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Abstract

Among Mediterranean marine life, benthic communities are possibly the most peculiar in terms of richness and endemic species. The distribution and structure of benthic fauna (sessile and vagile) is driven by environmental gradients that change with season, depth, the type of substrate and the interaction between organisms. The combined action of these multiple factors results in a high variety of assemblages and communities. This chapter focuses on the benthic fauna, with the aim to provide a broad description of the hard and soft bottom communities and the general trends of their characteristics and variability. Special emphasis is given to the ecological strategies of the fauna that inhabit in complex benthic ecosystems. The pressures and impacts on these benthic fauna and ecosystems, from alien species invasions, warming effects, ocean acidification and other direct and indirect human perturbations are also illustrated.

Keywords

Alien species invasions • Benthic communities • Benthic fauna • Complex benthic ecosystems • Ecological strategies • Endemic species • Environmental gradients • Hard and soft bottom communities • Human perturbations • Mediterranean marine life • Ocean warming and acidification • Sessile fauna • Vagile fauna

Introduction

The Mediterranean marine environment is characterized by a set of environmental factors that define its biota, especially in shallow communities. Extreme reduction of tides, transparent and blue waters, relatively high salinity and mean water temperature together with an evident seasonality with four recognizable seasons are the identity signals of

this temperate sea. These particular features renders the Mediterranean a very singular environment, and given the small extension of the Mediterranean (0.82 % of world oceans), with a very high marine biodiversity (between the 4 and 18 % of all marine species known) (Bianchi and Morri 2000). Among Mediterranean marine life, benthic communities are possibly the most peculiar in terms of richness and originality.

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Environmental Gradients

In marine Mediterranean benthic environments, the distribution of fauna is ruled by environmental gradients defined as: humidity (increasing from the atmosphere to the water); action-wave related factors (maximal at level zero and decreasing in both shoreward and seawater direction); water temperature and light intensity (decreasing with depth); etc.

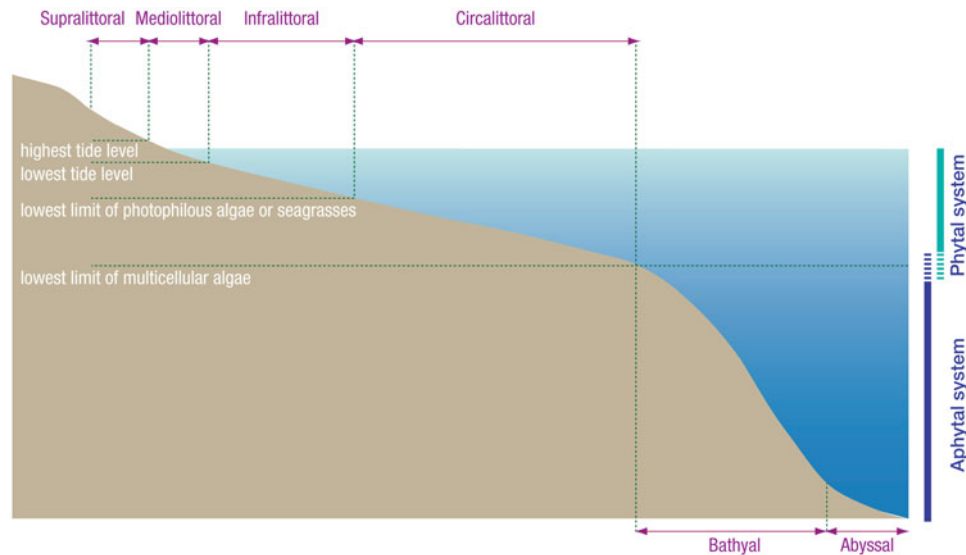


Fig. 12.1 Main benthic zonation of the Mediterranean Sea (Modified from Pérès 1982)

(Ros et al. 1985) (Fig. 12.1). Environmental changes are generally sharper along the vertical axis than along the horizontal plane especially in shallow areas. Other factors that change with depth such as the light spectrum, the water movement, the grain size of soft sediment (decreasing with depth), and the amount of hard substrates that are higher in shallow and shelf zones (Riedl 1971), play also an important role influencing the biota distribution.

The gradient on the vertical axis is often combined with a patchy heterogeneity in the horizontal plane caused mainly by the inclination, exposure to light, texture, type of substrate, orientation to predominant currents, etc. Concurrently, along these vertical gradients in shallow environments the plant-animal relationship changes with decreasing light. The macro-algae negatively impact on most of the sessile invertebrates by overgrowing in the shallower areas, or generating a canopy effect. These algae create a habitat for small and mobile fauna that finds shelter and food. All these factors generate diversity, which is enhanced by the increasing structural role of the organisms themselves, as plants and algae in the photic zone, the sessile animals in the aphotic zone. The variety of assemblages and communities results from the combined action of these multiple factors.

Mediterranean hard and soft-bottom communities were described from a qualitative and quantitative point of view on the studies of French pioneers in this field (Laborel 1961; Pérès and Picard 1964; Picard 1965; Laubier 1966; Bellan-Santini 1969; Guille 1971; Pérès 1982) and more recent reviewers (Ros et al. 1984, 1985; Fredj and Laubier 1985; Pérès 1985; Bellan-Santini et al. 1994; Bianchi et al. 2004; Ballesteros 2006). These classical papers identify the main coastal and shelf communities found in the western Mediterranean. Different assemblages are described by the

presence of key species following two main environmental parameters, bathymetry and substrate or sediment granulometry. In shallower areas the overlap of both parameters often occurs due to the presence of mixed sediments. In deeper habitats, bathymetry and granulometry are correlated due to a general decrease of hydrodynamism with depth, and communities generally extend over wider areas. No similar detailed community descriptions exist for the eastern Mediterranean and most papers (Karakassis and Eleftheriou 1997; Simbora et al. 2000, 2005; Simbora and Zenetos 2002; Chintiroglou et al. 2005) follow the previous mentioned classical works. A detailed and actual lists of the Mediterranean benthic communities for the establishment of national inventories of natural sites of conservation interest can be found in the synthesis of RAC/SPA (2006), a revised list is given by Fraschetti et al. (2008).

Spatial Trends and Variability

Zoobenthic Assemblages and Communities on Hard Substrata

Supralittoral

The supralittoral zone is never, or only very rarely, immersed. This habitat requires a relatively high degree of humidity that is supplied by the wave spray. Immersions occur mainly during heavy storms, though under certain conditions may be irregular because of the small tidal range. The upper part of this zone is only wetted very few times a year, whereas the lower part is almost continually splashed. The living community of this zone is homogeneous on a wide scale and has a very simple composition. The severe environmental conditions

have selected a few successful animal strategies. In the upper part of vertical rocky zones are common the herbivore littorinid gastropods (*Melaraphe neritoides*), cirripeds (*Chtamalus depressus*) and some detritivore mobile isopods (*Ligia italica*) (Pérès and Picard 1964; Ros et al. 1984).

Mediolittoral

The mediolittoral assemblages require or tolerate immersion and are adapted to the periodic ebb and flow of the intertidal zone. In the upper part of this zone humectation is due to the wave action and immersion is rare. In the lower part submersions are more frequent. The upper part is colonized by species of the supralittoral zone such as the very common molluscs strongly adhered to the rocks *Patella rustica* and decapoda (*Pachygrapsus marmoratus*) in crevices and sheltered areas. In the lower part animals can dominate the space (e.g. mussel belts, *Mytilus edulis*). On the rocky coast, cirripeds occupy the upper zone, often closely packed. On the lower region of rocky coasts live less tolerant animals, mussels and gastropods that cling to the wave-battered algal belts or hide into the crevices of encrusting algae belts. In areas with rich and dense communities of encrusting seaweeds many sessile species resist the wave action such as foraminifera (*Miniacina miniacina*), cnidarians (*Actinia equina*), sponges (*Hallichondria* spp.), hydrozoans (*Paracoryne huvei*) and many bryozoans, polychaetes, crustaceans (amphipods, isopods and some decapoda such as *Eriphia spinifrons*) and molluscs (Pérès 1967; Bouillon 1975; Ros et al. 1985; Morri et al. 1990).

Infralittoral

The infralittoral zone is characterized by an upper limit where species cannot endure emergence and by a lower limit marked by the disappearance of photophilic algae and marine phanerogams. The extension of this zone is highly variable, depending on substrate exposure, light penetration and turbidity. On rocky substrata the dominant species of fauna are associated to photophilic algal talus and phanerogams plants. Between the bases of the algal talus there is an encrusting animal community composed of skeletal material of polychaete worms, bryozoans and gastropods. Other encrusting species, sponges (*Myxilla rosacea*, *Hymedesmia* spp., *Phorbas topsenti*) and colonial ascidians, compete with the algae for the substrata. Sedentary species strongly attached to the rocky substrate such as molluscs (*Acanthochiton fascicularis*) are common, although crustaceans and members of others groups also occur (Bellan-Santini 1969; Ros et al. 1984).

A wide variety of species spend part of their life inside the rock crevices or in the interstices left or formed by others species. Examples of these include many polychaetes (*Nereis* spp., *Lepidonotus* spp., *Spirobranchus* sp., etc.), crustaceans (amphipods and isopods), molluscs (*Jujubinus gravinae*, etc.),

ophiurids (*Ophiotrix fragilis* and *Amphipholis squamata*) and also species that cling to the under face of boulders (*Coscinasterias tenuispina* or *Asterina gibbosa*). The complexity of this animal community increases with the endobiont species on sponges and ascidians.

There are other groups of species that move from one algal turf to another or adhering to the fronds or to sessile animals. The most common are amphipods (*Dexamine* spp., *Hyale* spp., etc.), but also isopods (*Cymodoce truncta*) together with picnogonids, molluscs, prosobranchs and opistobranchs gastropods and free-living polychaetes (e.g. *Platinereis dumerilii*). The algal fronds have also an important epiphytic community of sessile organisms such as hydrozoans with caprellids amphipods associated, bryozoans and encrusting tunicates.

On the algal talus there are other animals that compete for the space and develop large sizes such as cnidarians (*Aiptasia diaphana*, *Anemonia sulcata*, *Balanophyllia regia*) many hydrozoans and bryozoans (*Pentapora ottomulleriana*, *Turbicellepora magnicostata*). These species are chiefly substrate-occupiers, which compete strongly for the space. A second group of species, sessile molluscs (*Spondylus gaederopus*, *Ostrea edulis*) and tunicates (*Microcosmus sabatieri*, *Pyura dura*, etc.), are mainly substrate-suppliers that contribute to the spatial structuring of infralittoral communities. A final important group is the vagile fauna with species of different sizes that are highly mobile and linked in varying ways to the photophilic algae talus. Most of them are predators and include decapods (e.g. *Pilumnus hirtellus*, *Alpheus dentipes*), molluscs (*Octopus vulgaris* and many gastropods), echinoderms (e.g. *Paracentrotus lividus*, *Echinaster sepositus*) and many fishes of the families Gobiidae and Blenniidae (Ros et al. 1985).

Circalittoral

The circalittoral zone extends from the lower level of photophilic algae and sea-grasses to the end of the continental shelf. Fixed and colonial animals (sponges, cnidarians, bryozoans, tunicates) and red calcareous algae predominate on hard bottoms. The algae growing on coarse gravelly substrates coalesce the calcareous sediments to form a continuous, organogenous substrate on which the coralligenous community develops. This assemblage is the most structured and species-rich in the Mediterranean benthos. In general, the currents in the circalittoral zone are steady, though occasionally strong, and water is constantly cool. The plants are no longer the main contributors to the biomass, although its role is important as builders of the coralligenous (Ros et al. 1984; Uriz et al. 1993; Ballesteros 2006). The main variables delimitating these communities are changes in the relief, slope and substrata features in rocky habitats, grain size of the sediments, inter-specific competition and the alternation between hard and soft bottoms.

Three structural levels can be found in the circalittoral communities. The basal habitat with many species intermixes with algae in a reciprocal encrusting process. These species contribute to the community in two ways, as builders and bioeroders. One example (as a bioeroder) are the sponge species of the genus *Cliona*, which penetrate carbonate based organisms (Rosell et al. 1999; Cerrano et al. 2001; Rosell and Uriz 2002). The lower level is dominated by a high diversity of massive, erect and reptant species, such as sponges, cnidarians, bryozoans and tunicates, while the higher level contain the most visible and representative species. Their abundance in each habitat characterizes the so-called *facies*, being the contributors to the three-dimensional structure of these bottoms. Gorgonians (e.g. *Paramuricea clavata*, *Corallium rubrum* or *Eunicella singularis*), antipatharians (*Antipathella subpinnata*) (Bo et al. 2008, 2009), stylasterids (*Errina aspera*) (Salvati et al. 2010) and sponges (e.g. *Axinella polypoides*) are examples of this higher structural level (Fig. 12.2a, b, c). Other important components of the circalittoral communities are those species that move around the lower and higher levels (crustaceans, echinoderms or polychaetes). There is also a fauna specialized in occupying the higher levels as sessile epibionts or temporary residents. The coralligenous community is the more emblematic and developed of the circalittoral habitats, being a hot spot diversity habitat in the Mediterranean Sea (Laubier 1966; Fredj and Laubier 1985; Gili and Ros 1985a; Ballesteros et al. 1993; Ballesteros 2006).

Another very peculiar community in the Mediterranean circalittoral bottoms are the submarines caves. The fauna inhabiting in caves have a clear connection with the coralligenous but also with communities from deep waters (Riedl 1966; Uriz et al. 1992, 1993; Bianchi and Morri 1994; Bianchi et al. 1996). In this dark and cool habitats there is a continuously impoverishment of the particle concentration and the benthic cover from the open section to the darker parts of the caves (Gili et al. 1986; Martí et al. 2004) (Fig. 12.3). The walls are dominated by suspension feeders (sponges, cnidarians and bryozoans) and vagile fauna characterized by very specialized species of crustaceans and fishes (Bibiloni et al. 1989; Gili and Ballesteros 1991) (Fig. 12.2d).

Coralligenous assemblages are also found on soft isolated rocks or other rocky substrata (Fig. 12.2e). These latter assemblages can reach deeper areas, predominantly between 100 and 200 m depth. This particular community represents one of the most diverse assemblages in the Mediterranean shelf and slope even though these habitats have been destroyed by bottom trawling during decades. These rocky substrates are often covered with a silty sediment layer, and the sessile species have to penetrate through this sediment layer to attach to the hard substrate. The predominant species are suspension feeders such as gorgonians, alcyonarians, black corals, sponges and molluscs (True 1970; Gili and Ros 1985b; Uriz et al. 1992, 1993; Ballesteros 2006; Bo et al. 2011a, b).

Bathyal

Hard bottom communities in the bathyal domain are represented mainly by the cold-water coral community (Pérès 1985; Zibrowius and Taviani 2005; Bo et al. 2012). The deep-sea or cold-water coral community is found on hard substrates of the bathyal zone, between 200 and 1,000 m depth (Fig. 12.2f). These cold-water corals are only found when the slope is steep enough to expose hard substrates as vertical cliffs. The dominant species are the reef forming corals *Lophelia pertusa* and *Madrepora oculata*, which appear as scattered clumps along the slope. There is a rich associated fauna, the permanent species that live around or above the big boulders and rocks, and the temporal inhabitants such fishes and crustaceans that use this habitat as food source and nursery (Freiwald and Roberts 2005; Costello et al. 2005; Orejas et al. 2009; D'Onghia et al. 2010).

Zoobenthic Assemblages and Communities on Soft-Bottoms

Infralittoral

Infralittoral exposed soft-bottoms habitats are mostly sandy, with average grain sands depending on whether they are located in moderate or highly exposed areas. The predominant community, the *Beach sandy community*, usually covers bottoms from 5 to 7 m depth being colonized by several species of bivalves of the genus *Donax*, *Tellina* and *Lentidium*. Following the *Beach sandy community*, the so-called *Fine well-sorted sand community* (Pérès and Picard 1964) is the predominant one. This community has been recently named *Littoral Fine sands community* (Colombini et al. 2003; Labruno et al. 2007). Where high currents occur, fine sands are replaced by coarse sands and fine gravels, and the community changes to the *Littoral Coarse sands community*. This community contains a large diversity of bivalve species being *Spisula subtruncata* the most abundant one followed by polychaetes (*Ditrupa arietina*, *Owenia fusiformis*, and small spionids and paraonids). Under certain circumstances, these communities are densely colonized by sea-grasses (mainly *Cymodocea nodosa* and *Posidonia oceanica*) increasing spatial heterogeneity and therefore microhabitat availability. This process leads to an increase in diversity and abundance that causes a clear differentiation in the community structure. Finally, the *Littoral sandy mud community* is found in the deeper part of the infralittoral. In this zone a change in species composition is observed due to low current waters, which relates with more fine granulometry in the composition of sediment. Bivalves such as *Loripes lacteus* and *Tapes* spp. and crustaceans like *Pestarella tyrrhena* are among the characteristic species.

Infralittoral non-exposed soft-bottom habitats, on the other hand, are mostly dominated by silty sands and clays. This type of environments are generally found near river

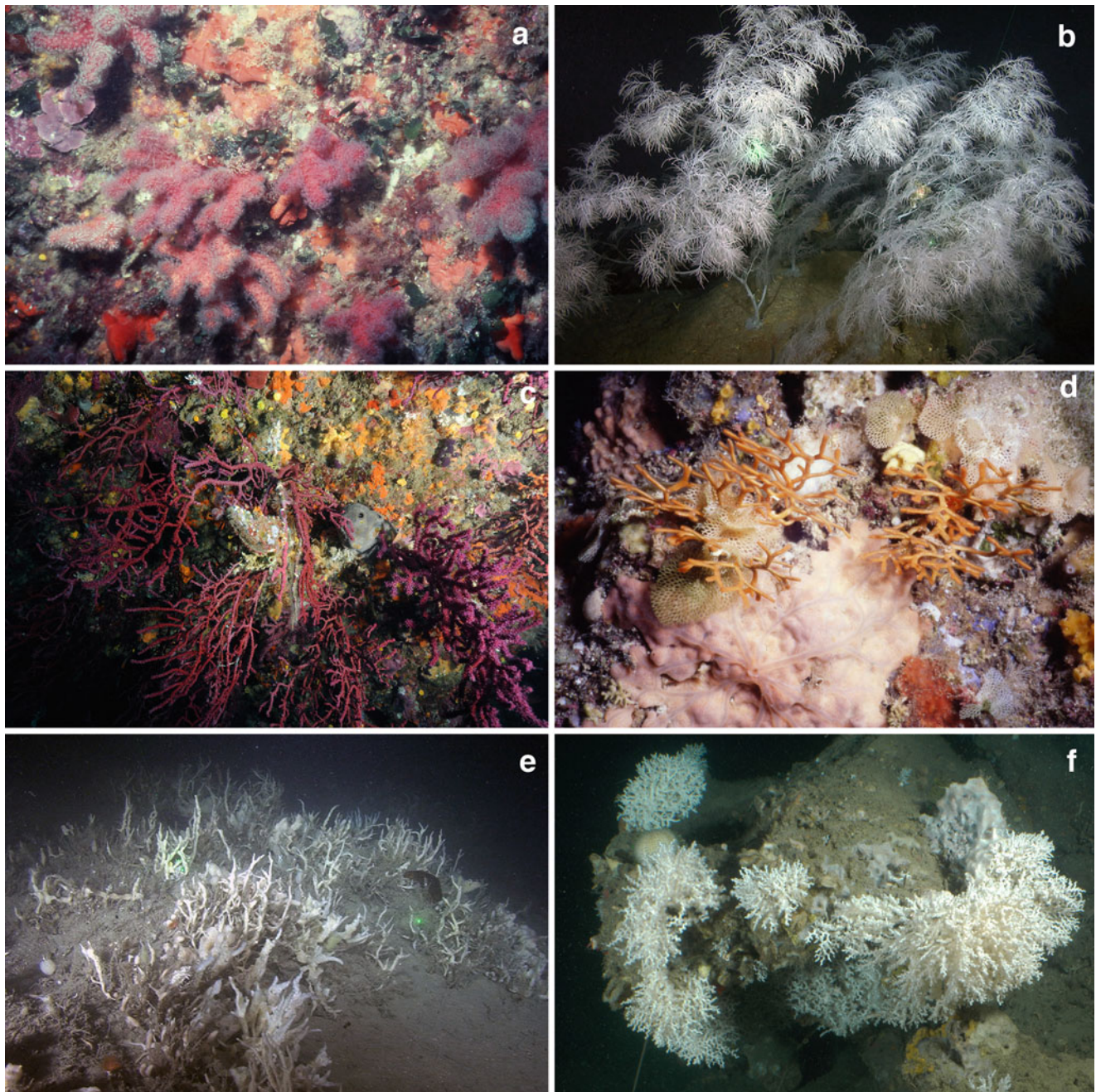


Fig. 12.2 Several examples of rocky bottom communities dominated by sessile organisms in the western Mediterranean: (a) cirralittoral community dominated by the alcyonarian *Alcyonium acaule* at 20 m depth in the Medes Islands (NW Mediterranean) (foto by J.M. Gili); (b) cirralittoral community dominated by the black coral *Antipathella subpinnata* at 120 m depth in Son Bou Canyon in Menorca Channel (NW Mediterranean); (c) coralligenous community dominated by the gorgonian *Paramuricea clavata* at 45 m depth in the Cap de Creus (NW Mediterranean) (Photo by Aldo Ferrucci); (d) cirralittoral community

located in the entrance of submarine caves in the NE Mallorca Island (NW Mediterranean) at 15 m depth dominated by the bryozoans *Smittina cervicornis* and *Retepora* sp. And the sponge *Spirastrella cuntatrix* (Photo by J.M. Gili); (e) community of deep rocky habitats at the end of the continental shelf of the Cap de Creus (NW Mediterranean) at 110 m depth, dominated by the sponge *Desmacidon fruticosum*; (f) community of depth cold-water corals dominated by *Madrepora oculata* at 200 m depth located at the Cap de Creus submarine canyon (NW Mediterranean) (Photographs b, e and f by JAGO-ICM-GEOMAR)

mouths and/or in deltas and coastal lagoon environments. The distribution of the species, assemblages and communities reflects the environmental gradients (i.e. granulometry, salinity and anoxic conditions) that can be found inside the

lagoon, and are mostly related with their communication with the open sea. Bivalve species such as *Cerastoderma edule* and *Scrobicularia plana*, polychaetes such as *Streblospio shrubsolii* and *Hediste diversicolor* and crustaceans such as

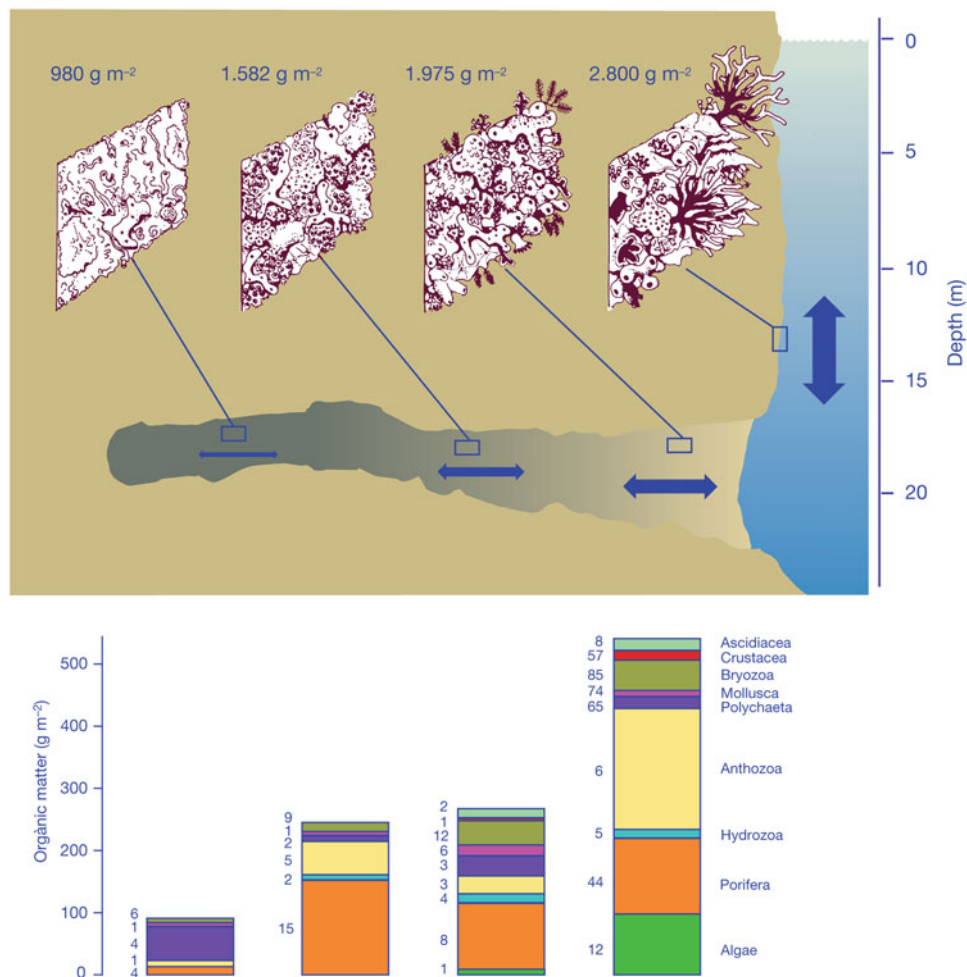


Fig. 12.3 Schematic representation of four Mediterranean circalittoral communities distributed from a vertical wall outside a cave to a horizontal one inside the cave. The number at the top of each representation is the community biomass in dry weight. The width and

direction of arrows roughly indicate the direction and intensity of water flow. The numbers on the side of each bar indicate the number of species within each group (Figure modified from Gili and Coma 1998)

Cyathura carinata and *Microdeutopus gryllotalpa* are some of the most important species.

An extreme environment in shallow waters is the hydrothermal vents. In the Mediterranean they occur in shallow depths of up to 115 m. The dominant sediment, called ooze, is mud with a high percentage of organic remains. These areas rely on primary production and benthic fauna is not distinct from the surrounding areas (De Biasi et al. 2004) except for the abundant gastropod *Cyclope neritea* in the bacterial mat areas (Dando et al. 1995).

Circalittoral

Circalittoral soft-bottom environments present a more complex situation (Somaschini et al. 1998). Pérès and Picard (1964) and Picard (1965) reported the presence of different circalittoral assemblages. On the other hand, Pérès (1967) and Salen Picard (1981, 1982) described many degradation detritic facies. And finally Guille (1971)

observed many transition zones among these assemblages, identifying only one circalittoral soft-bottom community with many sub-communities or facies. Other transitional zones, mostly between sandy and muddy bottoms, have been observed by other authors (Fèbvre-Chevalier 1969; Gambi and Fresi 1981; Falciai et al. 1983; Fresi et al. 1983; Zavodnik et al. 1985; Gravina 1986). All these aforementioned classifications were obtained basically with the help of dredges and box corers devices. Recent observations made with remote operated vehicles (ROV's) or small submarines have allowed to make direct observations on these soft-bottoms environments and discern also the fragile epifaunal species, which are usually observed in patches. Thus, by visual inspection of these habitats we can now classify all the communities found in circalittoral shelf environments, into four main large communities with many different assemblages and/or facies inhabiting them (Sardá et al. 2012).

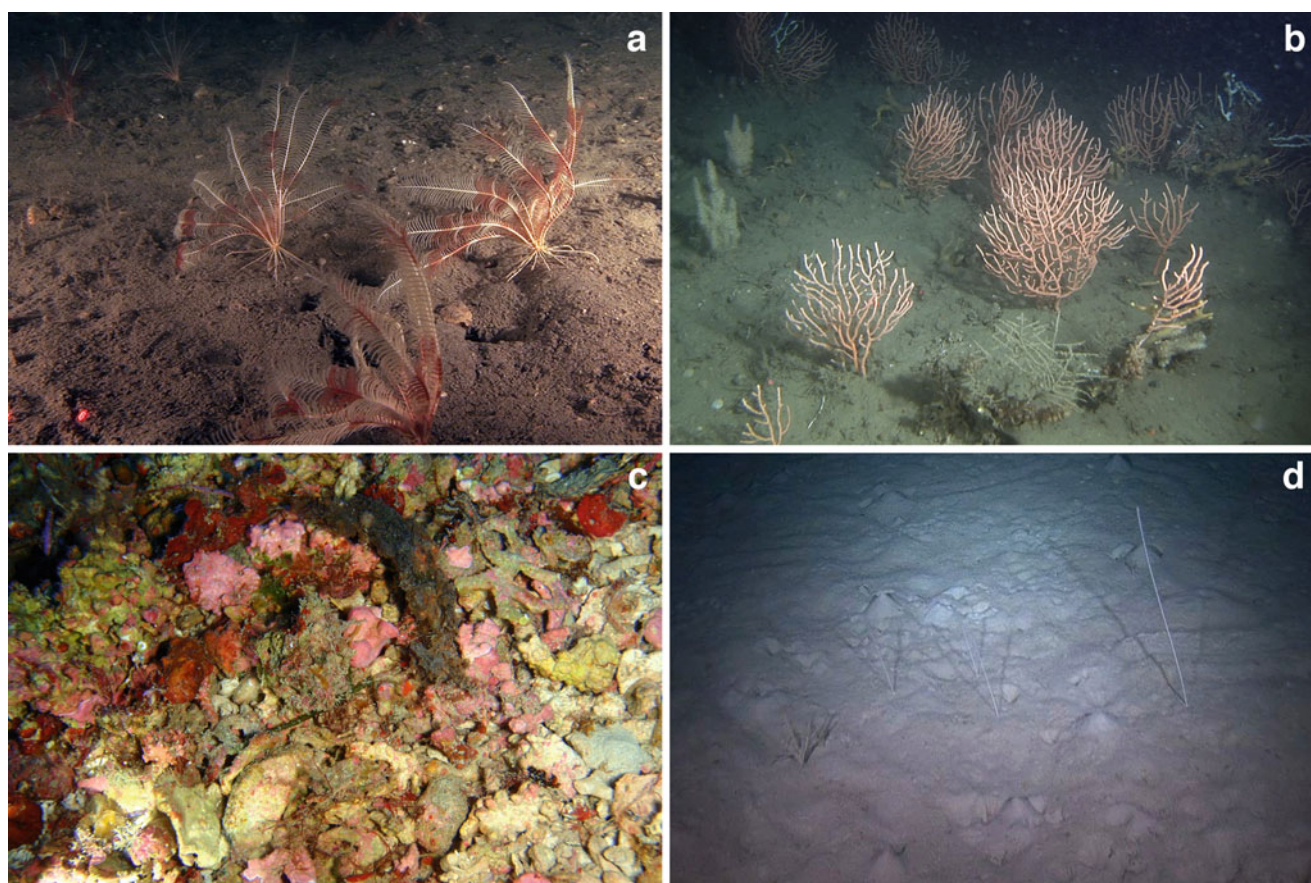


Fig. 12.4 Characteristic assemblages and zoobenthic communities on soft-bottoms: continental shelf detritic communities in the Cap de Creus (NW Mediterranean) at 120 m depth (**a**) facies with *Leptometra phalangium* at; (**b**) facies dominated by gorgonians *Eunicella* sp. and sponges (photographs a and b by NEMO-ICM-Gavin Newman);

(**c**) Maërl bed community at 52 m depth from Cabrera Island (NW Mediterranean) (photo by David Diaz); (**d**) communities of bathyal muds, facies with *Funiculina quadrangularis* in the Menorca channel (NW Mediterranean) at 140 m depth (Photo by JAGO-ICM-GEOMAR)

In the upper part of the circalittoral domain, the *Littoral sandy mud community* can also be found, although with a higher number of deeper species in the faunistic composition. *Continental shelf detritic communities* are the second large group of assemblages that can be found. The relative fraction of muds in their sediment composition determine different assemblages, from sandy detritic environments to more muddy. The presence of epifaunal species such as gorgonians, pennatulaceans (*Pennatula rubra*, *Pteroides spinosum*), alcionaria (*Alcyonium palmatum*), ceriantharia (*Cerianthus membranaceus*), crinoidea (*Leptometra phalangium*), ofiuroida (*Ophiotrix quinquemaculata*), and even terebelid polychaetes, determines the different facies of the same community (Fig. 12.4a, b). On continental shelf bottoms that meet the continental slope or submarine canyons, the proportion of mud decreases, dominating the gravel and rock substrata. In this zone, the present epifauna is more diverse with the presence of sponges and echinoderms. Finally, the *Platform mud community* is the largest

community that can be found occupying most part of the circalittoral environment. The composition is mainly silty sand sediments and clay, which vary between the terrigenous coastal mud in the upper part to the deep muds in the deeper part. The fauna is characterized by the endofaunal components with a large fraction being small polychaete species of genus such as *Tharyx*, *Monticellina*, *Prionospio* and *Lumbrineris* (Guille 1965; Desbruyères et al. 1972; Gili et al. 1987).

A very specific community that normally colonizes detritic environments in the upper part of the circalittoral is the well-known *Maërl bed community* (Fig. 12.4c). Maërl beds are mainly composed of free-living non-geniculate coralline algae (Corallinacea: Rhodophyta) that have an algal core and sandy granules or shells with a more or less regular and concentric growth around them. These structures develop and accumulate on soft-bottoms, influenced by laminar currents and gives a rich and diverse benthic community (Ballesteros 1994; Peña and Bárbara 2008).

Deep-Sea

Bathyal and Abyssal

Our knowledge on bathyal and abyssal soft-bottom communities is still scarce and few papers dare to work at a community level. The prevalent division presented by Pérès (1985) divides the slope communities into three horizons, the upper slope horizon extending to 400–500 m, the middle slope horizon that can extend until 1,200–1,400 m, characterized by compact muds and a high diversity, and the lower slope horizon that goes into the abyssal plains. Despite the reviews by Pérès 1985; Fredj and Laubier (1985) and Laubier and Emig (1993) quantitative data on faunal composition and ecological knowledge are generally scarce, although new studies on deep-sea habitats have led to valuable new knowledge on deep Mediterranean benthos (Boury-Esnault et al. 1994; Uriz and Rosell 1990; Tselepidis et al. 2000; Kröncke et al. 2003; Cartes et al. 2004; Ramirez-Llodra et al. 2008). Although it is accepted that Mediterranean deep-sea biodiversity should be high as shown by comprehensive biodiversity studies (Bianchi and Morri 2000; Coll et al. 2010; Danovaro et al. 2010), there is still few data to describe the different deep-sea communities. To present, bathyal facies are defined according to the compaction of the sediment. Sandy muds are quite frequent in the upper horizon whereas bathyal and abyssal muds constitute the largest bottom environments in the Mediterranean. Some of the characteristic species giving name to those facies include the cnidarians *Isidella elongata* and *Funicula quadrangularis* (Fig. 12.4d), the echinoderm *Bryopsis lyrifera*, the gastropod *Apporhais seressianus* and the sponges *Thenia muricata* and *Pheronema grayi*. Fishes and crustaceans (mainly decapods and peracarids) are particularly abundant (Cartes et al. 2004; Sardà et al. 2004; Galil 2004). The communities inhabiting these bottoms can be different to those found in world oceans due to a shallower average depth, high deep-water turnover rates, higher temperature and extreme oligotrophy with low nutrient concentrations, especially in the eastern part. All these key issues together are forecasting also a unique large percentage of endemic species.

From the continental shelf to the abyssal plain, soft bottoms environments are located on the continental slopes and/or submarine canyons. Organic matter originating in the water column and on the continental shelf flows along the canyon axis and sinks together with inorganic particulate matter. As a consequence, organic and inorganic debris, and large accumulations of sediments can be observed on the floor of submarine canyons (Canals et al. 2006). These deposits are responsible for distinct species assemblages and higher faunal densities and biomass in comparison to nearby non-canyon. In addition, canyons can hold littoral species carried down by the adventive inputs, be responsible for local upwelling and occasionally the presence of benthic species in the

water column, acting as a source and reservoir of endemic species (Gili et al. 1998, 2000; Sardà et al. 2010). The environmental conditions in submarine canyons may vary greatly from one location to another. Physical conditions such as strong bottom currents are responsible of resuspension, and seasonal changes in the particle rain may result in a habitat heterogeneity that could be comparable to that of tropical forests or rocky coasts (Grassle 1989).

Cold Seeps

Cold seep biological communities relying on chemosynthesis and associated to mud volcanoes and faults have been relatively recently discovered in the southeastern Mediterranean Sea, south of Crete and Turkey (in the Mediterranean ridge and Anaximander mountains) and north of Egypt at the Nile Seep-Sea Fan at depths ranging from 500 to 2,000 m. Cold seep habitats are extremely heterogeneous in structure and composition, linked to the different reduced microhabitats and substrate types in carbonate crusts and sediments. Faunal assemblages associated with Mediterranean cold seeps are still relatively unknown. Bivalves and tubeworms associated with endosymbiotic and chemoautotrophic bacteria characterize the structure of the faunal assemblages of cold seeps, as well as numerous gastropods. Described symbiont-bearing species include the polychaetes *Lamellibrachia anaximandri*, *Siboglinidae monilifera*, the bivalves *Myrtea amorpha*, *Lucinoma kazani*, *Idas modiolaeformis*, *Thyasira striata* and *Isorropodon perplexum* (Salas and Woodside 2002; Olu-Le Roy et al. 2004; Werne et al. 2004; Duperron et al. 2008; Ritt et al. 2010). Other megafaunal species of exceptional size compared with their background counterparts include the sponges (*Rhizaxinella pyrifer*) and crabs (*Chaceon mediterraneus*) (Olu-Le Roy et al. 2004).

The benthic cartography of the Mediterranean benthic habitats according to EUNIS (European Nature Information System) habitat classification can be found at <http://jncc.defra.gov.uk/page-5020> (Fig. 12.5).

Ecological Strategies

Most benthic Mediterranean bottoms are considered complex habitats and thus with many ecological niches. Due to substrata features, environmental factors and the role of the organisms themselves, the structural and dynamic complexity of sea bottoms enables the presence of many different habitats and organisms with diverse ecological strategies. Besides its precise role in the community, species fall into a bionomic or ecological continuum among the so-called *r* and *K* strategies (Pianka 1970; Margalef 1974). According to Hiscock and Mitchell (1980) any species may be summarized into the following four strategies: long-lived species

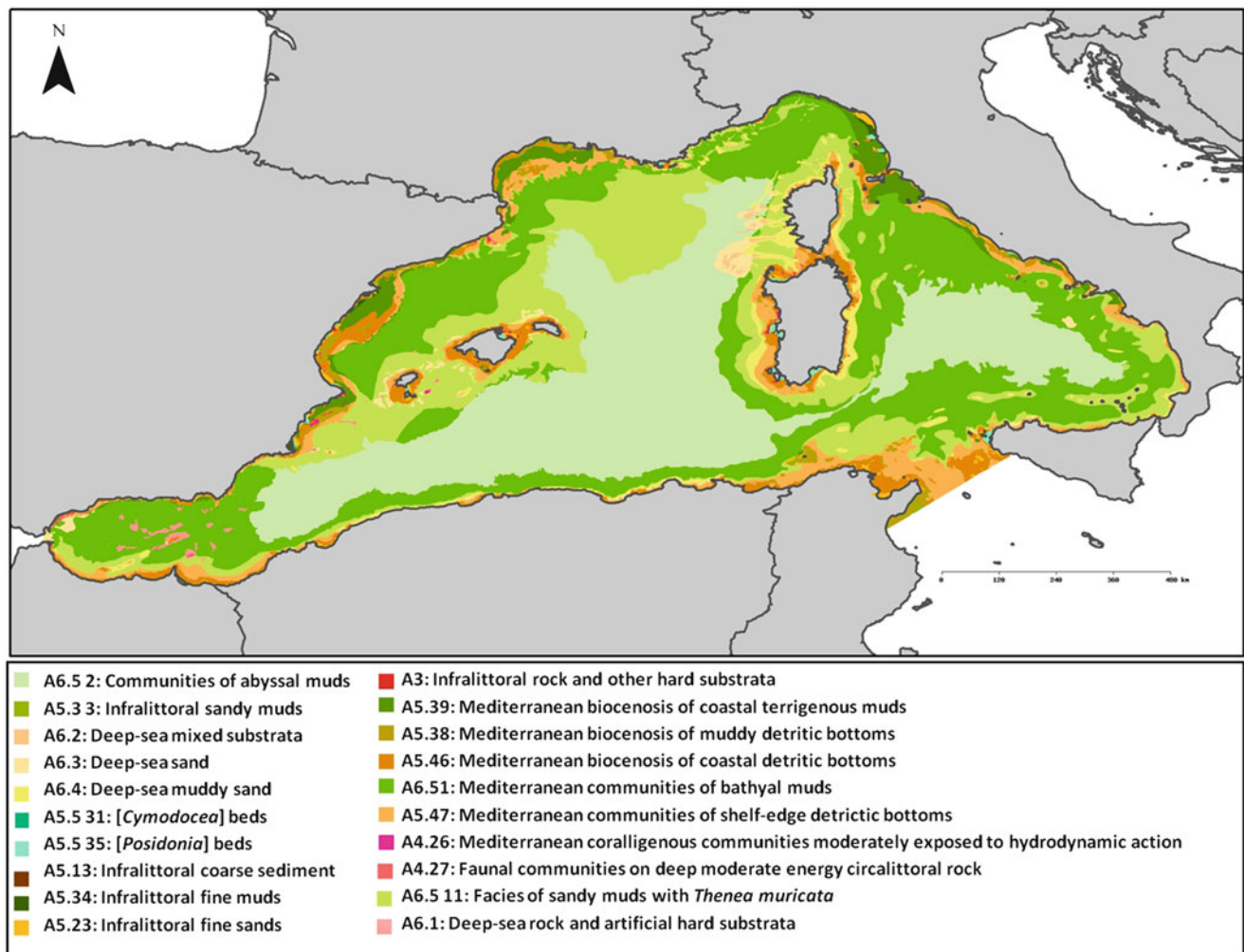


Fig. 12.5 Benthic cartography (EUSaMap) from the Northwestern Mediterranean following EUNIS classification (Adapted from <http://jncc.defra.gov.uk/page-5020>)

(moderate to big size, which stabilize and characterize the community; e.g. the bio-constructors); seasonal species (appear only at certain times of the year but have an important impact or role in the communities); opportunistic species (high reproductive potential, they can temporally monopolize the space); and species that respond to small alterations in the environmental conditions (usually with a known and variable temporally structural significance).

In general, both ecological strategies r and k , follow clear trends and are very representative of Mediterranean zoobenthos. R -strategist represents the opportunistic, fugitive, pioneer and generalist species. They exploit the lack of organization and environmental stability, with a high offspring production; the vast majority inevitably disappear. They are highly adaptable and frequent in unstable and stressed environments. On the other hand, the k -strategist exemplifies the specialists or strategists. They can stabilize their populations in a given environment, and produce few very protected offspring that are well adapted to ecological stable environments. In sessile modular species they also can reproduce asexually.

In the Mediterranean zoobenthos the ecological strategies can be summarized in the following trends:

At the upper littoral levels, the benthic strategies favoured are those that tend to counteract the mechanical stress associated with these shallow habitats. The balance between high illumination rates results in productive and dense algae communities that support a diverse and rich fauna. Because of the seasonal variations in algal cover, and the high environmental stress, most species have high reproduction rates, production and fast turnover. There are also diverse animal strategies colonizing the hard substrates, the algae or plant talus, especially by the vagile species.

At intermediate levels such as the circalittoral, the current stress is not mechanical but refers to light availability. Light decline reduces plant capacity to occupy the space, and therefore the competition with animals, especially sessile fauna, is maximal. The supply of food is adequate because of the continuous hydrodynamic regime and the oversupply of plankton and benthic production from the upper layer communities. The degree of organization is high. Many species are builders,

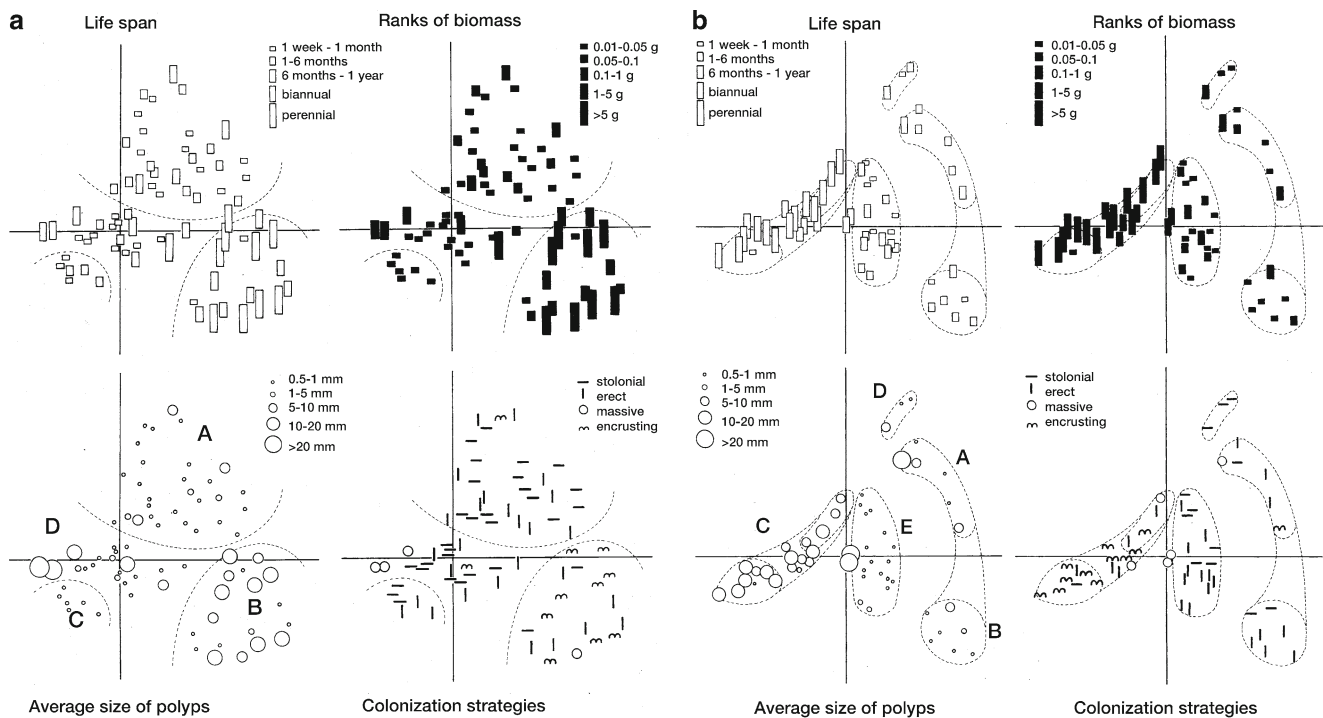


Fig. 12.6 Two examples of ecological strategies present in the different communities from an extensive survey in the Medes Islands (a) and along the Catalan coast (b) (NW Mediterranean). The 104 benthic cnidarian species considered have been ordered by means of a Principal Component Analysis (Figure modified from Gili et al. 1989, see this paper for more information and species list). (a) A mediolittoral community and assemblages of photophilic algae; B circalittoral community mainly

coralligenous assemblages; C assemblages of species growing on algae and phanerogams communities; D species of wide distribution in rocky shallow communities. (b) A mediolittoral community; B same assemblage but species forming dense populations; C circalittoral communities, coralligenous and submarine caves assemblages; D mediolittoral community mainly phanerogams meadows; E supralittoral and mediolittoral shallow communities dominated by species with photophilic algae

having high production rates and investing in three-dimensional structures. They have moderate to slow growth rates and a slow turnover. At deeper levels (e.g. the deep circalittoral, dark caves or shelf-break communities) the stress is greater due to high sedimentation and the scarce food supply. In these environments only animal assemblages can survive, mainly *k*-strategists, and their adaptation is often determined by the acquisition of far-reaching specializations (Fig. 12.6).

In shallow and deep benthic communities there is a convergent trend among the different groups towards a few adaptive options, which are themselves diverse according each particular community (Zabala and Ballesteros 1989). The most suitable strategy for spatial competition is the most common trophic guild, the filter feeding. This strategy may be found through solitary or colonial sessile organization, with or without a skeleton, and ultimate growth to a maximal size, being most of them *k*-strategists. They have long life cycles, efficient capabilities for filtering and defence, and a large capacity for covering the ground. At this ecological model the advantages of colonial vs. solitary strategies must be also considered, as an alternative and complementary way for successional colonization and population stability (Jackson 1977). At the other extreme are the individual

organisms, vagile and of limited growth, with short life cycles, high reproductive capacities, with planktonic and long-lived larvae, clearly *r*-strategists. They are minor competitors and prefer unstable surface levels. They opportunistically cover any area that is left open or, when occupying more stable substrates, show strong spatial and temporal fluctuations (Ros et al. 1985; Gili et al. 1989).

Temporal Variability

Seasonal variations are common phenomena in all marine ecosystems. In the Mediterranean, these changes are controlled by climate driven processes and anthropogenic forcing (Duarte et al. 1999). Life cycles of marine organisms show marked seasonal patterns in growth, reproduction and abundance. In the water column, these seasonal cycles are directed by factors, such as photoperiod, light intensity, food availability, oxygen, salinity and temperature. All these factors influence the energy expenditure in marine organisms both planktonic and benthonic. It is therefore a challenge to integrate the effects of multiple factors, as well as their interactive effects, to determine seasonality in the life cycles of marine organisms.

Plankton and Benthic-Pelagic Coupling

The composition and dynamics of plankton communities display strong seasonal changes (Longhurst 1998). In the Mediterranean, periods of water stratification and lower levels of water motion that reduce the biological activity follow high productive seasons. In temperate seas, spring season is considered a key period because it concentrates the majority of the total annual primary and secondary production (Margalef 1985). In autumn or early winter a second short productive period also occurs, although the primary productivity drops (Ribera d'Alcalá et al. 2004) and the seston becomes highly refractory (Grémare et al. 1997; Rossi et al. 2003), having a very low availability for a wide range of organisms. From the end of winter and beginning of spring the primary production is high (Estrada 1996) and many zooplanktonic groups display their maximal peaks of abundance (Sabatés et al. 1989; Calbet et al. 2001). This general tendency throughout the water column has also been observed in close bottom planktonic communities (Ribes et al. 1999; Rossi and Gili 2005). Planktonic communities receive a major input of detrital and dissolved organic matter from river run-off and from benthic debris coming from macroalgae and phanerogams, which influence the biological production (Thomsen and van Weering 1998). Besides the organic input, the near-bottom water layer is also subject to highly variable turbulence that influences the plankton and seston dynamics (Wainright 1990; Rossi and Gili 2009). Recent data on suspension feeders from benthic communities corroborate this seasonal patterns for planktonic communities (Coma et al. 2000).

Boero et al. (1996) and Marcus and Boero (1998) transferred to ecology a host of biological research on the life cycles of many planktonic species with benthic resting stages. Marine systems function based on pulses of production during which some species become very abundant for short periods. Phytoplankton blooms, followed by zooplankton blooms are the engine of all marine systems. Especially in coastal waters, many planktonic species spend the adverse season in the benthos, as resting stages. The pulses, thus, are based on the hatching of the resting stages and on its match with favorable conditions (Boero 1994). The resting stage banks of the benthos are the real potential for the expression of biodiversity in the plankton. Pati et al. (1999) suggested that the predation of the meiofauna on the benthic resting stages of plankton might play a keystone role in regulating the diversity of plankton pulses. The role of resting stages in benthic-pelagic coupling might well be enhanced by the down- and upwelling currents generated by marine canyons (Della Tommasa et al. 2000). Many gelatinous plankters do have benthic stages and the dynamics of their populations rely on benthic processes (Boero et al. 2008). These crucial aspects of benthic pelagic

coupling are still vastly unexplored and represent a new frontier in marine ecology.

In shallow waters, it is proved that the seasonal environmental variability both in the water column and near-bottom are closely linked and determine biological processes. Sedimentation, re-suspension, vertical mixing and nutrient fluxes conduct the coupling between plankton and benthic systems. At the same time, benthic organisms have a great influence on the dynamics of water column providing nutrients coming from regeneration processes in shallow and estuarine areas (Valiela 1995). However, in deeper communities the benthic-pelagic coupling is seasonally asymmetrical with surface events, although ecological processes are still linked with the biological production in surface layers (Gori et al. 2012).

Seasonality in the deep-sea may be less pronounced, but can be easily evidenced by the increased seasonal influx of detritus into these areas. With the exception of some extreme environments such as the cold seeps, found in the eastern Mediterranean region, most deep ecosystems in the Mediterranean depend completely on alloctonous organic and inorganic inputs (Cartes et al. 2004). Danovaro et al. (1999) reported mass fluxes at equal depths being up to two orders of magnitude higher in the Western Mediterranean (Gulf of Lions) than in the Eastern Mediterranean (Cretan sea). The 10 % of the carbon in surface waters is exported to 1,000 m depth in the Western Mediterranean, but only 2–3 % in the Eastern Mediterranean, and the bacterial densities are four times higher in the former than in the latter. The same authors also reported different efficiencies in the transfer of organic matter to the deep-sea between the west and the east, 10 % and 1 % respectively. This has deep implications in terms of benthic-pelagic coupling. The general conclusion from the research carried out in these environments, mainly in the NW Mediterranean deep waters (Cartes et al. 2001, 2008; Fanelli and Cartes 2004;), indicates that seasonal peaks in primary production or particulate organic matter translate into seasonal peaks of secondary production in the deep-sea.

Algae Dominated Communities and Sea-Grass Communities

Most habitats in temperate regions exhibit seasonal peaks in the standing stock of algae in late spring throughout summer and with minima in winter (Murray and Littler 1984). In most communities, these seasonal patterns involve changes in community structure (Mann and Lazier 2006), and strongly influence functional processes (Boudouresque 1971). There is also a shift in the time of production and biomass peaks, which take place in spring in shallow sublittoral algal communities, and in summer in the deeper assemblages. However

this scenario changes when the communities suffer the effect of fish and urchin predation, which modify benthic communities and affect the composition, abundance and dynamics of shallow sublittoral algal communities. At high densities and during the production phase of the algae, sea urchins display an overgrazing activity that reduce the algal biomass because of the patchy distribution and denudation by the urchin, especially on erect talus. In extreme cases of predation, grazers reduce totally the erect stratum of fleshy algae, resulting in a monotonous assemblage of encrusting algae and in a reduction of algal communities seasonality (Velarque 1987; Sala et al. 1998a, b). In the Mediterranean fishes are not the dominant predators and have less effect on algal abundance and seasonal variability than sea urchins (Velarque 1990). However, overgrazing the populations of fleshy erect macroalgae by fishes facilitates the increase in biomass of chemically defended or less competitive species assemblages, which disguise the natural community patterns (Sala and Boudouresque 1997). In seagrasses, the seasonal changes in meadow structure, shoot density or leaf surface and biomass, have an influence on the species composition and abundances of associated vagile fauna like polychaetes and fish, which are in turn influenced by the ecology and life cycle of single species like recruitment and migrations (Francour 1997; Gambi et al. 1998).

Vagile Fauna

The sessile components of benthic communities are associated with the morphological and physical characteristics of the seabed. These features determine seasonal periods of growth alternated with periods of inactivity and dormancy (Coma et al. 2000). In contrast, much of the fauna that lives close to the bottom exhibits varying degrees of mobility, from crawling gastropod molluscs, starfishes and sea urchins to highly mobile mysidacea and fish. These organisms perform seasonal migrations through a vertical gradient, avoiding high temperatures in summer and looking for food during winter in shallower habitats (San Vicente and Sorbe 2003; Bellan-Santini et al. 1994). Another group that moves seasonally are the bottom dwelling fishes and their migrations are linked to certain habitat types, and even to different regional areas (García-Rubies and Macpherson 1995). Such variation in habitat use can be attributed to different life history stages. Juveniles burrow into the substratum to evade predation, but the adults use a wider range of habitats such as big boulders or caves (Planes et al. 2000; Macpherson and Raventos 2005).

On the other hand, larval stages of many invertebrate and fish species use transitory habitats as an area for shelter and feeding. Many of these habitats occur in hard bottom communities associated to the sessile species that cover

temporally the substrata. The most common types of habitats are macro-algal and sea-grass beds where species find also refuge (Bruno and Bertness 2001). Occasionally, communities dominated by animals as bryozoans, gorgonians, corals and polychaetes play a similar role and have a great strategic importance for species that inhabit them (Bellan-Santini et al. 1994; Pederson and Peterson 2002). During periods of high growth of the foliage and thalli, meadows of macro-algae provide shelter and protection to different stages of many marine species that are most vulnerable to predation. Such habitats are essential in explaining the life cycles of species and also the seasonal and inter-annual variations in populations that synchronize their larval stages with the factors affecting the opportunities to colonize ephemeral habitats.

In deeper soft-bottoms environments of the continental shelves, there is a clear lack of knowledge in the temporal dynamics. One of the few studies that have been carried out in the Mediterranean on this topic (de Juan and Cartes 2011) showed a marked seasonal variability linked to the high phytoplankton production in spring. The springtime production supplies organic matter to the benthos, inducing a higher infaunal abundance. There was also a reduction in the infaunal crustacean abundance and species richness in late summer. These changes were attributed to two factors, the establishment of the thermocline (which could limit the availability of organic matter to the seabed), and the high water temperatures (which caused the production of phytoplankton exudates and accumulation of mucilaginous aggregates over the seabed).

The low food input into the deep-sea results in scarce food resources, high food partitioning, highly diversified diets, and very complex trophic webs. It can also be observed a trend towards a decrease of feeding intensity with depth for decapods and fish, which suggests a reduction on the metabolic activity with increasing depth (Carrasón and Cartes 2002; Fanelli and Cartes 2004).

Animal-Dominated Communities

There are great differences in the temporal changes in the structure and dynamics between algal-dominated and animal-dominated communities. Shallow algal communities show the largest temporal changes, though it is difficult to establish a clear seasonal pattern. When the cover area is partitioned between algae and animals, they both find favourable conditions for growing in the spring to summer period for algae, and autumn to winter for animals (Garrahou et al. 2002). In deeper communities, dominated by animals, few structural seasonal changes have been observed and these might be detected only in the physiological parameters of animal populations such as reproduction periods or slowly

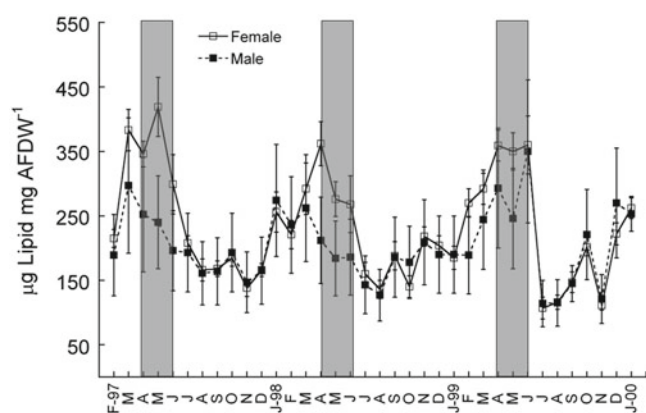


Fig. 12.7 Three years cycle of the lipid contents in the gorgonian *Paramuricea clavata*. Shadow areas indicate reproduction period (Figure modified from Rossi et al. 2006a). The marked seasonality of food quality and availability is reflected in the energy storage of mediterranean benthic suspension feeders. Food constraints and reproductive traits are reflected in summer (reproduction and aestivation process), and in autumn (low quality seston). Reproduction success is tightly related with the energy storage capability

growth patterns (Turon and Becerro 1992; Garrabou et al. 2002; Blanquer and Agell 2008; De Caralt et al. 2008). In these animal-dominated communities the abundance of ephemeral organisms and the trophic ecology of perennial ones are closely related, in response to summer and late autumn food shortages of the water column (Rossi et al. 2006a). Ingesta and assimilation may vary seasonally with seston concentration and quality, depending on the feeding strategy (Coma et al. 2000; Jordana et al. 2001; Rossi and Gili 2005).

In the Mediterranean, the seasonal variation of environmental factors such as temperature, food availability and photoperiod can cause shifts in the resource allocation of benthic organisms (Caswell 1989). From an energetic point of view, organisms change the seasonal pattern of energy invested in reproduction, growth and maintenance influencing the food storage (Rossi et al. 2006a) (Fig. 12.7). In general, the main energy output coincides with the reproductive period at the end of the most successful feeding period, especially spring and early autumn (Coma et al. 1998). The seasonal variation in the biochemical composition of the tissue of an organism may be interpreted as a record of the water column productivity fluctuations in the benthic community. It has been shown in gorgonians that the effect of seasonal fluctuations in seston quantity and quality were apparent in the protein, carbohydrate, and lipid tissue concentration values (Rossi et al. 2006a; Gori et al. 2007; Rossi and Tsounis 2007). Other approaches include the shift of the resource allocation into defensive mechanisms by species that grow in high competitive communities. In sponges, higher competitive pressure in the shaded environment results in increased investment in defensive/supportive (mineral and organic)

structures and a lower investment in somatic growth and reproductive output of larvae (Uriz et al. 1995).

Another seasonal strategy related to the energetic constraints is a predictable pattern of temporal dormancy. In the Mediterranean, summer dormancy predominates, in contrast to cold temperate seas, which are characterized by winter dormancy (Sardá et al. 1999; Garrabou 1999; Coma et al. 2000; Betti et al. 2012; Di Camillo et al. 2012). The physiological changes related with this resting state help the organisms to survive in adverse weather conditions and food scarcity. The plasticity of many sessile invertebrates allows them to withstand net energy deficits by digesting themselves until additional food becomes available (Gili and Coma 1998). Biochemical composition in Mediterranean gorgonians (Rossi et al. 2006a; Rossi and Tsounis 2007) shows periodic summer minimum energy storage of lipids and proteins, as well as a drop in late autumn-early winter. These observations agree with the expected physiological changes associated to summer and late autumn energy shortage (Grémare et al. 1997; Rossi et al. 2003), and with an annual pattern of investment in growth and reproduction of gorgonian species. Seasonal dormancy phenomena have been related not only with energetic constraints but also with physiological adaptations to exceptional changes in water temperature ranges (Sulak et al. 2007). The presence of resting stages is a common mechanism in marine organisms, which can remain inactive for long periods, acting as biodiversity reservoirs. The importance of life cycle dynamics in structuring marine communities contributes to explain seasonal fluctuations not only in benthic but also in phyto- and zooplanktonic communities (Boero et al. 1996).

Tendencies

The Mediterranean Sea is one of the most important biodiversity hotspots of the world with many different species and natural resources (Bianchi and Morri 2000; Coll et al. 2010). However, it is increasingly compromised by human activities, something that is accentuated by its semi-enclosed configuration, which restricts its communication with the open ocean. Human pressures on this environment are increasing habitat and species destruction to become a priority issue for policy-makers. In fact, Mediterranean Sea has been identified as a hotspot of sea warming effects, ocean acidification, alien species invasion and other direct and indirect human perturbations, being considerably more impacted than other places of the world (Durrieu de Madron et al. 2011). Increasing demographic and economic developments make the general panorama of the Mediterranean benthic communities complex, since several factors are synergically acting at population and community levels.

Directly Man-Induced Pressures

Fishing Activity

The fishing activity in the Mediterranean is characterized by the multi-specificity of catches and the absence of large single stocks, especially in the demersal regime (Farrugio et al. 1993). Although artisanal fleets and gears constitute the most important fisheries in the Mediterranean, nowadays there is a tendency in the development of semi-industrial fleets, mainly of trawl fishing. Five thousand two hundred and seventy four trawlers operate in Mediterranean waters, fully exploiting the continental shelves and upper slopes of the basin (FAO 2011). Bottom trawling shows the least degree of selectivity with the widest-range impact on different organisms of the ecosystem due to habitat destruction and modification (Demestre et al. 2000), and displays the largest impacts on some demersal target species and non-target groups (i.e. small organisms discarded and juveniles of vulnerable species such as rays and demersal sharks). At present, trawl fisheries constitute probably the most acute direct problem for soft-bottom and detritic habitats, but was an evident source of destruction in other communities like *Posidonia oceanica* or *Cymodocea nodosa*. Together with species like hake (*Merluccius merluccius*) or the anglerfish (*Lophius piscatorius*) and other demersal fishes, the most common catches of bottom trawlers are crustaceans. Except for the Norwegian lobster (*Nephrops norvegicus*), the scientific assessments carried out on the red shrimp (*Aristeus antennatus*), the giant red shrimp (*Aristeomorpha foliacea*) and the pink shrimp (*Parapenaeus longirostris*) are giving alarms for overexploitation and the highly damaging effect on the accompanying fauna and surrounding environments (General Fisheries Commission of the Mediterranean 2012).

Common illegal practices in Mediterranean trawling include using nets with a smaller mesh opening than the permitted, fishing in prohibited zones and seabeds and using engines with a higher power than officially declared. Their catches also include abundant by-catch and discards. Though theoretically it would be simple to analyze the intensity of trawling in the Mediterranean using the track of the fleet with positioning systems, the reality is that data does not exist or it is not available. Studies in the North Sea showed that the area trawled by these vessels each year is equivalent to the size of the entire sea (Leth and Kuijpers 1996), and this figure could be similar for the continental shelves in the Mediterranean. The impact of trawling on the ecosystem can be categorized into two basic factors: (a) the selectivity of fishing techniques, with regard to the target species and to catching young fish and other sea animals that do not correspond to the target species, and (b) the habitat destruction, physical and biological consequences of the fishing arts on the bottom (Fig. 12.8a, b).

The selectivity depends on the mesh size used and its shape. The larger the size of the mesh opening of the net, the

greater the selectivity, whereas diamond shapes generally tend to result in poorer selectivity than square shaped ones. However, other reports have demonstrated that the selectivity of fishing techniques depends more on the target species (behavior, life cycle, etc.) than on the size of mesh used (e.g. young mullet, Tokaç and Tosunoglu 1996). Although selectivity depends on the shape of the species caught, it is also highly affected by the large amounts of rubbish taken in the catch. A survey conducted on a Norway lobster trawler fishery in the Mediterranean showed that one piece of rubbish was brought up per six Norway lobsters (Ragonese et al. 1994). Rubbish is becoming an alarming problem in fisheries.

The physical impact of bottom trawling on ecosystems is also very high, reducing the complexity of benthic communities (Auster 1998). All the components involved in trawling have the capability to affect the seabed, the net, the chains, the weights and, especially, the doors. These can go various centimeters into the seabed (up to 30 cm depth) depending on the sediment and the technique used, damaging benthic ecosystems (Collie et al. 2000; de Juan et al. 2007, 2011). All trawl components show a huge impact on soft-bottom environments yielding less species selectivity than other fishing techniques, damaging the substrate and its sessile species, and increasing its slow recuperation. The reduction of invertebrates (echinoderms, polychaetes and molluscs) in trawled zones reach up to 65 % when compared with areas where this kind of fishing has not taken place (Bergman and Hup 1992).

Trawling can create also similar effects to eutrophication, increasing the presence of opportunist species in benthic environments. The reduction of biomass in these zones, when compared with an area where trawling has not taken place, can be ten times greater, especially with regard to fish species. Additionally, trawling discards can give rise to episodes of anoxia on the seabed, increasing the mortality of target species (Browder 1981) and causing changes in the structure and composition of these species (Chan and Liew 1986). The effect of discards can be noted on other taxonomic groups of fauna as marine birds. Discards may support a demographic explosion of the most opportunistic species to the detriment of other, more vulnerable ones (Garthe and Hüppop 1998), producing also changes in habitats, behavior and reproduction. Trawling also affects the water column and the ecosystem in general, by changes in biogeochemistry and the nutrient effluents caused by the resuspension of sediments, nutrients and pollutants, as well as damage to the invertebrates that are responsible for irrigating, compacting and oxygenating the seabed (Schwinghamer et al. 1996). The increase in turbidity can also influence the photosynthetic capacity of plants, with the resultant decrease in their distribution and productivity in the photic zone (Caddy 2000).

In general, trawling on soft-bottom habitats affects the most to long-living epibenthic species and less the infaunal

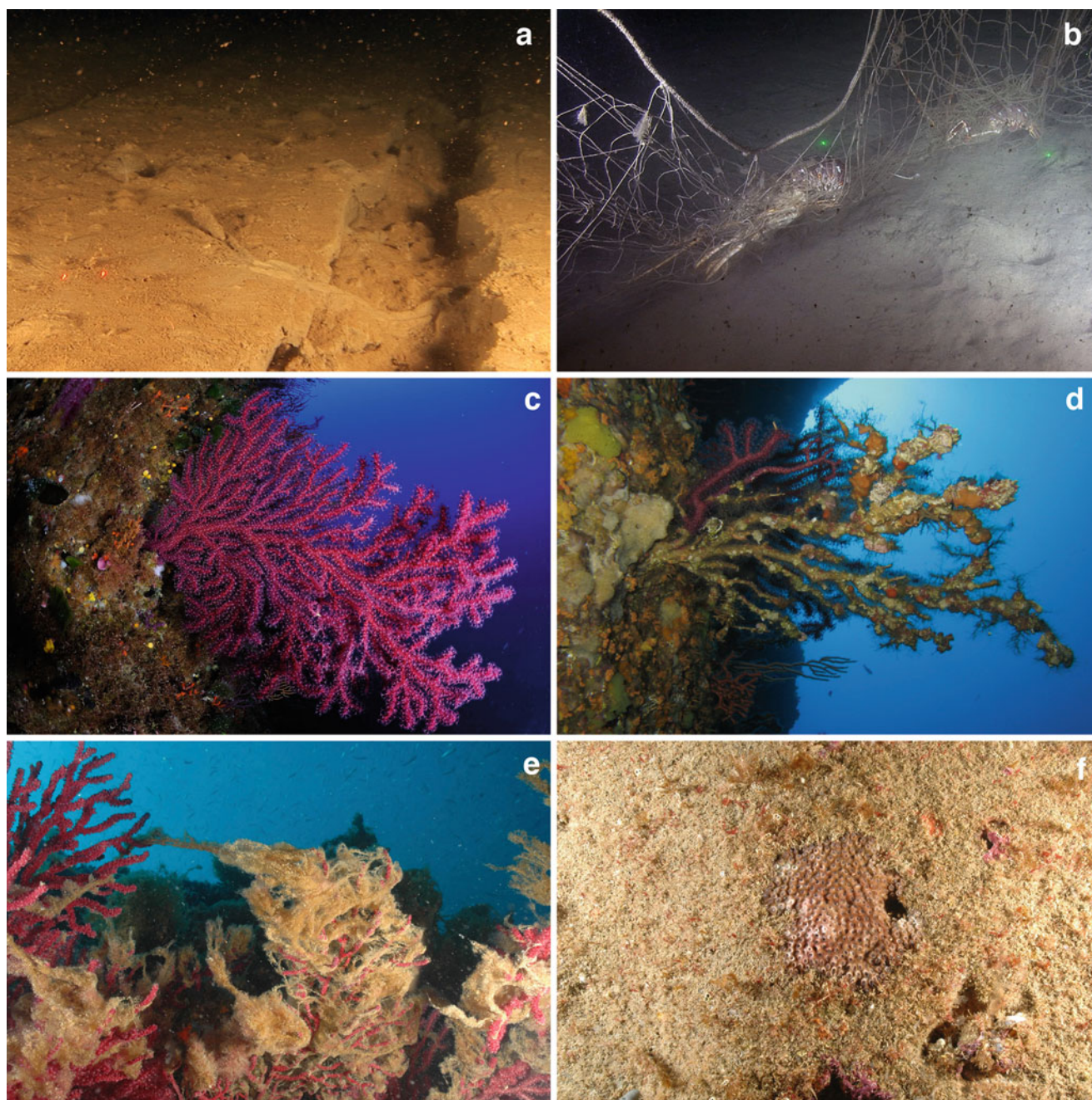


Fig. 12.8 Examples of perturbations: (a) trawl marks and (b) gosh net entangling adult lobsters *Palinurus elephas* (Photographs a and b by NEMO-ICM-Gavin Newman) as examples of direct human perturbations by fishing in the Cap de Creus continental shelf (NW Mediterranean) at 110 m depth; mass mortalities events affecting *Paramuricea clavata* at 20 m depth in Corsica (Central Mediterranean) (c) healthy colony and (d) a colony showing almost complete loss of

tissue, the denuded axis have been colonized by different epibiotic species (Photographs c and d by MedRecover Marine Conservation Research Group); (e) mucilage aggregations on gorgonian *Paramuricea clavata* at 20 m depth, Montgrí Coast (NW Mediterranean); (f) invasive species *Oculina patagonica*, colony found at 15 m depth in Medes Islands (NW Mediterranean) (Photographs e and f by Núria Teixidó)

ones. Consequently the oldest and longest living species are the scarcest in trawled areas, while younger, more short-lived species are the most abundant (Tuck et al. 1998). The effects of trawling in the long-term could also favor small passive filter-feeders over larger active filter-feeder species. Effects of trawling are as important as those produced by

strong natural perturbations (Pusceddu et al. 2005). Trawling may have a very high impact on important and unique habitats of long-term formation, seagrass beds, maërl habitats, and deep coral reefs. In deep-sea, the impact of trawling on species assemblages could be even greater. Because these areas are not regularly subjected to natural changes, as

frequently as in shallower waters, are more vulnerable to artificially induced changes (Langton and Auster 1999).

Nutrient Increase

Disease and mucilage formation are phenomena that are directly attributed to nutrient increase in the Mediterranean Sea. The mucilage phenomenon has been affecting different areas of the North-Western Mediterranean during the last decades (Mistri and Ceccherelli 1996a; Giuliani et al. 2005) (Fig. 12.8e). The first record was in 1991 in the Tyrrhenian Sea (Innamorati et al. 1993), but it has been spreading in other areas during the last 20 years (Pusceddu et al. 2009). This phenomenon, in which different algae form a compact bloom that covers benthic communities (Giuliani et al. 2005), has a direct effect on suspension feeders, covering during a prolonged time their feeding structures. Entire populations can be affected, being the extent of the injuries negatively correlated with the size of the colonies (Mistri and Ceccherelli 1996a). However, as in the previously described hot waves mass mortalities, the recovery of the colonies were also observed after 2 years of the event (Mistri and Ceccherelli 1996b). An indirect effect of hypoxia (and even anoxia) is also observed because of the oxygen depletion by bacterial respiration (Schiaparelli et al. 2003). Is not clear which is the origin of the mucilage, neither if is related with local contamination (high nutrient concentration), but it is certain that has effects on the pelagic and benthic functioning (Pusceddu et al. 2009).

Another phenomenon related with the microbiological or viral attack in hard bottom suspension feeders has been described in sponges (Gaino et al. 1992). The disease apparently produced by bacteria, made profound alterations on the skeleton with bacterial damage fibres (Cebrian et al. 2011). Commercial sponge beds were heavily damaged, especially in shallower areas, and because of its intensive harvesting, were locally depleted (Pronzato and Manconi 2008).

Harvesting

Commercial sponges and red coral are the most affected animal species by direct impact on hard bottom substrates (Pronzato and Manconi 2008; Tsounis et al. 2010). *Spongia*, *Hypospongia*, and *Corallium rubrum*, have been exploited for thousands of years. However, the most intense harvesting period is centred in the last two centuries. Sponges also suffered a devastating disease that dropped dramatically the landings and the commercialization of these species (Pronzato and Manconi 2008). Other sponge species have been recently identified as animals of pharmacological interest (like *Dysidea avara*), threatening the resource to extract the target metabolites (Pronzato et al. 2000). Red coral has also been harvested in a completely unsustainable manner (Tsounis et al. 2007), because no biological parameters are considered in the actual fishery models. The intense harvesting

and mass mortalities may collapse this resource at a local level in the first 50 m depth, due to a synergic effect (Garrahou et al. 2001; Santangelo et al. 2007). Even if there is a real effort to recover both harvested suspension feeders organisms (Pronzato et al. 2000; Bramanti et al. 2007; Linares et al. 2012; Benedetti et al. 2011), there is still a long way to manage properly these overharvested species. Other important harvesting activities that may cause severe direct or indirect impact on rocky benthic invertebrate assemblages and their habitat as in the case of the edible sea urchin *Paracentrotus lividus* (Sala et al. 1998a, b; Pais et al. 2007) and the rock-boring date mussel *Lithophaga lithophaga* (Fanelli et al. 1994; Guidetti et al. 2003).

Local Impacts

Local impacts on suspension feeders due to the direct action of humans have also important consequences. Sala et al. (1996) found that the bryozoan *Pentapora fascialis* was more exposed to SCUBA diver's action in frequented than in non-frequented areas. The same perturbation (dead or partially injured colonies) or the lack of populations recovery were found in a long term monitoring of the gorgonian *Paramuricea clavata* and red coral *Corallium rubrum* (Coma et al. 2004; Linares et al. 2012). SCUBA diving may be re-directed to a more respectful and appropriate diving behaviour (Bramanti et al. 2011). However, simple actions like bubbling near the colonies during the spawning period may cause the loss of sexual products before the fecundation process occurs, and therefore damaging the entire population (Tsounis et al. 2012).

Other not so evident damages in suspension feeders assemblages are caused by line fishing, which may affect more than 30 % of the gorgonians in highly frequented areas by amateurs or professionals (Bavestrello et al. 1997; Bramanti et al. 2011). Lines denude the axis of the animals, which favours the development of epibiont aggregates. Mechanical stress has also been recorded, damaging colonies that can be partially or totally broken. These kind of injuries have an effect on the gonadal output and in the energy storage capability of gorgonians that may produce less potential recruits (Tsounis et al. 2012). Other negative local impacts are those performed on sea-grasses by the anchoring of boats from recreational boating that causes mechanical damage and habitat loss (Francour et al. 1999; Milazzo et al. 2004; Lloret et al. 2008).

Natural and/or Indirectly Man-Induced Pressures

Increasing Temperature

The temperature increase observed in recent decades in the ocean has also been observed in the Mediterranean Sea. Two significant mass mortalities due to a heat wave (1999 and

2003) have been detected and their impact in hard bottom communities quantified (Cerrano et al. 2000; Perez et al. 2000; Garrabou et al. 2009). In these mass mortality events, the so-called animal forest were affected in the first 10–50 m depth in a wide range (more than 1,000 km of coast in the second heat wave), partially or totally killing gorgonians, corals, sponges or bryozoans. Affected colonies also recorded extensive attacks of microorganisms (protozoan and fungi) (Cerrano et al. 2000) (Fig. 12.8c,d). The anomalous high temperatures, the energetic constraints associated with water column stability conditions and pathogens developments, were the most probable causes of mortality (Bally and Garrabou 2007; Coma et al. 2009; Vezzulli et al. 2010). Other mass mortality events have been reported in the Mediterranean (Bavestrello et al. 1994; Harmelin and Marinopoulos 1994; Maldonado et al. 2010; Cebrian et al. 2011), although in previous outbreaks the number of affected species and/or spatial scale concerned was lower than in the above-mentioned 1999 and 2003 mass mortalities.

Several time series have examined the effects of the heat waves on different organisms especially in the coralligenous communities. Linares et al. (2008) showed the warming effect on the reproductive output of the gorgonian *Paramuricea clavata*, being the most affected colonies those with less gonadal production. Bramanti et al. (2005) observed a drop in the recruitment of shallow red coral patches, probably a consequence of the partial or total mortality of the colonies (Garrabou et al. 2001). Alternatively, not all the areas recovered in the same way after the heat wave. Unlike in the Port Cros National Park (Linares et al. 2005), *Paramuricea clavata* had high recruitment rates and tissue recover in the Eastern Ligurian Sea (Cupido et al. 2008, 2009), showing that population dynamics of gorgonians may differ with local environmental factors (Bramanti et al. 2009). Also the autoecology of the species is a key factor to understand the capacity to recover, being *Eunicella singularis* the species that showed the best recovery in the above-mentioned area (Fava et al. 2010). Recently, genetic studies demonstrated significant genetic structure between populations at small spatial scales (tens and hundreds of meters), suggesting that gene flow is highly restricted (Ledoux et al. 2010; Mokhtar-Jamäi et al. 2011). These results indicate that recovery of populations from large perturbations is very likely only based in local processes.

Ocean Acidification

Another less understood but probable damage suffered by the benthic communities due to the climate change in the Mediterranean sea will be the ocean acidification effects. Ocean acidification is predicted to impact all areas of the oceans and affect a variety of marine organisms (Durrieu de Madron et al. 2011). The diversity of responses among

species prevents clear predictions about the impact of acidification at the ecosystem level (Hall-Spencer et al. 2008; Kroeker et al. 2011).

Organisms like polychaetes or amphipods seem to be non-affected by the future acidification panorama, but decapods or gastropods may suffer severe impacts on its calcareous structures (Kroeker et al. 2011). Other calcareous organisms may be extremely affected by future ocean acidification, as shown by Lombardi et al. (2011) in the bryozoan *Schizoporella errata*. In this suspension feeder, the putative defensive polymorphs (avicularia) were significantly fewer, and retarded growth of zooidal basal and lateral walls was evident at low pH. Other studies show the effects of the chemical balance alteration in micronutrients essential for the physiological needs of bryozoans. In *Myriapora truncata*, prolonged low pH exposition increases the enrichment of Mg in outer layers, enhancing the skeleton vulnerability to dissolution. Alternatively, the symbiotic anthozoan *Cladocora caespitosa* seems to be non-affected by pCO₂ increase. So, the common belief that calcification rates will be affected by ocean acidification in all calcifier organisms may not be the common rule (Rodolfo-Metalpa et al. 2010). In fact, much work is needed to better understand the potential impact of pCO₂ increase, not only in the physiology of organisms but also at the community and between organism interaction levels.

Easterly Wind-Storms

Easterly wind-storms occur frequently and have high intensity in the Western Mediterranean Sea (Mendoza et al. 2011). The immediate effect of these storms is a direct mechanic perturbation on the benthic fauna and flora. Pluri-annual algal canopies like *Cystoseira zosteroides* may be heavily affected by autumn storms, but their recovery depends upon local population size structure, mortality and recruitment (Navarro et al. 2011). The changes produced in the algal and sessile animal composition, as well as in the abundance of vagile organism, may be crucial for the survivorship of higher trophic levels.

But there is also another less evident effect of easterly wind-storms that influences benthic communities. Storms affect resuspension modifying the composition of the organic fraction of settling particles, decreasing the labile fraction of particulate organic matter (Grémare et al. 1997; Rossi et al. 2003). The storm may result in a transitory increase of the abundance of fine particles at the water-sediment interface, coating these particles with highly refractory matter (Grémare et al. 2003). Even if in the deep coastal shelf and in submarine canyons such storms may mobilize particles suitable for benthic organisms (Puig et al. 2001; Sardà et al. 2009), in near coastal shallow areas can give rise to a shortage in food availability. The decrease in food availability because of high resuspension and heavy river runoff particle

transport rises the food stress level in passive suspension feeders (Rossi et al. 2006b).

Biological Invasions

Biological invasions in marine habitats represent one of the main factors of human-induced global changes (Occhipinti-Ambrogi and Savini 2003). The Mediterranean Sea has been subjected to introductions of non-indigenous species by ship traffic and aquaculture several centuries ago, but it has been during the last hundred years when these impacts have been accelerating (Galil 2000). Besides the Suez channel opening in Egypt. Also, the proliferation of artificial hard structures has been a key factor for the spreading of many species (Bulleri and Airoldi 2005), as well as the transformation of benthic areas by different direct or indirect human intrusions (Coma et al. 2011). An updated checklist of marine alien species within each subregion of the Mediterranean Sea, along with their acclimatization status and origin has been recently provided by Zenetos et al. (2010). A total of 955 alien species are known in the Mediterranean, the vast majority of them have been introduced in the Eastern Mediterranean (718), less in the Western Mediterranean (328) and Central Mediterranean (267), and least in the Adriatic (171), being this numbers underestimated. Excluding microalgae, for which knowledge is still insufficient, aliens have increased notably the total species richness of the Mediterranean Sea by 5.9 %. A total of 134 alien species are classified as invasive or potentially invasive (108 are present in the Eastern Mediterranean, 75 in the Central Mediterranean, 53 in the Adriatic and 64 in the Western Mediterranean). Invasive species presence indicates that they have spread, are spreading or have demonstrated their potential to spread elsewhere, and have an adverse effect on biological diversity, ecosystem functioning, socio-economic values and/or human health in invaded regions. A large portion of these invasive species are benthic species.

One of the most studied invasions of hard bottom suspension feeders is the *Oculina patagonica* case (Fig. 12.8f). This species is a new immigrant from the Southwest Atlantic to the Mediterranean Sea, which has now a widespread distribution even in the eastern Mediterranean (Fine et al. 2001). Coma et al. (2011) observed a longterm series of expansion in this symbiotic anthozoan, as well as the abundance of *Paracentrotus lividus*, the main grazer of macroalgae in hard bottom substrates. Their results show that part of the increasing presence of *Oculina patagonica* may be explained by the increase of sea urchin abundance, which creates a barren rock suitable for the settling of the alien species (Coma et al. 2011). Sponges have also been reported to invade the Mediterranean. The calcareous sponge *Paraleucilla magna* is proliferating in the western Mediterranean since 10 years ago (Guardiola et al. 2012) and its origin remains unknown. In general, the first stages of colonization and the capacity to

survive during the settling process have been observed as key factors to better understand alien species success on hard bottom substrates (Rius et al. 2009a, b).

In summary, Mediterranean benthic communities have been perturbed and changed by human activities since the beginning of the civilization. With the progressive increase in human population in the coastal zone, the impact has increased especially on the coast but also along the continental shelf. Today, signs of disturbances caused by man activities can be seen in almost all regions of the Mediterranean Sea. Both trawling and pollution drastically affect the loss of diversity and benthic habitat reduction. The anthropogenic effects must be added to those produced by global warming that affect especially the shallow populations and may favor the proliferation of invasive species. The conservation of the Mediterranean requires urgent measures such as marine protected areas and a proper change in its management, based on rigorous scientific knowledge (Riell 1980; Sala 2004). Benthic communities, especially those dominated by animals, have been unfairly ignored in management plans and conservation all around the world (Arntz et al. 1999).

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