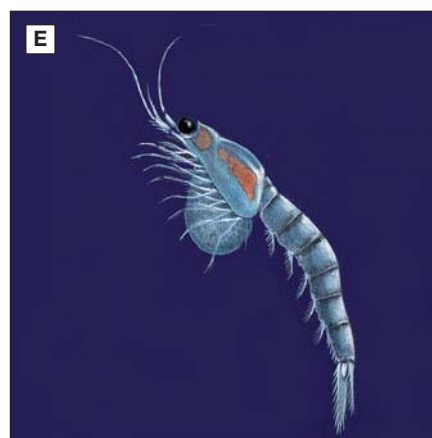
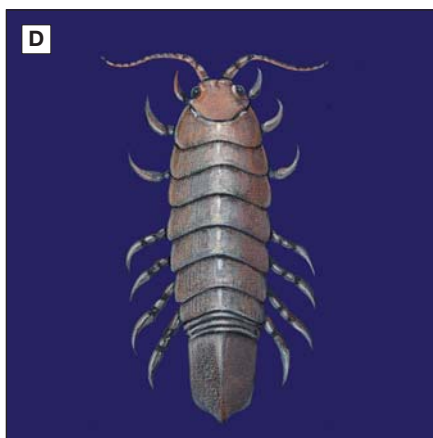
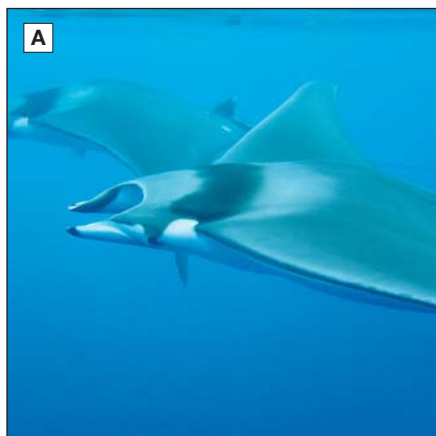


Fig. 29 (p. 34):

Crustacea:

- A) Copepods,
female of *Centropages kroyeri*.
Photo: Stéphane Gasparini, Laboratoire
d'Océanographie de Villefranche.
- B) Euphausiids,
- C) Amphipods,
- D) Isopods,
- E) Mysids,
- F) Ostracods,
- G) Decapods (larval stage of *Sergestes* sp.)



B



C



E



F

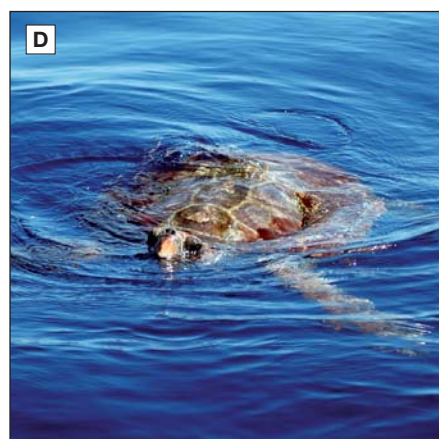


Fig. 30 (p. 35):

Nectonic species.

A) *Mobula mobular* ;

B) *Mola mola*, by V. Fossat, 1878. Coll. Muséum d'Histoire naturelle de Nice ;

C) *Thunnus thynnus*, by V. Fossat, 1878. Coll. MHNN ;

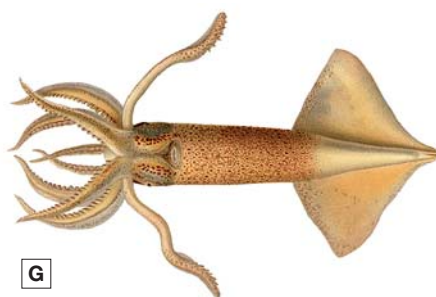
D) *Caretta caretta*,

E) *Prionace glauca*, by V. Fossat, 1879. Coll. MHNN ;

F) *Coryphaena hippurus*, by V. Fossat, 1879. Coll. MHNN ;

G) *Onychoteuthis banksii*. Joubin, L., 1900. Céphalopodes provenant des campagnes de la Princesse-Alice. *Résultats des campagnes scientifiques accomplies sur son yacht par Albert I^{er} prince souverain de Monaco*, Fascicule XVII, planche XII ;

H) *Stenella coeruleoalba*.



G



H

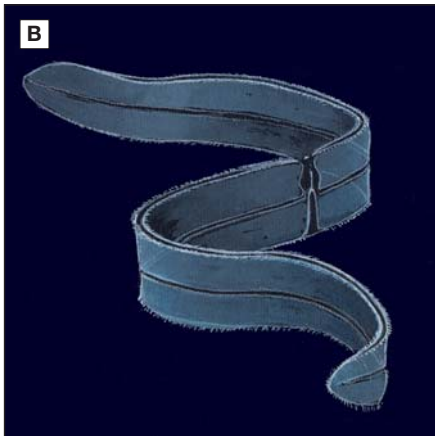
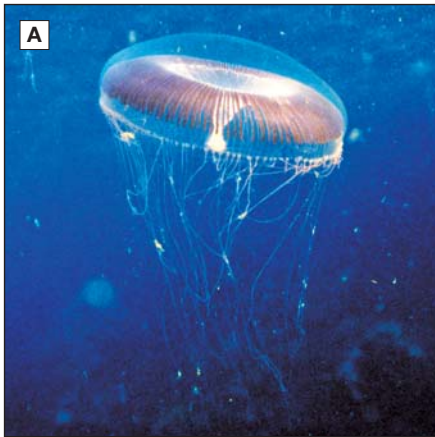


Fig. 31 (p. 36):

A) Cnidaria, *Aequorea forskalea*.

Photo: Olivier Le Corre.

B) Ctenophores, *Cestus veneris*.

C) Urochordata (tunicates), *Pyrosoma* sp.



Fig. 32 (p. 37): Mesopelagic fishes.

A) Gonostomatidae: *Cyclothone* sp.
(from Zugmayer, 1911).

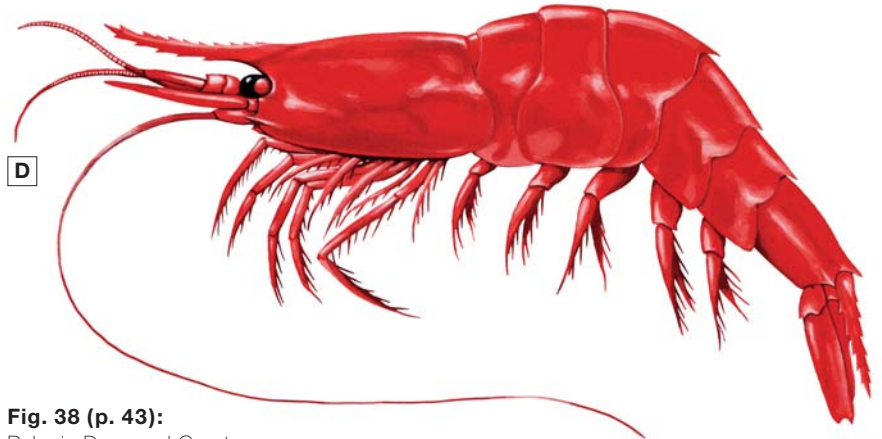


Fig. 38 (p. 43):

Pelagic Decapod Crustaceans.

D) *Acantheephyra pelagica*.



Fig. 42 (p. 45):

An Isaacs-Kidd Mid-water Trawl (IKMT) hauling on board after a mesopelagic tow.

Photo: Laure Mousseau, Enseignement UPMC-OOV.



Fig. 41 (p. 45):

Argyropelecus hemigymnus.

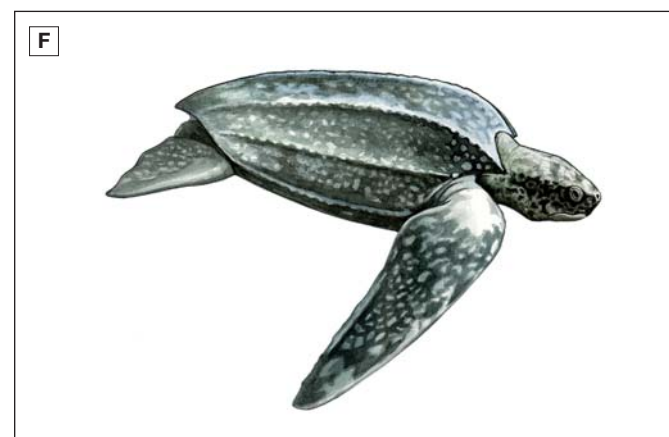
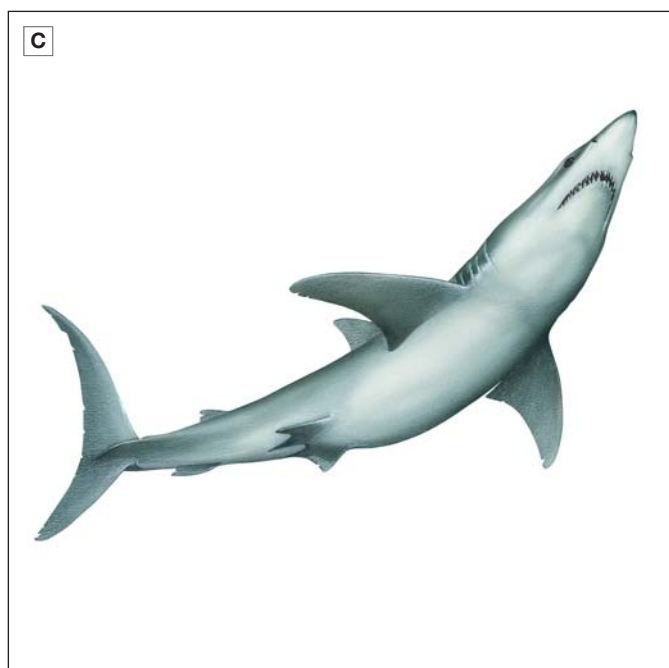
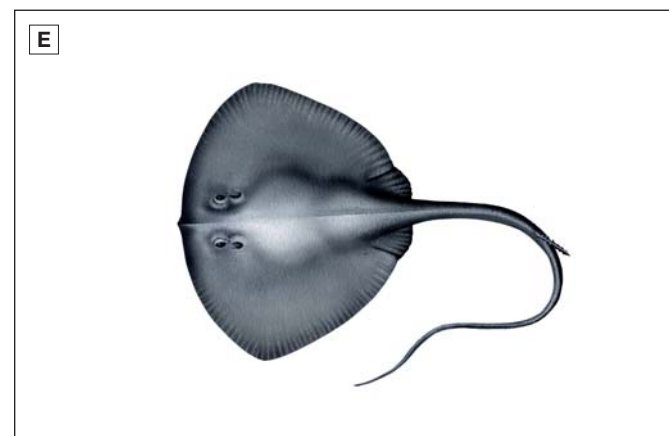
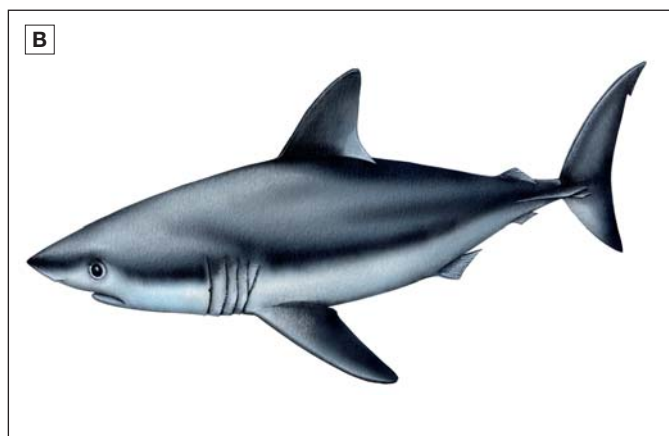
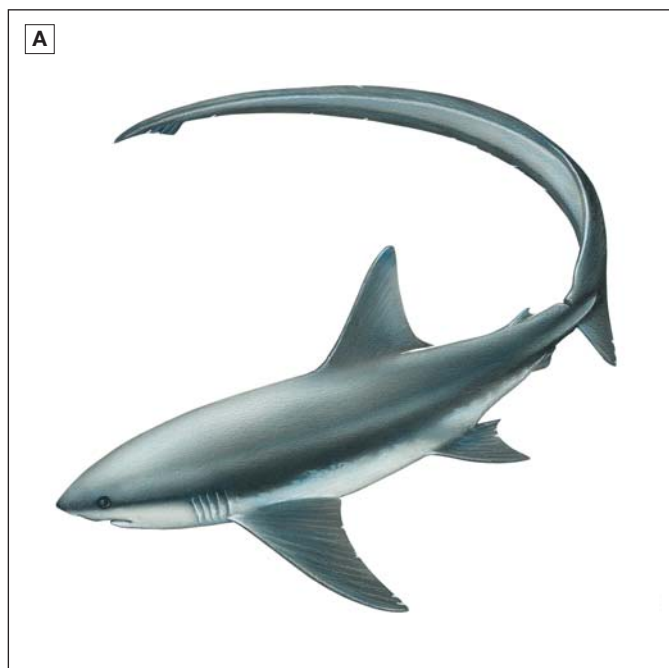


Fig. 47: Pelagic sharks, rays and turtles (p. 48):

A) *Alopias vulpinus*, size: common 400 cm;

B) *Lamna nasus*, size: common 250 cm;

C) *Isurus oxyrinchus*, size: common 250 cm;

D) *Cetorhinus maximus*, size: common 500 cm;

E) *Pteroplatytrygon violaea*, size: common 150 cm.

F) *Dermochelys coriacea*, size: common 140 cm.

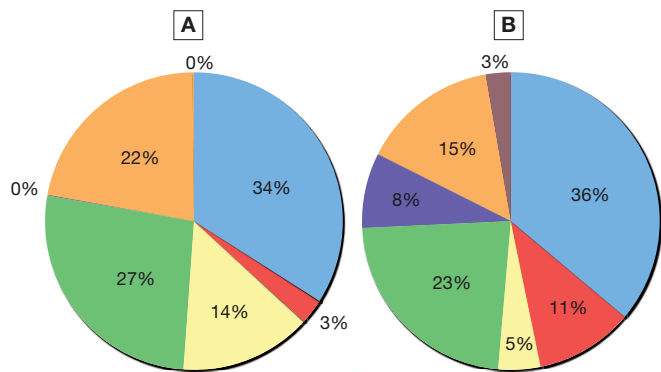


Fig. 48 (p. 51): Cumulative percentage of prey composition (A) and prey occurrence (B) as found in the stomachs of several top pelagic predators (Astruc, 2005; Orsi Relini *et al.*, 1992; Orsi Relini *et al.*, 1995; Pulcini *et al.*, 1992; Würtz *et al.*, 1992; Würtz and Marrale, 1993).

mesopelagic cephalopods
neritic cephalopods
mesopelagic fishes
neritic small pelagic fishes
benthopelagic fishes
mesopelagic crustaceans
jelly macroplankton

Fig. 49 (p. 51): Teuthophagous cetaceans:

- A) Risso's dolphin, *Grampus griseus*, size: maximum 4 m;
B) Sperm whale, *Physeter catodon*, size: male maximum 18 m, female maximum 12 m;
C) Cuvier's beaked whale, *Ziphius cavirostris*, size: maximum 7 m.

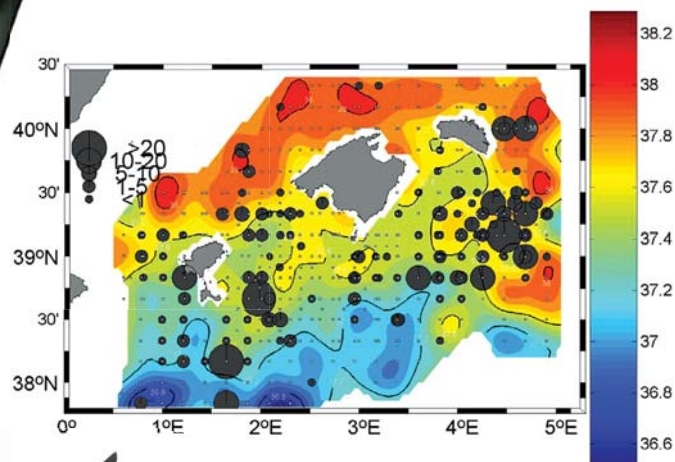
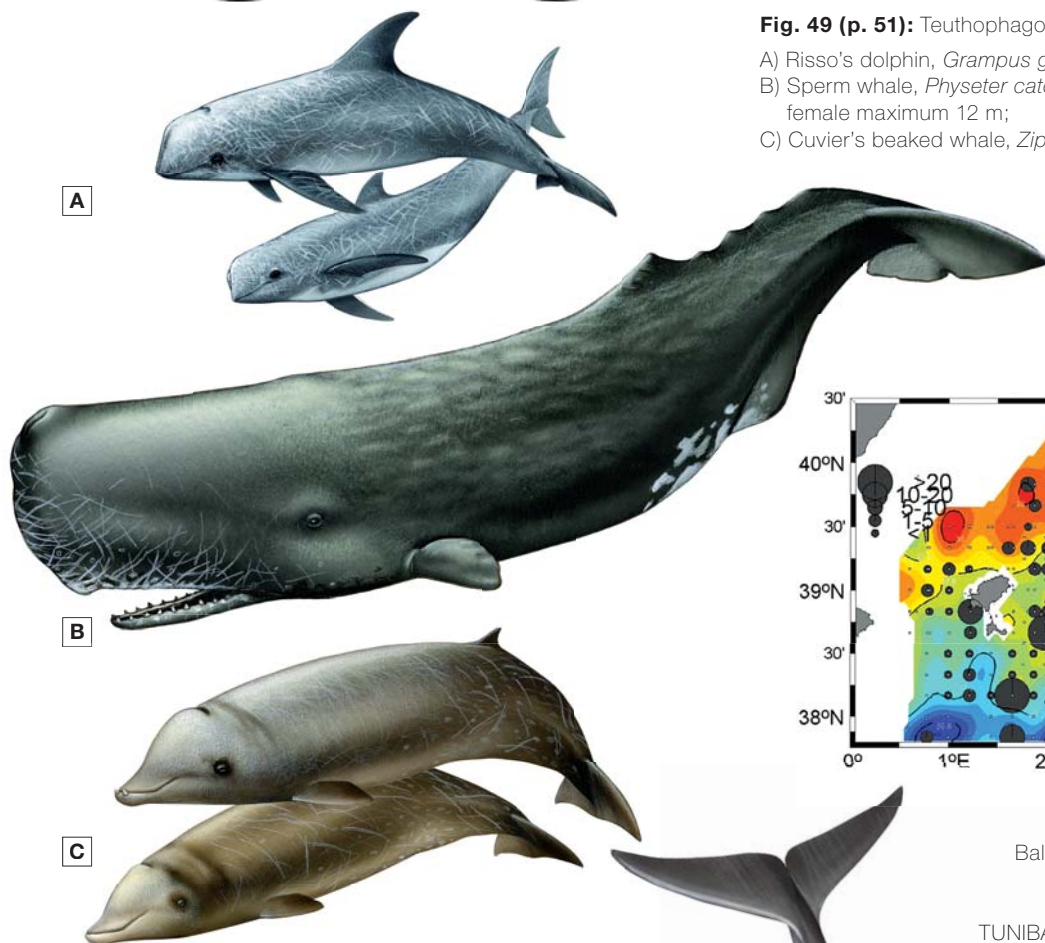


Fig. 55 (p. 54): Balearic spawning grounds of bluefin tuna. Larvae concentration related to salinity, according to the data from 2001-2005 TUNIBAL campaigns (Garcia *et al.*, 2002a, b, c; Alemany, 2008).

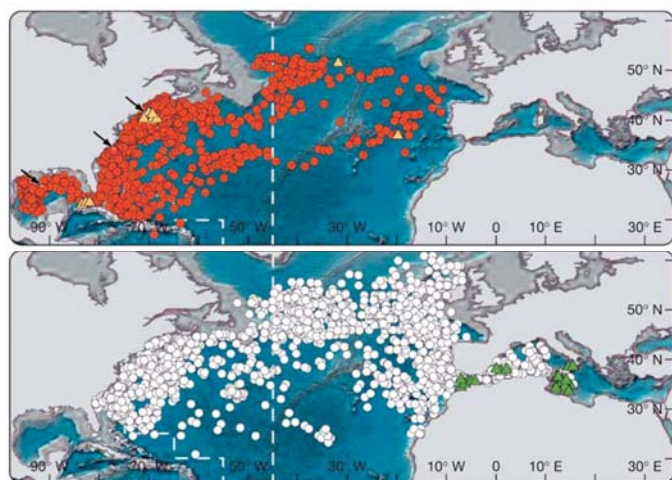


Fig. 52 (p. 53): Results of Atlantic Bluefin tuna electronic tagging campaigns (Block *et al.* 2005) show that eastern stock specimens do not reach the Mediterranean Sea spawning grounds (A) and western stock specimens do not reach the Gulf of Mexico spawning grounds (B).

Fig. 62 (p. 59):

Fin whale
(*Balaenoptera physalus*).

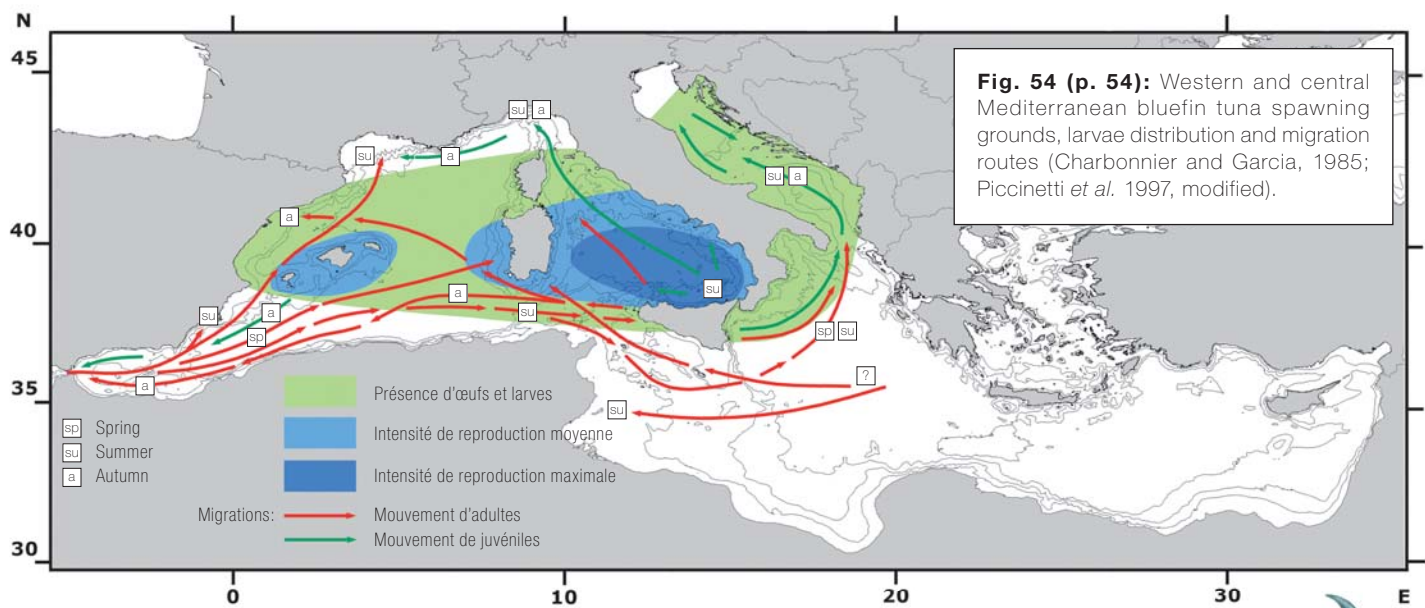


Fig. 60 (p. 57): White shark (*Carcharodon carcharias*) distribution in the Mediterranean sea, according to Fergusson and Compagno (1996). Blue intensity is proportional to the relative shark abundance.

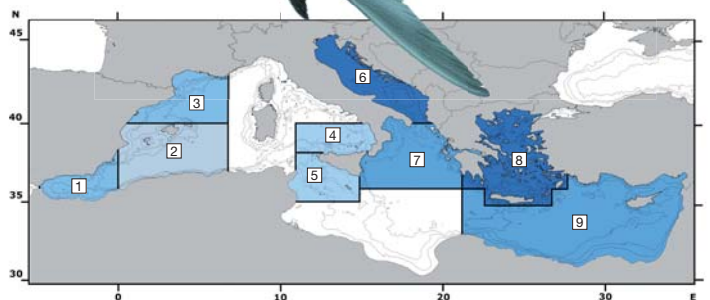
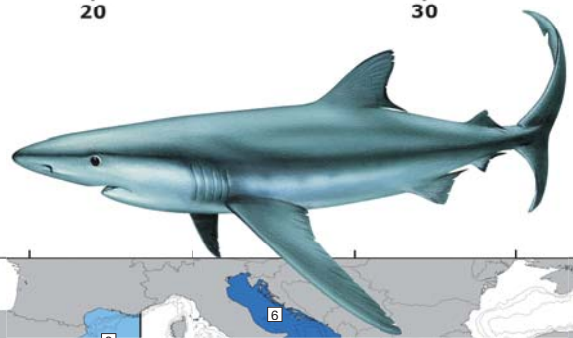
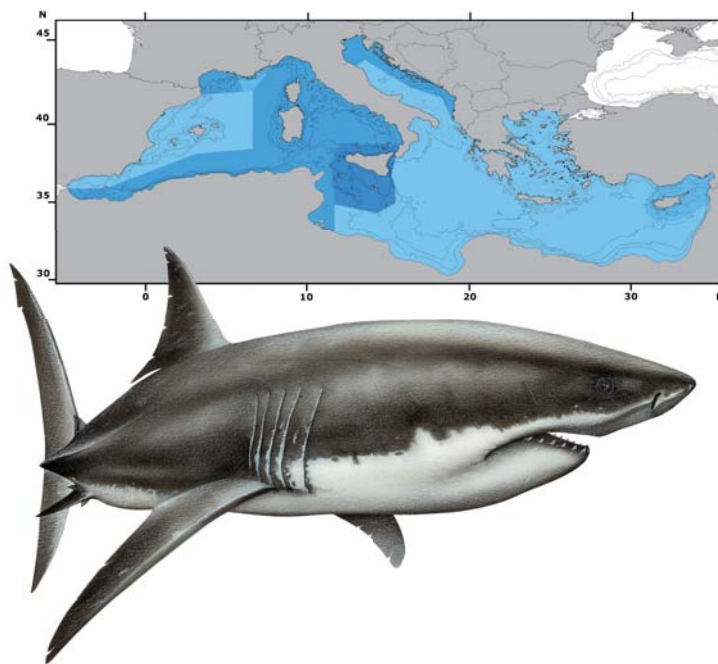


Fig. 58 (p. 57): Map of relative shark abundance in nine areas of the Mediterranean Sea according to the study on shark bycatch in swordfish fisheries during the period 1998–2000 (Megalofonou *et al.*, 2005, modified). Main species represented in the catches was *Prionace glauca*. 1) Alboran Sea, 2) Balearic Islands area, 3) Catalan Sea, 4) Tyrrhenian Sea, 5) Straits of Sicily, 6) Adriatic Sea, 7) Ionian Sea, 8) Aegean Sea, and 9) Levantine basin.

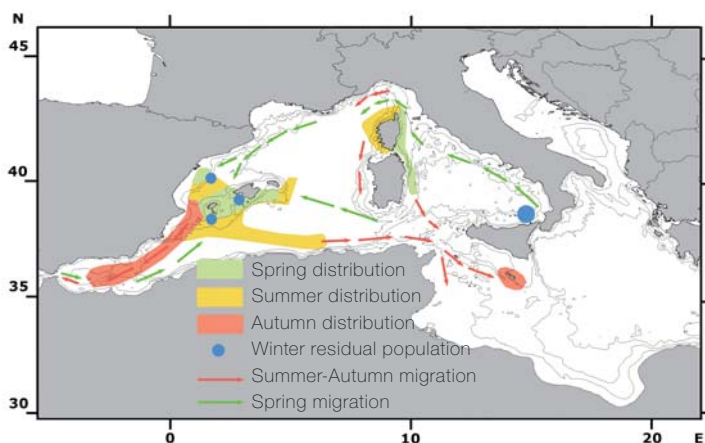


Fig. 61 (p. 58): Loggerhead turtle (*Caretta caretta*) migration routes and distribution in the western and central Mediterranean Sea. From Camiñas (2004), modified.



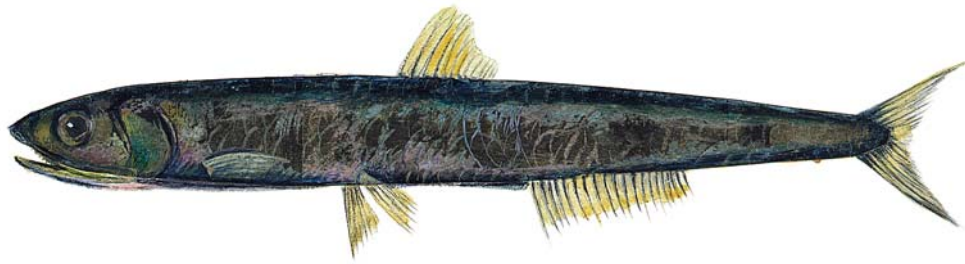


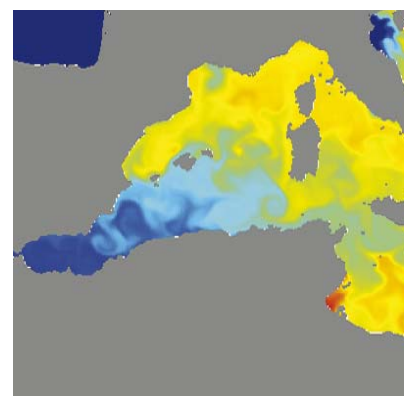
Fig. 65 (p. 61):

Anchovy, *Engraulis encrasicolus*,
by V. Fossat, 1842. Coll. Muséum
d'Histoire naturelle de Nice.



Fig. 66 (p. 62):

Sardina, *Sardina pilchardus*,
by V. Fossat, 1877. Coll. Muséum
d'Histoire naturelle de Nice.



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FOR CONSERVATION OF NATURE

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