Marine biodiversity in the mediterranean: status of spicies, populations and communities [1]

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Abstract : The Mediterranean Sea, probably thanks to the narrowness of its communication with the Atlantic, to its east-west orientation and to its geological history, constitutes a hot-spot of marine species diversity. It does not appear to be the case that what we see is an artefact linked to the pressure of scientific investigation being greater than for other regions of the world. The number of species actually inventoried in the Mediterranean Sea can be estimated at about 12 000 species; it is greater in the western than in the eastern basin. The fauna and flora of the Mediterranean are mainly of Atlantic origin. They encompass a rather high number of endemics, most of them being relatively recent (neo-endemics). A very few biota from the former Tethys Sea are present, e.g. the seagrass *Posidonia oceanica* which plays a major role in the modern Mediterranean, of which it is emblematic. Finally, there are about 400 introduced species in the Mediterranean. Most of them are lessepsians immigrants: they entered the Mediterranean *via* the Suez Canal, after its opening in 1869. Many other species introduced to the Mediterranean arrived through fouling and clinging on ships' hulls. Since the 1970s, aquaculture has been another major source of species introduction. The Mediterranean Sea harbours a large variety of communities, as a function of depth, substrate, mean irradiance, water movement and the annual range of temperature. Some of these communities are unique, giving the Mediterranean its touch of originality: the *Posidonia oceanica* meadow, between the mean sea level and a depth of 25-40 m, the coralligenous community, mainly buit up by crustose corallines in sciaphilic biotopes, the *Litophyllum byssoides* rim, at the bottom of the mediolittoral zone, the vermetid platform and the *Neogoniolithon brassica-florida* algal reef, typical formations of the warmest parts of the Mediterranean. These communities are sensitive to coastal development, pollution, water turbidity, mooring, trawling and/or diving. No marine species seems, at the moment, to have totally disappeared from the Mediterranean. However, two of them are critically endangered: the monk seal *Monachus monachus* and the giant limpet *Patella ferruginea*. Many other species dramatically declined during the twentieth century, e.g. *Cystoseira* spp. (Fucophyceae), the mollusc *Pinna nobilis*, the seahorse *Hippocampus ramulosius* and the sea-turtle *Caretta caretta*. Unfortunately, recent data are more or less totally lacking for most Mediterranean species, so that it is impossible to assess the status of their populations.

Résumé : La Méditerranée, sans doute en raison de l'étroitesse de sa communication avec l'Atlantique, de son orientation Est-Ouest et de son histoire géologique, constitue un "hot-spot" (point chaud) pour la diversité spécifique marine. Il ne semble pas qu'il s'agisse d'un artéfact lié à une pression de recherche qui serait plus forte que dans d'autres régions du monde. Le nombre d'espèces effectivement inventoriées en Méditerranée est de l'ordre de 12 000. La diversité spécifique est plus élevée dans le bassin occidental que dans le bassin oriental. L'origine de la faune et de la flore méditerranéennes est principalement atlantique. Elles comportent également un nombre relativement élevé d'endémiques, la plupart d'origine relativement récente (néo-endémiques). En revanche, très peu d'espèces reliques de l'ancienne Téthys sont présentes. L'une d'entre elles est emblématique de la Méditerranée, dont elle est du reste endémique, la phanérogame *Posidonia oceanica*. Enfin, La méditerranée héberge environ 400 espèces introduites. La plupart d'entre elles sont des immigrants lessepsiens, c'est à dire des espèces qui sont entrées en Méditerranée *via* le canal de Suez, après son ouverture en 1869. Beaucoup d'autres espèces introduites sont arrivées en Méditerranée sur les coques de bateaux (fouling et clinging). Enfin, depuis les années 1970s, l'aquaculture est devenue une voie majeure d'introduction. La Méditerranée abrite une grande diversité de communautés, en function de la profondeur, du substrat, de l'irradiance moyenne, de l'agitation et de la temperature. Certaines de ces communautés traduisent l'originalité de la Méditerranée : l'herbier à *Posidonia oceanica*, entre le niveau moyen et 25-40 m de profondeur, le coralligène, édifié principalement par des corallinacées encroûtantes dans les biotopes sciaphiles, l'encorbellement à *Litophyllum byssoides*, à la base du médiolittoral, et enfin le trottoir à vermets et les récifs à *Neogoniolithon brassica-florida*, formations caractéristiques des secteurs les plus chauds de la Méditerranée. Ces communautés sont vulnérables à l'urbanisation littorale, la pollution, la turbidité, les ancrages, le chalutage et/ou la plongée sous-marine. Aucune espèce marine ne semble, pour le moment, avoir totalement disparu en Méditerranée. Cependant, deux d'entre elles sont en danger critique : le phoque moine *Monachus monachus* et la patelle géante *Patella ferruginea*. Beaucoup d'autres espèces ont régressé fortement au cours du 20° siècle, e.g. *Cystoseira* spp. (Fucophyceae), le mollusque *Pinna nobilis*, l'hippocampe *Hippocampus ramulosius* et la tortue *Caretta caretta*. Malheureusement, les données récentes les concernant manquent souvent, de telle sorte que le statut de leurs populations ne peut pas être établi.

INTRODUCTION

The geological history of the Mediterranean, together with its geomorphology and environmental conditions, are important features for understanding its present day biodiversity.

The Mediterranean is an almost closed sea: the Straits of Gibraltar, by which it communicates with the Atlantic Ocean, are only 14 km wide and 320 m deep. It also communicates with the Black Sea (via the Bosphorus). Lastly, the digging of the Suez Canal (1869) allowed the Mediterranean to communicate with the Red Sea again. This communication route had been closed for 12-13 million years (Ma) (ROGL and STEININGER, 1984; STANLEY, 1986; ROGL, 1998). This link, nowadays 120-125 m wide and 13-15 m deep, is negligible as regards the mass of water concerned, but of major consequence from the biological viewpoint, with the massive entry of Red Sea species into the eastern Mediterranean (POR, 1978, 1990). The shallowness of the Gibraltar threshold prevents the very cold water from the Arctic, which flows southwards along the bottom of the Atlantic, from entering the

Mediterranean. Thus the temperature of the water in the Mediterranean, instead of progressively dropping with depth (as happens in the Atlantic), is constant (about 13° C) all year round (HOPKINS, 1984).

In the Mediterranean, evaporation stands at 3 500 cubic kilometres a year. The rivers (mainly the Rhône, Po, Nile and Ebro) only bring in 350 km³/a, and rainwater 850 km³/a. The deficit in water is thus some 2 300 km³/a, which represents, spread out over the whole of the Mediterranean, a slice of water about 1 meter thick (TCHERNIA, 1978). According to BETHOUX and GENTILI (1998), its actual thickness lies between 78 and 96 cm. Without the water coming in from the Black Sea (via the Bosphorus: 200 km³/a) and particularly from the Atlantic (via Gibraltar: 2 100 km³/a), the Mediterranean would dry up (in about 3 000 years). For reasons of thermal and mechanical balance, some 35 000 cubic km³/a flow in via Gibraltar (at the surface, for this is less salty water: 36.2-36.3‰), and 32 900 km³/a flow out (at depth, for this is saltier water: 37.9-38.4‰) (TCHERNIA, 1978). The average sea-level of the Atlantic is slightly higher than that of the Mediterranean (3 cm in July, 11 cm in January). The Red Sea is also slightly higher than the Mediterranean (24-40 cm), so that the water in the Suez Canal generally runs from the Red Sea towards the Mediterranean (which is important for migratory species; see below).

In the Miocene (Messinian) age, between 5.6 and 5.3 Ma ago, Gibraltar was closed several times, and the Mediterranean Sea more or less dried up each time. During these "Messinian crises", layers of salt and gypsum were laid down, with a thickness of up to 3 500 m. In all, 1 million km³ of salt were laid down (HSU, 1972; HSU et al, 1977; PERES, 1985; KRIJGSMAN et al., 1999;

Table I. Partial assessment of the number of species (or taxa) of Mediterranean fauna and floraa (see text for references). Pelagic algae are not taken in consid-eration. *= benthic species only. **= estimate.

Phylum	Number ofspecies
Porifera	622
Cnidaria	420
Ctenophora	23
Echinodermata	144
Mesozoa	11
Nemertinea	112
Nematoda	150
Rotifera	35
Gastrotrichia	118
Kinorhyncha	23
Nematomorpha	1
Gnathostomulida	5
Chaetognatha	20
Priapulida	3
Annelida*, **	791
Myzostomida	4
Echiurida	6
Sipuncula	33
Brachiopoda	15
Entoprocta	19
Ectoprocta**	494
Mollusca**	2 026
Tardigrada	18
Arthropoda**	1 938
Pogonophora	1
Phoronidea**	5
Hemichordata	5
Chordata	244
Loricifera**	1
Vertebrata	694
Cyanobacteria	165
Rhodophyta	816
Fucophyceae	255
Chlorophyta*	209
Phanerogama	9
TOTAL	9 435

McKENZIE, 1999). After the reopening of Gibraltar, the Mediterranean filled up over 100 years (McKENZIE, 1999). Over the past 500 000 years, eleven anoxic crises have occurred in the eastern Mediterranean deep water, the last one 7 000-9 000 years ago, resulting in the deposition of black and organic-rich layers of sediment (sapropels). These crises were due to the stoppage of dense water formation in the Adriatic Sea, following sealevel and/or freshwater input changes (BETHOUX, 1993; BETHOUX and GENTILI, 1998). During the ice ages, contrary to what has sometimes been suggested, there does not seem to have been any inversion of the inflow and outflow currents at Gibraltar (BETHOUX, 1993).

The Mediterranean is often considered as a tideless sea, which is wrong. Semidiurnal tides do occur, though their amplitude is generally small (30-40 cm) by world ocean standards, with the exception of the northern Adriatic and the Gulf of Gabès (up to 150 and 180 cm, respectively). Finally, the surface water layer (0-100 m) is oligotrophic, due to the poor input of water (and therefore nutrients) by rivers and run-off.

The overwhelming value of biodiversity (species diversity and community diversity, the latter hereafter referred to as ecodiversity), as an indication of environmental health and for the functioning of the biosphere is now widely recognized, not only by academic scientists, but also by the mass media, decision makers and public opinion (LAWTON, 1994; BIANCHI, 1996; CULOTTA, 1996; BOUCHER, 1997; GRIME, 1997; NAEEM and LI, 1997; AARTS and NIENHUIS, 1999; BIANCHI and MORRI, 2000; NAEEM et al., 2000; HENRY et al., 2001). Unfortunately, marine biodiversity, especially in the Mediterranean, has received only a very small fraction of the attention accorded to terrestrial environments (BIANCHI, 1996; ORMOND, 1996). Not only do the species definitely recorded from the Mediterranean clearly represent only a small part of those that actually occur there, but the present status (how many? where? on the increase or on the decrease?) of most of them is virtually unknown, with the exception of a few emblematic species, mainly sea mammals and sea turtles.

Species diversity in the Mediterranean

In the Mediterranean Sea, the number of animal species actually inventoried (strictly marine and brackish lagoon species; **Table I**) can be estimated at about 8 000 species (data from in particular FREDJ and LAUBIER, 1985; FREDJ and MAURIN , 1987; PANSINI, 1990; FREDJ et al., 1992; RELINI, 1992; SEGUIN et al., 1992; BOUDOURESQUE, 1995; BIANCHI, 1996; BOUDOURESQUE, 1997a; PANCUCCI-PAPADO-POULOU et al., 1999; BIANCHI and MORRI, 2000; Medifaune®).

As far as the macrophytes are concerned, only the Phanerogama (9 taxa; HARTOG, 1970), benthic Chlorophyta (209 taxa; GALLARDO et

al., 1993) and the Fucophyceae (255 taxa; RIBERA et al., 1992) have been recently inventoried. Considering that the ratio between the number of Rhodophyta and that of Fucophyceae (R/P ratio; FELDMANN, 1938) should be around 3.2 (**Table II**), one can extrapolate 816 taxa of Rhodophyta. One can therefore assess at some 1 500 the macrophyte species (including Cyanobacteria) (**Table I**).

Table II. Relationship between the number of taxa and stages of Rhodophyta and Fucophyceae (R/P ratio) in the Mediterranean.

Region	Reference	Number of Rhodophyta	Number of Fucophyceae	R/P Ratio
Alexandria (Egypt)	ALEEM (1993)	141	48	2.9
Aegean Sea (Greece, Turkey)	ATHANASIADIS (1987)	274	91	3.0
Tunisia	BEN MAIZ et al. (1987a)	245	82	3.0
Pyrénées-Orientales (France)	BOUDOURESQUE et al. (1984b)	311	113	3.0
Corsica (France)	BOUDOURESQUE and PERRET-BOUDOURESQUE (1987)	318	102	3.1
Algeria	PERRET-BOUDOURESQUE and SERIDI (1989)	292	95	3.1
Sicily (Italy)	GIACCONE et al. (1985)	423	136	3.1
Var (France)	BOUDOURESQUE and PERRET-BOUDOURESQUE (1979)	319	102	3.1
Naples (Italy)	FURNARI (1984)	289	91	3.2
Balearic Islands (Spain)	RIBERA-SIGUAN (1983)	275	79	3.5
Catalonia (Spain)	BALLESTEROS (1990)	315	90	3.5
South-east of Spain	SOTO (1987)	276	71	3.9

Bearing in mind work done more recently than these estimates of numbers of fauna and flora, and of the taxonomic groups they fail to take account of (e.g. bacteria other than Cyanobacteria, Diatomophyceae, Dinophyceae), the number of species reported in the Mediterranean must be around 12 000 (GIACCONE, 1974; FREDJ and MEINARDI, 1989; RELINI, 1992; BOUDOURESQUE, 1995, 1997a).

Be that as it may, the biodiversity of the Mediterranean, like that of the world's other seas and oceans, remains largely unknown. Every year, several dozen new species are reported (or described for the first time) in the Mediterranean. In the present state of knowledge, all thinking on biodiversity must therefore rely largely on hypotheses.

Table III. Numbers of taxa and stages of marine Chlorophyta, Fucophyceae and Rhodophyta in some regional seas. ᵃ= Values calculated from authors' data. ᵇ = Number of Rhodophyta extrapolated from the number of Fucophyceae and an average R/P ratio of 3.2. ᶜ = Number of Rhodophyta extrapolated from the number of Fucophyceae and an average R/P ratio of 3.1. ᵈ = "Doubtful" species have been taken in consideration. ᵉ = Including freshwater species. For the oceanic coasts, surface area is calculated by multiplying the length of the coast by a 500 km width (half the average width of the Mediterranean Sea). Tropical West Africa: from Gambia to the equator. From BOUDOURESQUE (1997a).

| Sea	Surface area in x1000 km²	Chloro-Phyta	Fuco-Phyceae	Rhodo-phyta	TOTAL	Reference
Greenland Sea	1 200	96	136	135	367	SOUTH and TITTLEY (1986)[a]
North Sea	570	136	214	362	712	SOUTH and TITTLEY (1986)[a]
Baltic	420	128	90	111	329	PANKOW (1971)
Black Sea	420	80	80	129	289	RIBERA et al. (1992)[a]; GALLARDO et al. (1993)[a]; ZINOVA (1967)
South-East USA	500	65	59	200	324	SCHNEIDER and SEARLES (1991)[a]
Mediterranean (without Black Sea)	2 500	209	255	816	1 280	RIBERA et al. (1992)[a]; GALLARDO et al. (1993)[a, b]
Western Mediterranean	820	185	220	704	1 109	Idem
Adriatic	130	129	156	390	675	Idem and GIACCONE (1978)
Eastern Mediterranean	1 550	125	141	437	701	RIBERA et al. (1992)[a]; GALLARDO et al. (1993)[a, c]
South Australia Sea	3 500	123	231	786	1 140	WOMERSLEY (1984, 1987)
Tropical West Africa	1 900	71	61	231	363	LAWSON and JOHN (1987)[a, c]
Gulf of Mexico	1 500	122	62	230	414	TAYLOR (1960)[a]
Caribbean Sea	2 800	159	73	330	562	TAYLOR (1960)[a]
Total number		3 600[a]	1 500	5 000	9 100	BOURRELLY (1972)[a]; BOLD and WYNNE (1978)[a]; MARGULIS and SCHWA-RTZ (1985)[a]; STRASBUR-GER et al. (1988); LUNING (1990); NORTON et al. (1996)
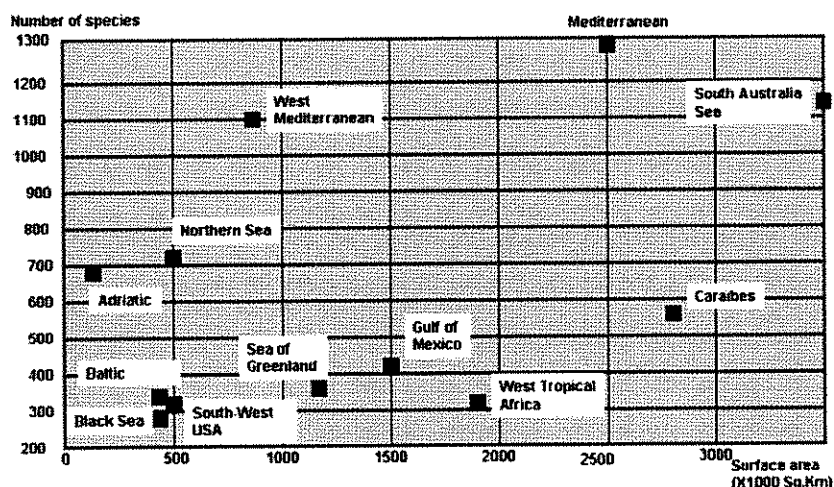
Fig. 1 : Relationship between species diversity of the flora (macrophytes) and the surface area of some regional seas or parts of oceans.

All in all, the Mediterranean fauna and flora seem particularly rich, and it does not appear to be the case that what we see is an artefact linked to the pressure of scientific investigation being greater than for other regions of the world (**Table III** and **Figure 1**). While the Mediterranean only represents less than 0.8% of the world ocean area, and less than 0.3% of its volume, its fauna and flora represent 7% of described species, with strong differences according to the groups considered. For the Chlorophyta, for example, at least 6% of known marine species occur in the Mediterranean. For the Fucophyceae (an almost exclusively marine group), 17% of the 1 500 species described in the world (BOLD and WYNNE, 1978; RIBERA *et al.*, 1992; NORTON *et al.*, 1996; BOUDOURESQUE, 1997a) occur in the Mediterranean. This percentage is 10% for sponges: 622 species in the Mediterranean, out of the 6 000 known species (BERGKIST, 1978; PANSINI, 1990; Nicole BOURY ESNAULT, pers. comm.; Elena VOULTSIADOU KOUKOURA, pers. comm.). It is 10% for the Annelida (FREDJ *et al.*, 1992). Conversely, the Echinodermata are relatively poorly represented, with only 2% of world species (TORTONESE, 1985; FREDJ *et al.*, 1992). Naturally, these percentages must not be compared only on the basis of the relative size of the Mediterranean in terms of surface area: most of the species present not being endemic, it is normal that they are higher than this relative size. They must be compared with other regional seas of comparable size (**Table III, Fig. 1**), although the comparison is hard to perform (surface area, coastline, exploration pressure, and age of inventories vary greatly from one area to the next). Moreover, one might think that the Mediterranean has been particularly well explored, but we believe this is doubtful.

The only region in the world that compares with the Mediterranean in the species diversity of its marine flora is the southern coast of Australia (LUNING, 1990; **Table III, Fig. 1**). As a result, the Mediterranean Sea may be considered as a hot spot of marine species diversity (SARA, 1985; WALLE *et al.*, 1993; BOUDOURESQUE, 1995; BIANCHI, 1996; BOUDOURESQUE, 1997a; BIANCHI and MORRI, 2000).

The distribution of this biodiversity is not homogenous within the Mediterranean (**Table IV**): 38% of the invertebrate fauna (FREDJ, 1974; FREDJ et al., 1992), 75% of the fishes (FREDJ and MAURIN, 1987) and almost all the algal species are confined to the 0-50 m bathymetric zone.

Table IV. Bathymetric distribution of the Mediterranean fauna: number of species observed below a given depth, as a percentage of total fauna. From FREDJ, (1974) and FREDJ et al. (1992).

Below (metres)	Number of species (as percentage)
0	100 %
50	63 %
100	44 %
150	37 %
200	31 %
300	25 %
500	18 %
1000	9 %
2000	3 %

As regards the benthos, this bathymetric zone only represents about 5% of the Mediterranean surface area. Conversely, less than 10% of Mediterranean animal species are present below a depth of 1 000 m, and less than 3% below 2 000 m (FREDJ, 1974; FREDJ *et al.*, 1992). The relative poverty of the fauna in the bathyal and abyssal zones constitutes a distinctive feature of the Mediterranean. It is due to the fact that, after the Messinian crises, deep Atlantic species were prevented from recolonizing the Mediterranean by the shallowness of the Gibraltar threshold. Moreover, these deep water species find the thermal state of the deep waters of the Mediterranean, with the temperature barely dropping below 13°C, very unlike that of the Atlantic, where the temperature can be much lower (PERES and PICARD, 1964; PERES, 1985; BELLAN-SANTINI and POIZAT, 1994).

Table V. Number of species (and percentage compared to the Mediterranean overall) of Fu-co-phyceae in the various sectors of the Mediterranean and in the Black Sea. Calculated from the data of RIBERA et al. (1992).

Sector	Number of species	%
North western	161	61%
Tyrrhenian Sea	183	69%
North Africa	119	45%
Adriatic	160	60%
Greece and Turkey (Mediterranean)	122	46%
Levantine basin	74	28%
Black Sea	80	30%

North-Western = continental Spain, the Balearic islands and continental France. The Tyrrhenian Sea = western Italy, Corsica, Sardinia, Sicily. North Africa = Morocco, Algeria and Tunisia. Levantine basin = Syria, Lebanon, Israel, Egypt and Libya.

The species diversity of the Western Mediterranean is greater than that of the Eastern Mediterranean: 51% greater for the Fucophyceae (calculated from the data of RIBERA *et al.*, 1992) and nearly 100% greater for the fauna (FREDJ, 1974). The fact that the scientific investigation effort has been less intensive in the Eastern Mediterranean cannot alone explain this difference. Within the Eastern Mediterranean, biodiversity is greater in the Aegean Sea (Greece and Turkey) than in the south and the Levantine basin (Syria, Lebanon, Israel, Egypt and Libya) (**Table V**).

The reasons for the general richness of Mediterranean flora and fauna are to be found in their origin. One of the reasons for this wealth is doubtless the coexistence, in the Mediterranean, of species from the warm and boreal Atlantic, the tropical Atlantic and the Indo-Pacific (FREDJ, 1974; SARA, 1985; BIANCHI, 1996; BIANCHI and MORRI, 2000). Another reason is its exceptional rate of endemism (see below). As far as the bathyal fauna is concerned, it is made up of two types of species (PERES and PICARD, 1964):
- Atlantic epibathyal species, which tolerate a temperature of 12 -13°C.
- Shallow water species, tolerating depth, which can therefore go far down into deep waters since the thermal factor is not restrictive there.

Characteristics of the Mediterranean flora and fauna

Endemic species

The Mediterranean (and more especially the western Mediterranean) appears to be a particularly active centre of endemism. On the basis of 560 species of Hydrozoa, walking Decapoda, Echinodermata and Ascidia, PERES and PICARD (1964) estimate that the rate of endemism is over 29%. On the basis of 1 882 species of invertebrates and fishes, FREDJ (1974) and FREDJ and MAURIN (1987) estimate it at 19% (**Table VI**) and on the basis of 4 238 species of invertebrates and fishes, FREDJ *et al.* (1992) put it at almost 29%. These ratios are probably underestimates: most recent studies of species occurring both in the Mediterranean and the Atlantic ocean lead to the conclusion that Mediterranean and Atlantic populations are genetically distinct (e.g. the sea turtle *Caretta caretta* and the whale *Balaenoptera physalus*: LAURENT *et al.*, 1993; BEAUBRUN, 1995)

The rate of endemism varies according to the taxonomic group. It is, for example, zero for Sipuncula (PANCUCCI-PAPADOPOULOU *et al.*, 1999). It is greater among Echinodermata than among Mollusca (**Table VI**). It is 46% among Porifera (sponges), with a concentration of endemic species in the 0-200 m bathymetric zone (PANSINI, 1990; Nicole BOURY-ESNAULT, pers. comm.). Among the Ascidia, the rate of endemism is 50%. Doubtless, the reason for this is the short lifetime of the pelagic larvae of sponges and Ascidia. PERES and PICARD (1964) note that the rate of endemism is very logically in inverse proportion to the species' ability to move around. Though seabirds are not considered here, it is of interest to note that 90% of the species nesting around the Mediterranean are endemics (ZOTIER *et al.*, 1999). Finally, among algae, the rate of endemism is 20% (GIACCONE, 1974).

Table VI. Number and percentage of endemic species (or taxa) for some phyla of Mediterranean fauna. Data from FREDJ and MAURIN (1987) for fishes, and from FREDJ (1974) for other groups.

Phylum	Number of species of endemics	Number of endemics	Percentage
Echinodermata	134	32	24 %
Priapulida	1	0	0 %
Polychaeta Errantia	371	88	24 %
Echiurida	6	1	17 %
Sipuncula	20	4	20 %
Brachiopoda	15	2	13 %
Mollusca	401	65	16 %
Crustacea Decapoda	286	52	18 %
Pogonophora	1	1	100 %
Phoronidea	4	0	0 %
Hemichordata	5	2	40 %
Fishes	638	117	18 %
Total	1 882	364	19 %

The rate of endemism also varies according to sector. It reaches 26%, for example, for algae in Sicily (GIACCONE and GERACI, 1989). It is higher in the western Mediterranean (78% of Mediterranean endemics occur here) than in the eastern basin (23% only) (FREDJ *et al.*, 1992).

Mediterranean endemism appears much more clearly at the level of species than that of genus; this is recent endemism, or neo-endemism (FREDJ *et al.*, 1992). The Messinian crises, during which the Mediterranean more or less dried up (some 5.6-5.3 Ma ago), with the disappearance of a large part of its biota, are without doubt the cause of this. After these crises, some 5.3 Ma ago, the Mediterranean fauna and flora had to reconstitute itself on the basis of Atlantic stocks. The *Cystoseira* genus (Fucophyceae) is a good illustration of the speciation phenomena, which took place then. The Atlantic species, penetrating into the Mediterranean, evolved to give birth successively to several species and varieties, becoming increasingly distinct from the original Atlantic form the further from the Straits of Gibraltar they occurred (SAUVAGEAU, 1912a, 1912b; FELDMANN, 1958; GIACCONE, 1971a). For example, the Atlantic species *Cystoseira tamariscifola*, which penetrates into the Mediterranean along the southern coast of Spain, and especially along the coasts of North Africa, is then replaced at that point by a whole sequence of endemic and vicariant taxa, distributed to a greater or lesser extent from west to east from Gibraltar onwards: *Cystoseira mediterranea, C. amentacea* var. *stricta, C. amentacea* var. *spicata, C. amentacea* var. *amentacea* (GIACCONE, 1971b; RIBERA *et al.*, 1992). All in all, the *Cystoseira* genus contains 21 species endemic to the Mediterranean (GIACCONE, 1991).

Paleo-endemics are much rarer in the Mediterranean. The Rhodophyta *Rissoella verruculosa* probably belongs to this category. It is taxonomically very isolated, belonging to a monospecific genus and even a monogeneric family (KYLIN, 1956). The discovery of an extra-Mediterranean population (Canary Islands; AFONSO CARILLO and SANSON, 1999) does not invalidate its status as Mediterranean paleo-endemic. Rather, it illustrates the way paleo-endemics survived the Messinian crises, possibly thanks to extra-Mediterranean refuges (see below). The *Rodriguezella* genus is also endemic to the Mediterranean. *Laminaria rodriguezii*, similar to a Pacific species, must also be considered as a paleo-endemic (FELDMANN, 1934; STAM *et al.*, 1988). One of the Mediterranean species of the *Cystoseira* genus, *C. sedoides*, confined to the coasts of Algeria, Tunisia, and the Island of Pantelleria (Italy), could be a paleo-endemic, unlike most of the other Mediterranean species of the genus (GIACCONE, 1991). Some paleo-endemics probably result from the fragmentation of the old Tethys Sea, which gave rise to the Mediterranean. This may be the case for the Mediterranean Phanerogama *Posidonia oceanica*. The closest modern species are the

Australian *P. australis, P. ostenfeldii* and *P. sinuosa.* All modern *Posidonia* are probably descended from the Tethys dwellers *P. cretacea* and *P. parisiensis* (LARKUM and HARTOG, 1989). In the same way, the sponge *Discorhabdella hindei,* closer to *D. incrustans* from New Zealand than to *D. tuberosocapitata* from Azores, could be a pre-Messinian relict (BOURY-ESNAULT *et al.,* 1992). FREDJ *et al.* (1992) note that for the fauna, Mediterranean endemism is only 1-2% at the level of the genus.

Why is endemism so active in the Mediterranean? According to LUNING (1990), the compartmentalization of this sea (and its 46 000 km of coast) into fairly isolated sectors is probably the reason. In addition, the fluctuations of sea water temperature during the Quaternary, in an east-west orientated sea, where the species were unable to simply slip from north to south (and vice versa) to find the required temperature, unlike the Atlantic species, and the obligatory changing of ecological niche which resulted from this, probably also played their part. This is what PANSINI (1990) suggests for the sponges. We notice that, in the case of marine flora, the richest region in the world, along with the Mediterranean, is the southern coast of Australia (**Fig. 1**), also east-west oriented (LUNING, 1990). Lastly, the gene flow through the Gibraltar Straits was cyclically interrupted (when the Atlantic range of the species no longer included Gibraltar), allowing speciation to happen in the Mediterranean. All in all, in the phrase coined by BIANCHI (1996), the Mediterranean has functioned as a "diversity pump" from the Atlantic.

Such a high level of endemism does not hold for other regions of the world. There are no endemic algae in the Baltic Sea (SCHWENKE, 1974; RUSSELL, 1985), because it has been far too unstable: non-existent 18 000 years ago, freshwater 12 000 years ago, salt 10 000 years ago, not very salty 9 000 years ago, then increasingly salty over the last 7 000 years (DIETRICH and KOSTER, 1974). In the islands of the Atlantic, algal endemism is extremely low, perhaps because of the fluctuations of temperature which occurred with every ice age: 1% in Madeira, 3% in the Canary Islands, 3% in the Azores, 4% in the Cape Verde Islands (PRUD'HOMME VAN REINE and HOEK, 1988; LUNING, 1990), 5% in the Arctic, and 7% in tropical West Africa. Easter Island, the most isolated island in the Pacific, has an algal endemism of only 14% (BØRGESEN, 1924; SANTELICES and ABOTT, 1987).

Some rare regions of the world present a rate of endemism comparable to or greater than that of the Mediterranean. It is about 20% for fishes of the temperate South African Atlantic (BRIGGS, 1974), 33% for algae in the Arctic (LUNING, 1990) and in the temperate and cold regions of the Pacific coasts of South America (SANTELICES, 1980), 35% for algae in the Gulf of California (DAWSON, 1960), 43% for algae in New Zealand (PARSONS, 1985), and lastly 70% for algae in the southern coasts of Australia (WOMERSLEY, 1984, 1987).

The Messinian element

When the Mediterranean dried up, the only species to have survived were those that were able to live in hypersaline water, or in brackish water at the mouths of rivers, or in extra-Mediterranean refuges. These species, which we term the "Messinian element", are thus mostly species which today live in coastal lagoons. This is probably the case for Ostracods of the *Cyprideis* genus, and the fishes Cyprinodontidae of the *Aphanius* and *Valencia* genera: *Aphanius iberus*, a very rare species in Spanish and Algerian lagoons (GARCIA-BERTHOU and MORENO-AMICH, 1991), *Aphanius fasciatus*, a slightly commoner species that is widespread in the lagoons of the western Mediterranean, and *Valencia hispanica*, endemic in Spanish lagoons and fresh water (MAURIN and KEITH, 1994).

The case of the marine Phanerogama *Posidonia oceanica* is probably to be considered among the Messinian species. We do know that species of the *Posidonia* genus have occurred in the seas of Europe since the Cretaceous period: *Posidonia cretacea, P. perforata,* and *P. parisiensis* (STOCKMANS, 1932). As far as *P. oceanica* is concerned, its oldest fossilized remains date from the Pleistocene period, and are known in Sicily (RITTMANN, 1930), i.e. later than the Messinian crises. It is thus logical to think that *P. oceanica*, or its ancestor, managed to survive the Messinian crises. As its refuge cannot be sited in the Indo-Pacific (the communicating link was already closed), and since the Atlantic seems fairly unfriendly to *P. oceanica* (which disappears very abruptly in the neighbourhood of Gibraltar), we must suppose that this refuge was situated within the bounds of the Mediterranean; this was thus not entirely hypersaline or brackish in the Messinian age, since *P. oceanica* cannot tolerate such conditions. Saline conditions in the Messinian period were in fact certainly much more varied than was supposed some 15 years ago. It was perhaps in the Aegean Sea that a marine area survived serving as a refuge for "Messinian" species (POR and DIMENTMAN, 1985; GIACCONE, 1991).

The pantropical element

Pantropical species are species that are widespread in all the tropical seas in the world (Atlantic, Indian Ocean, Pacific). Before the Messinian crises, the Mediterranean was a tropical sea. Its tropical stock was destroyed during these crises. It was never reconstituted because, since the start of the Pliocene age (5 Ma), the boundary of the tropical zone fell far south of Gibraltar (at present around Senegal) and never approached it again, despite probable fluctuations (CIFELLI, 1976). Moreover, present day sea surface temperatures of Mediterranean waters are far lower than those of tropical waters: from 9 to 18°C in February (Northern Adriatic and Syria, respectively) versus always

above 20°C in tropical waters. Finally, during the ice ages, the average temperature of the Mediterranean fell considerably: about 2-3°C less than now at the start of the Pleistocene age, and 5-6°C at the end of the Pleistocene (THUNELL, 1979).

The tropical zone is defined firstly by its fauna and flora. It may also be defined by its warmth: the temperature there is over 25°C in summer and over 20°C in Winter. From this point of view, part of the Mediterranean (mainly the south eastern Mediterranean) enjoys a tropical thermal climate in summer, with temperatures slightly above 25°C; but in winter, the thermal climate of the whole Mediterranean is clearly temperate, with the highest temperatures, found in a very limited sector on the coasts of Israel and Egypt, hardly rising above 17°C (LIPKIN and SAFRIEL, 1971).

Pantropical species are therefore extremely rare in the Mediterranean (**Table VII**): the Rhodophyta *Acanthophora najadiformis*, is an example.

The Indo-Pacific element

The separation between the Mediterranean and the Indian Ocean happened some 12-13 Ma ago (STANLEY, 1986; ROGL, 1998), that is, well before the Messinian crises. It is, therefore, not surprising that the Indo-Pacific element should be very little represented among the Mediterranean's indigenous fauna and flora (**Table VII**).

In fact, most of the Indo-Pacific species encountered are "lessepsian immigrants" (POR, 1978), i.e. species introduced to the Mediterranean (see below) which entered the Mediterranean via the Suez Canal, after its opening in 1869. There are nearly 250-300 species in this category (BOUDOURESQUE, 1999a). One of the best known is the marine phanerogama *Halophila stipulacea* (HARTOG, 1970, 1972; LIPKIN, 1975; BILIOTTI and ABDELAHAD, 1990; ZIBROWIUS, 1993). We can also cite the rabbit fishes *Siganus luridus* and *S. rivulatus* (BAUCHOT, 1987; KTARI and KTARI, 1974; POR, 1978; QUIGNARD and BEN OTHMAN, 1978). For the fishes, the percentage of lessepsian immigrants is 7% (FREDJ and MAURIN, 1987). FREDJ *et al.* (1992) estimate it as 5% for the Mediterranean fauna as a whole and it rises to 12% if we only look at the eastern Mediterranean. POR (1990) considers that on a world scale, lessepsian migrations constitute the most important present day biogeographical event.

Almost all of the lessepsian immigrants have remained confined to the eastern Mediterranean, from the Nile Delta to southern Turkey, especially along the Levantine coasts. POR (1978, 1980) names this biogeographic region the "Lessepsian Province".

Table VII. Biogeographical affinities (as percentages) of the flora and some fauna groups in the Mediterranean. The demarcation, definition and designation of the elements vary from one source to another. (1) includes the "Messinian" element; (2) the "Senegalese" and the "central Atlantic" (the African and American subtropical shores of the Atlantic) elements; (3) North Atlantic in the wider sense; (4) species present in the Atlantic, the Indo-Pacific and the Mediterranean (not uniquely tropical); (5) not considered.

Taxonomic group	Algae (Sicily)	Sponges	Hydrozoa	Crustaceans and walking Decapoda	Echino-dermata	Ascidia	Whole fauna (4094 species)
Source / Element	GIACCO-NE and GERACI (1989)	PANSI NI (1990)	PERES and PICARD (1964)	PERES and PICARD (1964)	PERES and PICARD (1964)	PERES and PICARD (1964)	FREDJ et al. (1992)
Endemic (1)	26%	46%	27%	13%	26%	50%	29%
Pantropical	2%	3%	10%	2%	1%	5%	17% (4)
Indo-Pacific	3%	3%	0%	3%	1%	3%	4%
Tropical Atlantic	47%	6%	4% (2)	20% (2)	19% (2)	4%	
Temperate Atlantic		13%	42% (3)	57% (3)	50% (3)	32%	50%
Cold Atlantic	20%	21%					
Cosmopolitan	(5)	10%	17%	5%	3%	5%	(5)

The Atlantic element

Mediterranean flora and fauna are of basically Atlantic origin (**Table VII**). These species first entered to the Mediterranean at the end of the Messinian crises, when Gibraltar was reopened and the Mediterranean restocked. Within the Atlantic element, two main stocks are to be considered: the species of the temperate Atlantic, that is, those from the biogeographical area to which the Mediterranean today belongs, and which stretches into the Atlantic to the north and south of Gibraltar and then the species of the cold North Atlantic (**Table VII**). One can add a third element, much less important: that of the species of the subtropical Atlantic, which entered the Mediterranean during the warm phases between the ice ages, and of which some (the Gastropod *Lurida lurida*, for example) have survived.

During the ice ages, the species of the cold North Atlantic managed to enter the Mediterranean via Gibraltar (KOSSWIG, 1956). The low salinity of the Mediterranean was doubtless as important an element for their installation as the thermal factor, as PERES and PICARD (1964) pointed out. Most of them disappeared afterwards: this was so for the Molluscs *Cyprina islandica* (= *Arctica arctica*), *Modiolus modiolus, Mya truncata, Buccinium undatum, Chlamys islandica, Chlamys septemradiata* and *Panopea norvegica*, whose dead shells can still be found, at a depth of between 90 and 340 m, mainly in the Gulf of Lions, dating from 10 000-31 000 BP (BP = years before present; MARS, 1958; FROGET et al., 1972). Some of them have survived, finding refuge in the north of the western Mediterranean, the Adriatic, the Aegean Sea and in the

Black Sea. This is so for *Fucus virsoides* (Fucophyceae) in the north of the Adriatic, a neo-endemic, probably a descendant of *Fucus spiralis* and also for *Plocamium cartilagineum, Gymnogongus crenulatus* (Rhodophyta) and for *Desmarestia viridis* (Fucophyceae); the last named lives at depth in the Adriatic (ERCEGOVIC, 1948) and in the French Languedoc lagoons (VERLAQUE, 1981). The north Adriatic can from this point of view be seen as a refuge for species with boreal affinities (GIACCONE and GERACI, 1989). Conversely, the Strait of Messina, with its concentration of Atlantic species absent from most of the Mediterranean (the brown algae *Laminaria ochroleuca, Saccorhiza polyschides, Cystoseira tamariscifolia and C. usneoides* for example) may be considered to be a temperate Atlantic refuge.

Table VIII: Similarity between the algal flora (Fucophyceae taxa) of the Portuguese coasts (data from ARDRE, 1970) and that of the various sectors of the Mediterranean and the Black sea (data from RIBERA *et al.*, 1992). Data on the northern coasts of Morocco, being too sketchy, are not taken into account. The similarity index is SORENSEN's (1948).

Country or region	Total number of Fucophyceae	Number of Fucophyceae in common with Portugal	Similarity with Portugal
Continental Spain (Europe)	124	58	52%
Balearic Islands (Spain)	87	37	40%
Continental France	129	44	38%
Corsica and Sardinia	129	43	38%
Western continental Italy	113	40	38%
Sicily (Italy)	157	58	45%
Adriatic Sea	160	48	37%
Greece	102	39	39%
Black Sea	80	28	31%
Turkey (without the Black Sea)	76	35	40%
Lebanon, Syria and Israel	58	30	38%
Egypt	32	19	29%
Libya	51	23	30%
Tunisia	87	39	42%
Algeria	87	41	44%

All in all, the Mediterranean fauna thus presents a strong similarity to that of the Eastern Atlantic (European and African coasts). On the basis of 1 244 species (Echinodermata, Priapulida, Polychaeta errantia, Echiurida, Sipuncula, Brachiopoda, Mollusca, Crustacea Decapoda, Pogonophora, Phoronidea and Hemichordata), 66% of these species are in common with the Portuguese region, and 50% with the Mauritanian region. In contrast, only 18% of species are common between the Mediterranean and the Indo-Pacific (including recent immigrants via the Suez Canal: lessepsian immigrants) and 13% between the Mediterranean and the western Atlantic (American coasts) (FREDJ, 1974). Similarly, the Mediterranean's stock of fishes has 64% of species in common with the Portuguese region (FREDJ and MAURIN, 1987).

However, if we consider the regions of the Mediterranean taken in isolation, we notice that the similarity to the Atlantic is less than expected

(**Table VIII**): they only share between a quarter and half of their Fucophyceae species with Portugal.

Introduced species

There are about 400 introduced species in the Mediterranean, among which are almost 90 macrophyte algae (ZIBROWIUS, 1991, 1994; BOUDOURESQUE, 1994; BOUDOURESQUE and RIBERA, 1994; RIBERA, 1994; VERLAQUE, 1994; RIBERA and BOUDOU-RESQUE, 1995; BOUDOURESQUE, 1999a; VERLAQUE, 2001).

Most introduced species are lessepsian immigrants and they have been mentioned above, bearing in mind their Indo-Pacific affinities (POR, 1978, 1990; BOUDOURESQUE, 1999a). The entry into the Mediterranean of species from the Red Sea still continues. It is facilitated by low biodiversity in the eastern basin. In addition, these species reoccupy an area which they doubtless colonised in the past, and from which they were excluded by the crises experienced by the Mediterranean (partial drying-up at the time of the Messinian crises, cooling during the ice ages, anoxic crises). It would be possible, though somewhat difficult, to slow down this phenomenon, for example by placing locks or fresh water barriers in the Suez Canal, or by re-establishing the hypersaline barriers formerly constituted by the Bitter Lakes (BOUDOURESQUE, 1999a).

Many other species introduced to the Mediterranean arrived through fouling and clinging (i.e. on ships' hulls). This is the case with the Rhodophyta *Womersleyella setacea* and *Acrothamnion preissii* (CINELLI and SARTONI, 1969; VERLAQUE, 1994), the Scleractinia *Oculina patagonica* in Italian and Spanish ports (ZIBROWIUS, 1974; ZIBROWIUS and RAMOS, 1983) and the Bryozoa *Tricellaria inopinata* in the Venice lagoon (OCCHIPINTI AMBROGGI, 1991).

Since the 1970s, aquaculture has been another major source of species introduction. In a few cases, these are cultured species which have escaped, for example the clam *Ruditapes philippinarum* (MAZZOLA, 1992). In most cases, these are species that accompany aquaculture species. This is the case for all the Japanese species introduced into the Thau Lagoon (France) and the Venice Lagoon (Italy), then sometimes into the neighbouring open sea, via the spat of the Japanese oyster *Crassostrea gigas* directly imported from Japan or the transfer of oysters from one site to another (VERLAQUE, 1994, 2001): e.g. the Fucophyceae *Sargassum muticum, Undaria pinnatifida* and *Laminaria japonica* and the Rhodophyta *Chrysymenia whrightii* and *Antithamnion nipponicum* (PEREZ *et al.,* 1981; VERLAQUE, 1981, 1989; BEN MAIZ *et al.,* 1987b; VERLAQUE and RIOUALL, 1989; BELSHER, 1991; CURIEL *et al.,* 1995).

Ballast waters, taken on by ships in one sea, with all their planctonic flora and fauna and unloaded in another sea, are considered as a major present day vector of species introduction (CARLTON and GELLER, 1993; RIBERA and BOUDOURESQUE, 1995). They have been responsible for the introduction of the Ctenophora *Mnemiopsis leidyi* to the Black Sea. Subsequently, it entered the Mediterranean via the Bosphorus (KONOVALOV, 1992; GESAMP, 1997).

Fishing bait seems to be the cause of the introduction of *Fucus spiralis* (Fucophyceae) in a Languedoc lagoon (SANCHOLLE, 1988). Finally, release from aquaria, which is responsible for the introduction of very many species in fresh waters (WELKOMME, 1992), has also resulted in the introduction of the tropical Chlorophyta *Caulerpa taxifolia* along the coasts of the French and Italian rivieras, Tuscany, Sicily (Italy), the Balearic Islands (Spain), Croatia and Tunisia (MEINESZ and HESSE, 1991; BOUDOURESQUE and GOMEZ-GARRETA, 1992; BOUDOURESQUE *et al.*, 1995b; MEINESZ and BOUDOURESQUE, 1996; JOUSSON *et al.*, 1998, 2000; LANGAR et al., 2000; MEUSNIER *et al.*, 2001).

Few species introduced into the Mediterranean seem to have entered via Gibraltar, from populations previously introduced into the Atlantic. This is perhaps the case for the green alga *Codium fragile* (FELDMANN, 1956). It was thought that the same held good for the Rhodophyta *Asparagopsis armata*, but genetic studies have shown that the strain which is colonising the Mediterranean, did not have the same geographical origin as the Atlantic strain. The Mediterranean and Atlantic populations therefore represent distinct introductions, probably via fouling on ship hulls (GUIRY and DAWES, 1992).

Ecodiversity in the Mediterranean

Between forty and almost two hundred communities (assemblages, biocenoses or ecosystems) have been described in the Mediterranean, their number depending upon the authors, the definition they adopted for the concept of community and the method they used for community delineation (MOLINIER, 1960; PERES and PICARD, 1964; PICARD, 1965; PERES, 1967; BOUDOURESQUE, 1970; VAMVAKAS, 1970; AUGIER and BOUDOURESQUE, 1971, 1974; BOUDOURESQUE and CINELLI, 1971; LIPKIN and SAFRIEL, 1971; GAMULIN BRIDA, 1974; GIACCONE, 1974; AUGIER and BOUDOURESQUE, 1975; MAYHOUB, 1966; GIACCONE, 1977; KOCATAS, 1978; BALLESTEROS, 1982, 1984; BALLESTEROS *et al.*, 1984a, 1984b; BALLESTEROS I SEGARRA, 1984; BOUDOURESQUE, 1984; ROS *et al.*, 1985; LABOREL, 1987; BALLESTEROS, 1991; GIACCONE *et al.*, 1993; BELLAN-SANTINI, 1994; BELLAN-SANTINI *et al.*, 1994; BIANCHI and MORRI, 1994; ALIANI *et al.*, 1995; BIANCHI *et al.*, 1995; LUNDBERG and OLSVIG-WHITTAKER, 1998; among others).

These communities can be divided from top to bottom into five zones, whose bathymetric amplitude varies according to the hydrodynamism (especially in supralittoral and mediolittoral zones) or the limpidity of the water (the other zones). On hard substrates, the suite is as follows:

- The supralittoral zone is sited above mean sea level. It is the zone generally reached by sea spray. Here, living conditions are extremely harsh, so much so that this zone is relatively poor from the species diversity point of view. The most conspicuous species are the lichen *Verrucaria amphibia*, the crustaceans *Ligia italica* and *Euraphia depressa*, the gastropods *Littorina neritoides* and *L. punctata* and several species of epilithic and endolithic Cyanobacteria.

- The mediolittoral zone is sited astride mean sea level. It corresponds to the area of wave and tide motion. Here, living conditions are still very harsh but the number of species is slightly greater than in the supralittoral: e.g. the Rhodophyta *Rissoella verruculosa, Nemalion helminthoides, Porphyra leucosticta* and *Lithophyllum byssoides* (the species which builds up a rim usually named "trottoir"), the molluscs *Patella rustica* and *Monodonta turbinata*, the crab *Pachygrapsus marmoratus*, the cirriped crustaceans *Chthamalus stellatus* and *C. montagui* and several species of Cyanobacteria, different from those which dwell in the supralittoral zone.

- The infralittoral zone starts slightly below mean sea level and extends down to the lower limit of the *Posidonia oceanica* meadows, 25-40 depth (depending on the water transparency). This is the richest zone, from the point of view of both species diversity and ecodiversity. It harbours in particular many species of the genus *Cystoseira* (Fucophyceae).

- The circalittoral zone extends down to the lower limit of the photosynthetic algae. Here, light starts to be a limiting factor for the flora, so that only sciaphilic algae can live. In the Gulf of Lions, it can extend no further down than 45-50 m. But in the eastern Mediterranean and in the centre of the western Mediterranean, the circalittoral may extend down to a depth of 120 m.

- Lastly, the bathyal and the abyssal zones extend down to the lowest depth of the Mediterranean (more than 5 000 m). It is thus these zones which (as a percentage of the surface area) occupy the largest part of the Mediterranean.

A similar suite occurs on soft substrates. In addition to water movement and light, the grain size of the sediment and its origin (terrigenous versus biogenic) play a major role in the distributional pattern of soft substrate communities.

Among the most characteristic communities of the Mediterranean we should mention, for the mediolittoral zone, the *Lithophyllum lichenoides* rims, for the infralittoral zone the *Posidonia oceanica* meadows, and for the circalittoral zone the "Coralligenous community". In addition, we should mention two communities which sit astride the mediolittoral and infralittoral zones: the vermetid platforms and the *Neogoniolithon brassica-florida* algal reefs.

The Lithophyllum byssoides rim

The incrusting coralline *Lithophyllum byssoides* (Rhodophyta), previously known as *L. lichenoides* and *L. tortuosum*, lives at the bottom of the mediolittoral zone, i.e. slightly above mean sea level. Under conditions of dim light and strong surf exposure, e.g. in small coves, corridors, fends, crannies and along cliffs, it builds up rims, usually known as "trottoirs". They consist of a wide overhanging cornice with a flat or slightly depressed upper surface, ending in a salient rim with a vertical face (DELAMARE-DEBOUTEVILLE and BOUGIS, 1951; BLANC and MOLINIER, 1955; HUVE, 1963; PERES and PICARD, 1964; LABOREL, 1987; LABOREL et al., 1994a).

The *Lithophyllum byssoides* rim is a common feature in the northern and central parts of the western Mediterranean basin and the Adriatic Sea. The most spectacular rims are those of Grand Langoustier in Porquerolles Island (Var, France), Punta Palazzu (Scandola natural Reserve, Corsica) and Kvarner Gulf (Croatia). They are 2 m wide in places. *Lithophyllum byssoides* rims are less common in the south of the western basin and very rare in the eastern basin (HUVE, 1963; LOVRIC, 1971; ZIMMERMANN, 1982; BIANCONI et al., 1987; LABOREL, 1987; LABOREL et al., 1994a).

Datings by ^{14}C have shown that the building up of a *Lithophyllum byssoides* rim requires several centuries, even more than a thousand years, and a relatively stable (or just very slowly rising) sea level, which has rarely been the case over the last 30 000 years (LABOREL et al., 1983, 1994b).

The vermetid platform

The vermetid platform is mainly built by the close association of two species: a vermetid gastropod, *Dendropoma petraeum* (often referred to in biological papers as *Vermetus cristatus*) and an encrusting coralline alga, *Neogoniolithon brassica-florida* (= *N. notarisii*). These two species are completed by a number of epiphytic and endolithic species among which the sessile foraminifer *Miniacina miniacea* plays an important part as a cavity filler (PERES and PICARD, 1952; BLANC and MOLINIER, 1955; LABOREL, 1987).

The upper surface of vermetid platforms is more or less dry at low tide, in very calm weather, but always at a lower level than the *Lithophyllum byssoides* rim (LABOREL, 1987). Though isolated thalli of the latter species can be present at the upper edge of a vermetid platform, the two formations (*Lithophyllum byssoides* rim and vermetid platform) never coexist at the same place.

The structure of the vermetid platform is rather variable. Typically, it consists in a more or less wide horizontal platform extending near sea level and covered by shallow pools, a few centimeters deep. As a matter of fact, the platform is not built up by marine organisms but is an erosion form cut into the rock itself (sandstone or limestone). The biogenic structure itself lies at the sea edge of the platform, in the form of a more or less thick rim, often supported by short pillars and enclosing small cavities. The upper surface of the platform is covered by a thin layer of *Dendropoma petraeum* and *Neogoniolithon brassica-florida*. The shallow pools are inhabited by infralittoral algae as *Cystoseira* spp. and *Chondophycus papillosa*. (LABOREL, 1987; BOUDOURESQUE *et al.*, 1990).

The vermetid platforms are typical formations of the warmest parts of the Mediterranean. Best developed platforms are known from Sicily, Algeria, Tunisia, Crete, Lebanon and Israel. They also occur along the southern continental coasts of Spain and Italy up to the latitude of Rome, in Corsica, Sicily, etc. (PERES and PICARD, 1952; MOLINIER and PICARD, 1954; MOLINIER, 1955; FEVRET and SANLAVILLE, 1966; SAFRIEL, 1974; LABOREL, 1987; BOUDOURESQUE *et al.*, 1990). Some particularly remarkable vermetid platforms are considered by LABOREL (1987) as natural monuments and are worth protecting: Torre de Isola (Sicily), Tipasa (Algeria), Mikhmoret and Shikmona (Israel) and from Tyr north to Tripoli (Lebanon).

The Neogoniolithon brassica-florida algal reef

The *Neogoniolithon brassica-florida* algal reef is mainly known from the hypersaline lagoon of Bahiret-el-Bibane, in southern Tunisia. Here, it forms a wave resistant ridge 31 km long. Individual heads of mushroom shaped colonies of *N. brassica-florida* (= *N. notarisii*), averaging 0.9 m in diameter, coalesce to differing degrees. The reef is usually awash, but the remainder of the ridge is exposed only at lowest low water (THORNTON *et al.*, 1978; DENIZOT *et al.*, 1981; PERGENT and KEMPF, 1993). More localized and far less spectacular algal reefs have been recorded elsewhere in the eastern Mediterranean, e.g. in Greece and Turkey (HUVE, 1963; LABOREL, 1987). The *N. brassica-florida* algal reef of Bahiret-el-Bibane is therefore a unique case, with no other similar formation in the whole Mediterranean, which must be protected and gain the status of natural monument (LABOREL, 1987).

The Posidonia oceanica meadow

Posidonia oceanica meadows develop in the infralittoral, between the mean sea level and a depth of 25-40 m (according to water limpidity), and on soft as well as hard substrates (MOLINIER and PICARD, 1952). The largest meadows in the Mediterranean are those in the Gulf of Gabès (Tunisia), the bays of Hyères and Giens (Var, France), the eastern coast of Corsica, the western coast of Sardinia (giving the town of Alghero its name) and Sicily, near Marsala (BOUDOURESQUE and MEINESZ, 1982; BOUDOURESQUE *et al.*, 1994; PASQUALINI, 1997). The meadows surrounding Menorca (Balearic Islands) are thought to be particularly well conserved (VIDAL *et al.*, 1994). But on a Mediterranean scale, bearing in mind the narrowness of the continental shelf, the covered surfaces are modest: all the Provence and Côte d'Azur (France) meadows, for example, would fit into 16 km-sided square (PAILLARD *et al.*, 1993).

The *Posidonia* meadows, because of the length and density of the leaves (several thousand leaves per square metre) trap large amounts of sediment. The rhizomes react by growing vertically from a few millimetres to several centimetres yearly, thus erecting a "matte" formed of intertwining rhizomes and roots (very little putrescible) and the sediment which fills in the interstices. With time, the matte slowly rises above the initial level: up to 1 m per century, according to MOLINIER and PICARD (1952).

In sheltered bays, the rise of the matte can result in the meadow reaching the surface of the water: the foliage falls flat. Thus is formed a fringing-reef of *Posidonia*, which, progressing towards the open sea, becomes a barrier-reef, separated from the coast by a shallow lagoon (MOLINIER and PICARD, 1952).

Posidonia oceanica meadows are considered as the most important ecosystem in the Mediterranean (BOUDOURESQUE and MEINESZ, 1982; BOUDOURESQUE *et al.*, 1994). (i) The mattes stabilise the sediment. By trapping the sediment, the matte can rise from 1 metre per century to 1 metre per thousand years: the Roman wreck of the Gulf of Giens was thus protected under 2 m of matte. In addition, mattes are a sink for nutrients (ROMERO *et al.*, 1994) and carbon (PERGENT *et al.*, 1994). (ii) The meadows weaken the water movement (waves, swell) by 10 to 70%, so that they help protect the beaches (BOUDOURESQUE and JEUDY DE GRISSAC, 1983; JEUDY DE GRISSAC, 1984; JEUDY DE GRISSAC and BOUDOURESQUE, 1985; GAMBI *et al.*, 1989). (iii) The net primary production is considerable (leaves and rhizomes: 500-1 300 grams of dry mass (DM) per square metre per year (gDM/m²/a) at a depth of 1 m, 300 to 1 200 gDM/m²/a at 5 m, 150-300 gDM/m²/a at 20 m; roots: 80 gDM/m²/a at 4 m; epiphytes: 500-900 gDM/m²/a at 2 m), so that it is the origin of a very rich food web

(BOUDOURESQUE and MEINESZ, 1982; ROMERO-MARTINENGO, 1985; ALVAREZ, 1989; PERGENT-MARTINI et al., 1994; MAZELLA et al., 1995; among others). As a comparison, a Quercus ilex (evergreen oak) forest in Sicily has a primary production of only 775 gDM/m²/a (LEONARDI et al., 1992). (iv) Much (30-40%) of this production is exported to other ecosystems, in particular to the circalittoral and the bathyal (FRANCOUR, 1990; PERGENT et al., 1994, 1997). (v) It is (together with the coralligenous community) the main hot spot for species diversity in the Mediterranean (almost 20% of all known Mediterranean species, i.e. several thousand species, have been sighted here) (BOUDOURESQUE, 1995). (vi) It is a spawning area and nursery for many species, among them fishes of economic interest (JIMENEZ et al., 1996; LE DIREAC'H and FRANCOUR, 1996).

The coralligenous community

Like the *Lithophyllum byssoides* rim and the *Neogoniolithon brassica-florida* algal reef, the coralligenous community is a biogenic construction. It is mainly built up by crustose corallines (Rhodophyta) belonging to the genera *Lithophyllum* and *Mesophyllum* and by Bryozoa. It develops in sciaphilic biotopes, at a depth of between 20 and 70 m (up to 130 m in the eastern Mediterranean), either in "rims" (up to 2.5 m wide) in tiers along vertical walls, or as big rolls at the foot of the walls, or again as tables on the sub-horizontal substrates. Coralligenous constructions may grow to be several metres thick (PERES and PICARD, 1951; LAUBIER, 1966; PERES and PICARD, 1964; SARA, 1967, 1969; GILI and ROS, 1984; LABOREL, 1987). Like the *Lithophyllum byssoides* rim, growth is very slow (0.2-0.8 mm/a) and building such a structure requires several thousand years: in the Marseilles region and in Scandola (Corsica), SARTORETTO (1995) found ages of up to 7 140 BP (years before present).

After the *Posidonia oceanica* meadows, the coralligenous community constitutes the second most important hot spot of species diversity in the Mediterranean: the flora and especially the fauna there are indeed very rich, with in particular many endemics (LAUBIER, 1966; HARMELIN, 1990). Moreover, due to the large sponges, gorgonians and bryozoa it harbours and to the variety of their bright colours, the coralligenous community offers some of the most spectacular and most characteristic underwater scenery in the Mediterranean. As such, it constitutes the main diving sites in the Mediterranean and is therefore of great economic importance (BOUDOURESQUE, 1995).

Erosion of Mediterranean species diversity

The human activities likely to diminish species diversity and ecodiversity are coastal development (reclamation, harbours, artificial

beaches), fishing (commercial fishing, trawling, overfishing and amateur fishing), pollution (nutrients, organic matter, heavy metals, turbidity) and dumping (solid waste). These activities mainly affect the continental shelf, more particularly the infralittoral zone (from the sea level to 30-40 m depth), i.e. the main reservoir of biodiversity. They are unevenly distributed in the Mediterranean. For example, it is mainly in Catalonia (Spain; FOLCH I GUILLEN, 1988), País Valenciano (Spain; VERA REBOLLO, 1991), Languedoc-Roussillon (France; OLIVER, 1991), Provence - Côte d'Azur (MEINESZ et al., 1981, 1982; **Table IX**) and Liguria (Italy) that the surface area of seabeds undergoing reclamation is extensive.

Table IX: Percentage of surface area of infralittoral seabeds undergoing (and irreversibly destroyed by) coastal development (reclamation, harbours, artificial beaches) in the Provence- Côte d'Azur region. Data from MEINESZ and LEFEVRE (1976, 1978) and MEINESZ et al. (1981, 1982).

Bathymetric zone	Bouches du Rhône	Var	Alpes-Maritimes
0-10 m	25 %	10 %	18 %
0-20 m	18 %	6 %	12 %

Concern about human impact is dependent upon the degree of reversibility or irreversibility of the damage. Thus, coastal development, species introduction and species extinction are the greatest cause for concern, due to their irreversibility, at least at human scale.

For the time being, no species seems to have disappeared from the Mediterranean. Some have however disappeared from fairly extensive sectors and seem likely to disappear in the near future. This is the case for the monk seal *Monachus monachus*, formerly widespread around the whole of the Mediterranean, which now only survives in Greece, Turkey, Algeria, Morocco (including the Spanish Chafarinas Islands) and perhaps Libya and Croatia. It is, according to the WWF, one of the ten species in the world that are most threatened with extinction. During the last 25 years, its total numbers dropped from 1 000 to about 300 individuals, and of these 150-200 are in the Mediterranean (MARCHESSAUX, 1989a, 1989b; ANSELIN et al., 1990; RAMADE, 1990; REIJNDERS, 1997). The reasons for the monk seal's decline are (i) the reduction of its natural habitat (beaches, caves) because of coastal development and tourism (OZTURK, 1992), (ii) overfishing of the fish stock on which it feeds, which leads to individuals being scattered and stealing fish from fishers' nets (BOUDOURESQUE and LEFEVRE, 1988, 1992), and (iii) its being destroyed by fishers (JACOBS and PANOU, 1988); this destruction is a consequence of the previous point. A Mollusc, the giant limpet *Patella ferruginea*, is also on the brink of extinction. Formerly widespread throughout the western Mediterranean, of which it is an endemic, it now only survives in sparse populations in Corsica, Sardinia, Tunisia, Algeria and southern Spain (BOUDOURESQUE and

LABOREL-DEGUEN, 1986; LABOREL-DEGUEN and LABOREL, 1990, 1991a, 1991b; PORCHEDDU and MILELLA, 1991). Its decline has accelerated over the last 15 years. The reason for the disappearance of this large species (sometimes over 10 cm in diameter), which lives in the mediolittoral zone (i.e. slightly above mean sea level), is its being gathered by humans either for consumption or for use as bait.

Although not threatened with extinction in the immediate future, a number of species appear to be vulnerable. These are (i) naturally rare species, i.e. species whose numbers are slight and species whose sites are very localised, so that they are at the mercy of an even moderate increase in human impact, for example, urbanization, new port or aqua-culture facilities close to the sites of their populations. They are also (ii) species which are still relatively common but whose populations are dwindling rapidly. Several Red Books have inventoried some eighty vulnerable species in the Mediterranean (e.g. WELLS et al., 1983; BAGHDIGUIAN et al., 1987; BELSHER et al., 1987; DUGUY, 1987; FRETEY, 1987; LACAZE, 1987; QUERO et al., 1987; SCHEMBRI and SULTANA, 1989; BOUDOURESQUE et al., 1990; GROOMBRIDGE, 1993; MAURIN and KEITH, 1994; BOUDOURESQUE et al., 1996; MAYOL et al., 2000). Examples of rare species are the Chlorophyta *Penicillus capitatus* (BOUDOURESQUE et al., 1985), the Rhodophyta *Schimmelmannia ornata,* (SOLAZZI, 1968), the gastropod *Gibbula nivosa* (SCHEMBRI and SULTANA, 1989) and the fish *Pomatoschitus canestrini* (TORTONESE, 1975). Examples of species experiencing a steady and severe decline, at least in some parts of the Mediterranean, are the Fucophyceae *Cystoseira amentacea* and *C. zosteroides* (BELLAN-SANTINI, 1966; BOUDOURESQUE et al., 1990, 1996), the Mollusc *Pinna nobilis,* especially in the north western Mediterranean (VICENTE and MORETEAU, 1991), the seahorse *Hippocampus ramulosus* (KEITH and MAURIN, 1994) and the sea-turtle *Caretta caretta*. This turtle recently deserted its nesting sites in the western basin of the Mediterranean; the rare beaches it still frequents to lay eggs are in the eastern Mediterranean: e.g. Lampedusa (Italy), Zakhintos (Greece; the largest site) and Lara (Cyprus) (RAMADE, 1990).

If no species seems at this moment to have totally disappeared from the whole Mediterranean, this does not hold good at regional level. In the Venice lagoon, for example, where SCHIFFNER and VATOVA (1938) inventoried 141 species of algae, PIGNATTI (1962) only found 104 and SFRISO (1987) 95 (the research effort being of the same order). In fact, the qualitative change is still more profound in that many species have disappeared, replaced by species that tolerate pollution (SFRISO, 1987). In the Gulf of Izmir (Turkey), the increase of pollution between 1970 and 1986 caused a conspicuous decline in the number of Rhodophyta and Fucophyceae (**Table X**). In particular, all the species of the *cystoseira* genus disappeared. In contrast, the number of

Chlorophyta (green algae) species, a group which encompasses numerous opportunistic species, rose (AYSEL *et al.*, 1993). In the Gulf of Gabès (Tunisia), out of 22 species of crab inventoried between 1970 and 1980, only two were found again by ZAOUALI (1992). A third species, not previously recorded, was the recently introduced *Eucrate crenata*.

On land, certain human activities (traditional agriculture, grazing) are known to enhance ecodiversity and therefore species diversity. On the other hand, the withdrawal from agricultural land and the return to a uniformly stable climax result in a reduction in species diversity, with the possible elimination of certain rare species. Such a phenomenon can be seen for example in the Port-Cros National Park (Var, France). For the moment this problem does not seem to affect the sea. However, one may point out that in the Scandola Nature Reserve (Corsica), protection has resulted in an increase in species diversity and more sharply in the biomass of fishes (FRANCOUR, 1992), and at the same time ("cascade effect") a decrease in the species diversity of the benthic fauna, on which the fishes feed (BOUDOURESQUE *et al.*, 1992b).

Table X: Evolution of the algal flora in three sites in the Gulf of Izmir (Turkey). The species diversity of Fucophyceae (brown algae) and of Rhodophyta (red algae), minimal in the most polluted sites, dropped as pollution rose between 1970-1981 and 1981-1986. This is not so for Chlorophyta (green algae). Data from AYSEL *et al.* (1993).

	Moderately polluted		Polluted		Extremely polluted	
	1970-1981	1981-1986	1970-1981	1981-1986	1970-1981	1981-1986
Cyanobacteria	1	2	1	2	0	1
Chlorophyta	17	17	8	8	3	18
Fucophyceae	16	3	5	0	4	1
Rhodophyta	33	17	7	3	6	10
TOTAL	67	39	21	13	13	30

Impact of introduced species on species diversity and ecodiversity

The study of a large number of species introductions, in the terrestrial environment, has led to the conclusion that, as a mean, 10% of introduced species become invasive: this is the "tens rule" (WILLIAMSON and FITTER, 1996). An invasive species (also called a "pest") is an introduced species the abundance of which is conspicuous, or threatens native species or communities, or has dire economic consequences. It is difficult, or impossible, to predict whether or not an introduced species will become invasive: it is a matter of "ecological roulette", in the phrase coined by CARLTON and GELLER (1993).

Most attention has focused on environmentally damaging consequences resulting from alien invasive species in terrestrial and

freshwater environment. After habitat destruction, introduced species are the second greatest cause of species endangerment and extinction worldwide, and the first cause if only islands are taken into consideration (SIMBERLOFF, 1995; SCHMITZ and SIMBERLOFF, 1997).

In contrast, the marine environment has been very little studied. Nothing is known about the possible impact of most of the 400 species introduced to the Mediterranean. Available information concerns mainly the Chlorophyta *Caulerpa taxifolia* in the Western Mediterranean (MEINESZ and HESSE, 1991; BOUDOURESQUE *et al.*, 1992a; VERLAQUE and FRITAYRE, 1994; VILLELE and VERLAQUE, 1995; BELLAN-SANTINI *et al.*, 1996; BOUDOURESQUE, 1997b), the brown alga *Sargassum muticum* in the Thau lagoon, France (GERBAL et al., 1985), a few Lessepsian aliens (POR, 1978), and the comb jelly *Mnemiopsis leidyi* in the Black Sea (KONOVALOV, 1992 ; GESAMP, 1997). A few additional data are available on the Rhodophyta *Acrothamnion preissii* in Western Italy (PIAZZI et al., 1996), *Asparagopsis armata* in the north-western basin (SALA and BOUDOU-RESQUE, 1997) and *Womersleyella setacea* in Western Italy and in the Aegean Sea (AIROLDI *et al.*, 1995a, 1995b; ATHANASIADIS, 1997).

The conclusions which can be drawn from the available studies show that each introduced species constitutes a special case. According to species, the following has been observed (RIBERA and BOUDOU-RESQUE, 1995; BOUDOURESQUE, 1999a, 1999b): (i) Zero or slight impact. It is worth noting that this statement is just a hypothesis, since species whose impact is not conspicuous were not studied (ii) More or less drastic changes in the number and/or abundance of native species (RUITTON and BOUDOURESQUE, 1994; VERLAQUE and FRITAYRE, 1994; BELLAN-SANTINI et al., 1996). For example, along the French Riviera coasts, 6 species of parasites (Digenea) are present in the digestive tract of the fish *Symphodus ocellatus* (cumulative prevalence = 46%); at sites colonized by the introduced *Caulerpa taxifolia*, only 2 digenean species occur (cumulative prevalence = 2%) (BARTOLI and BOUDOURESQUE, 1997). In the Thau Lagoon (France), the Shannon diversity index is dramatically lower in the *S. muticum* forest than in indigenous communities (GERBAL *et al.*, 1985). (iii) Displacement of a native species occupying a close ecological niche. For example in the Thau lagoon, the introduced brown alga *Sargassum muticum* has more or less replaced another brown alga, *Cystoseira barbata*, as well as its accompanying flora (GERBAL *et al.*, 1985). Along the Levantine coasts, the introduced asteroid *Asterina wega* appears to have locally replaced the native, ecologically similar *Asterina gibbosa* (POR, 1978). The native prawn *Penaeus kerathurus*, which supported a commercial fishery throughout the 1950s, has now virtually disappeared; it is replaced by *P. japonicus* (GELDIAY and KOCATAS, 1972; SPANIER and GALIL, 1991). (iv) Several native species along the Levantine coasts

have been competitively displaced towards deeper waters by introduced competitors, e.g. the red snapping shrimp *Alphaeus glaber*, the red mullet *Mullus barbatus* and the hake *Merluccius merluccius*, have been displaced by the shrimp *Alphaeus rapacida*, the goldband goatfish *Upeneus moluccensis* and the brushtooth lizardfish *Saurida undosquamis*, respectively (POR, 1978). (v) Changes in the functioning of native ecosystems, due to an introduced species which acts as a keyspecies. For example, the presence among Lessepsian immigrants of large herbivore fishes, *Siganus luridus* and *S. rivulatus*, makes highly probable a strong impact on the functional processes of the ecosystems of the Eastern Mediterranean. Indeed, the Mediterranean is a sea characterised by a rather low level of herbivory (BOUDOURESQUE, 1999a, 1999b). (vi) Displacement of native ecosystems, due to the setting up of a totally new ecosystem. This is the case of the *Caulerpa taxifolia* meadow, which can take the place of a most of the indigenous communities of the infralittoral zone, e.g. *Cystoseira* photophilic communities, sciaphilic communities and the seagrass *Cymodocea nodosa* meadow (BOUDOURESQUE *et al.*, 1992c; VERLAQUE and FRITAYRE, 1994; BOUDOURESQUE *et al.*, 1995b; BOUDOURESQUE, 1997b; RODRIGUEZ-PRIETO, 1997; RELINI et al., 1998a; HARMELIN-VIVIEN *et al.*, 1999; RODRIGUEZ-PRIETO, 1999).

There is a common empirical opinion that species introductions do not result in species deletion but instead in species enrichment: "one species more! what good news for biodiversity!" As a matter of fact, this opinion is not supported by scientific data: the fate of most native species is generally unknown. This is the case in the eastern Mediterranean (BOUDOURESQUE, 1999a) as well as in the Thau Lagoon (VERLAQUE, 2001). It is clear, however, that some introduced species can enhance species diversity, at least in some habitats and at a local scale (alpha diversity). This is the case for coastal lagoons, ports and polluted sites, which are often the sites of both arrival and acclimalization of introduced species, since they harbour the main sources of introduction (e.g. aquaculture, unloading of ballast waters, ship hulls covered with fouling) and whose species diversity is generally low. The invasion by *Caulerpa taxifolia* provides a relevant example. It results in a decrease of fish diversity in habitats with high structural complexity (e.g. *Posidonia oceanica* meadows and coralligenous community), but in contrast increases this diversity in habitats with low structural complexity (e.g. sand bottoms and *Cymodocea nodosa* meadows). In fact, it induces homogeneization of the habitats and of their fish fauna, so that, at regional level, species diversity (beta diversity) is actually lower than before the invasion (see RELINI *et al.*, 1996, 1998a, 1998b; HARMELIN-VIVIEN *et al.*, 1999). In the same way, the native terrestrial mammal fauna of Corsica does not exceed 6 species. Since the Neolithic age, most native species had disappeared, but introductions brought the

number of species to 20 (an increase in species diversity ?). However, this set of 20 species is nearly the same in all Mediterranean islands. Before introductions and extinctions due to human impact, nearly 50 species of mammals, most of them endemic for a given island, inhabited the Mediterranean islands (a decline in species diversity !) (MENNESSIER, 1998). Clearly, species diversity is not just a matter of number of species. If this were in fact the case, zoos and botanical gardens would be the paradigm of biodiversity (BOUDOURESQUE, 1999b).

Erosion of Mediterranean ecodiversity

The Lithophyllum byssoides rim

The *Lithophyllum byssoides* rim is sensitive to pollution (especially hydrocarbons). The platforms have died in the Pyrénées-Orientales region, in the area of Marseilles (France) and in the Gulf of Palermo (Sicily): bio-erosion (perforating organisms) no longer being compensated for by bio-construction, they are progressively eroded and end up disappearing (LABOREL *et al.*, 1994a; RIGGIO *et al.*, 1994). Bearing in mind the slowness with which they are built up, this disappearance must be considered irreversible from the human point of view (even when the causes of the death are believed to have been removed).

Lithophyllum byssoides rims are also threatened by constant treading: the platform of Punta Palazzu (Scandola natural Reserve, Corsica), well popularized as a high value natural monument, is visited by growing numbers of tourists who arrive there in rubber dinghies. The crustose corallines die if they are walked over too often. In addition, at the side of the platform, rope marks can be observed (dinghy moorings). For these reasons, upon request of the Scientific Committee of the Scandola Reserve, access to the Punta Palazzu *L. byssoides* rim is now prohibited.

Finally, the rising of the mean sea-level, resulting from global warming (PERNETTA and ELDER, 1992), threatens in the long term the *L. byssoides* rims. The building up of this bio-construction is linked to a stable or very slowly rising sea-level (see above).

The vermetid platform

Vermetid platforms are vulnerable to domestic pollution, low salinity rainwater and oil slicks. Sediment laden waters, as a consequence of coastal development (urbanization or setting up of littoral roads), may kill vermetid formations by siltation (LABOREL, 1987; BOUDOU-RESQUE *et al.*, 1990). Such seems to have been the fate of an original and interesting vermetid platform on the southeastern coast of Turkey (between Cevlik and Samandaj), with oysters associated to the vermetid *Dendropoma petraeum* (LABOREL, 1987). In northwestern Corsica, fine

vermetid formations have been killed and completely covered by sediment generated by production of asbestos (LABOREL, 1987). In other parts of the Mediterranean (e.g. Lebanon), vermetid platforms have been buried under reclamations. In addition, over-frequent walking over by tourists and amateur fishermen damage the vermetids (BOUDOURESQUE et al., 1990).

The Posidonia oceanica meadow

The *Posidonia oceanica* meadows have dwindled considerably, in particular in the vicinity of the large urban centres: e.g. Athens, Naples, Genoa, Nice, Toulon, Marseilles, Barcelona. They are dwindling both at their lower limit (rising because of the water turbidity and the resulting deficit in light) and at intermediate depths. In Italy, Ligurian meadows have lost about 10-30% of their surface area (BIANCHI and PEIRANO, 1995; PEIRANO and BIANCHI, 1995). In the Alicante region (Spain), RAMOS-ESPLA et al. (1994) estimate that 52% of the surface area has been lost. In Marseilles (France), close to 90% of the meadows mapped by MARION (1883) have today disappeared. In the Bay of Toulon (France), the meadows have almost completely disappeared (BOURCIER et al., 1979). This is also the case in the Gulf of Gabès (Tunisia) (HATTOUR et al., 1993; PERGENT and KEMPF, 1993). The causes are as follows (BOUDOURESQUE and MEINESZ, 1982; PERES, 1984; PAILLARD et al., 1993; BOUDOURESQUE et al., 1994):

- Industrial and urban pollution (*P. oceanica* is very sensitive to this), in particular detergents and nutrients (AUGIER et al., 1984; PERGENT-MARTINI et al., 1995, 1996).

- Turbidity, in reducing the limpidity of the water and the penetration of light to the deep. Phytoplanktonic blooms, whose importance is accentuated by eutrophy, experience the same consequences. The result is a rising of the lower limit. In the Bay of Cassis (Bouches-du-Rhône, France) the lower limit has risen from 35 to 23-28m (BOURCIER, 1982).

- Mooring of small boats. This phenomenon is not recent and the fleets of ships, galleons and caravels of past centuries, which frequently moored all along the Mediterranean shores, no doubt explain certain patches of dead matte such as those which occupy the centre of the bays of Port-Man and Port-Cros (Port-Cros Island, Var, France) (AUGIER and BOUDOURESQUE, 1970b; BOUDOURESQUE et al., 1980b). In Elbu cove (Scandola, Corsica), 68 000 shoots of *P. oceanica* are torn up in one year by anchors over an area of 1.4 ha (BOUDOU-RESQUE et al., 1995).

- Trawling. Trawling is normally forbidden less than three nautical miles from the coast (e.g. France, Italy, Tunisia), above the 50 m isobath

(Spain, Italy, Gulf of Tunis, Algeria) or 20m (the rest of Tunisia), so that, in principle, trawling is impossible over most of the *P. oceanica* meadows. In practice, this legislation is not respected. The meadows with bare rhizomes (frequently the case because of the lack of sediment) are particularly vulnerable (BOUDOURESQUE *et al.*, 1988; PAILLARD *et al.*, 1993). Trawling in the area of Alicante (Spain) is responsible for almost half the surface area diminution in the meadow (RAMOS-ESPLA *et al.*, 1994).

- Explosives. Throughout the north-western Mediterranean coasts, there are circular patches of dead meadows, which have been caused by underwater explosions: bombs dropped at the time of the World War II or fishing with dynamite (PAILLARD et al, 1993; PERGENT-MARTINI, 1994; PASQUALINI *et al.*, 1999, 2000). Recolonisation is excessively slow since, 50-60 years after the event, the recolonisation is still far from complete (MEINESZ and LEFEVRE, 1984; PERGENT-MARTINI, 1994; PERGENT-MARTINI and PASQUALINI, 2000).

- Coastal development: ports, artificial beaches and reclamations over *P. oceanica* meadows (MEINESZ and LEFEVRE, 1976, 1978; BOU-DOURESQUE and MEINESZ, 1982). For example, the extending of the port of Golfe-Juan (Alpes-Maritimes, France) has destroyed about 15 ha of meadows. The artificial beaches of Le Mourillon (Toulon, France) covered 20 ha of meadows (ASTIER, 1984).

- The laying of underwater cables and pipes. Their 'burying' (= placing in a trench) leads to a diminution of the meadows on either side of the trench, which subsequently becomes wider. For example, between the Lerins Islands (Alpes-Maritimes, France), in a shallow and exposed site, the laying in 1992 of an electric cable over 760 m has destroyed, directly and indirectly, 2.7 ha of meadows (CHARBONNEL *et al.*, 1995). In Cannes (Alpes-Maritimes, France) the laying of a water pipe 1500 m in length has had similar effects, destroying 2.1 ha of meadow (MOLENAAR, 1994). On the other hand, the laying of pipes or cables directly on the meadows (i.e. without trench) has only a negligible effect, because *Posidonia* rhizomes grow and cover them up rapidly (CHARBONNEL *et al.*, 1995).

- Alteration of the sediment flow. A groyne perpendicular to the coastline results (in relation to coastal drift) in upstream hypersedi-mentation and a shortage in sediment (with baring of the rhizomes) downstream. The average maximum growth of orthotropic rhizomes being around 5-7 cm per year (BOUDOURESQUE *et al.*, 1984a), the vegetative apexes are buried and die if the annual sediment input exceeds 5-7 cm. On the other hand, the bared rhizomes are vulnerable to water movement and to trawling. In both cases, the *P. oceanica* meadows can be destroyed.

Most barrier-reefs have been destroyed by harbour development. Such a barrier-reef perhaps existed in the Lacydon, the former "Vieux Port" of Marseilles, and at Port-Vendres (Pyrenées-Orientales, France). BOURCIER *et al.* (1979) offer the hypothesis that barrier-reefs existed in the past in the bays of La Seyne and Le Lazaret (Var, France). The most recently destroyed barrier-reef is that of Bandol (Bouches-du-Rhône, France) (PERES and PICARD, 1963). The only two typical barrier-reefs which still exist in France are those of Le Brusc (MOLINIER and PICARD, 1952) and the bay of Port-Cros (AUGIER and BOUDOU-RESQUE, 1970a). They remain threatened (see below). One can add two small barrier-reefs: at the island of Sainte-Marguerite (Alpes-Maritimes, France) and at San Fiurenzu (Corsica) (BOUDOURESQUE *et al.*, 1985). In Spain, one can cite the barrier-reef of Puerto de Sanitja in Menorca (VIDAL *et al.*, 1994).

It might be thought that the *Posidonia* barrier-reef in the bay of Port-Cros, situated in a National Park since 1963, has been saved. In fact, it has been shown that this reef has been continuously eroded since the beginning of the 20th century (AUGIER and BOUDOURESQUE, 1970a; BOUDOURESQUE *et al.*, 1975, 1980a). The causes are as follows: (i) The pollution of the bay, (ii) overuse by amateur sailors; more than 200 boats have been counted there in a single day in August; besides the pollution created by this veritable floating village, numerous amateur sailors overestimate the depth and come to grief on the reef; in disengaging, they contribute to the erosion of the reef. Since 1981, a cordon of buoys has protected the bathing area at the back of the bay, and at the same time the barrier-reef; but now it is windsurfers, and the damage caused by windsurfing beginners, which constitute a problem. (iii) Overgrazing by sea-urchins, whose numbers have on occasion soared (most recently in the 1970s), maybe in relation to the overfishing of their predators (Sala *et al.*, 1998).

Natural recolonisation by the *P. oceanica* meadow, after its destruction and if the causes are no longer operative, is very slow. Near Marseilles (Le Plateau des Chèvres), an area of 1.13 ha destroyed by a bomb in 1942 was not entirely recolonised in 1999, almost 60 years later: 0.32 ha of sand remain without *Posidonia* (PERGENT-MARTINI AND PASQUALINI, 2000). Through extrapolation, it is reasonable to suppose that it will only be in around 2020 that recolonisation will be completed, that is after nearly 80 years. In the Alpes-Maritimes (France), MEINESZ (1995) estimates that the time necessary for the recolonisation of lost areas would be 3 000 years.

The coralligenous community

Reduction in limpidity in waters (pollution, turbidity) and silting constitute the main threats to the coralligenous community. It is worth

adding, locally, the excessive visits by scuba divers: erosion by contact of coralline algae and Bryozoa (*Retepora* in particular), non-intentional breaking of gorgonians by beginners and deliberate tearing off of the red coral *Corallium rubrum* and the gorgonians *Eunicella* and *Paramuricea* (HARMELIN and MARINOPOULOS, 1994; HARMELIN, 1995; SALA *et al.*, 1996; MAURIS *et al.*, 1999).

At the end of the summer 1999, from Liguria (Italy) to Provence (France), a mass mortality outbreak severely affected a wide array of sessile filter-feeder invertebrates from the coralligenous community: e.g. sponges (*Hippospongia communis* and *Spongia officinalis*), the red coral (*Corallium rubrum*), gorgonians (*Paramuricea clavata, Eunicella singularis, E. cavolinii*), ascidians and bryozoans. Exceptionally high and constant temperatures throughout the water column (23-24°C for over one month, down to 40 m) could have created an environmental context favourable to this mass mortality (PEREZ *et al.*, 2000; ROMANO *et al.*, 2000). This event is an ominous reminder of what could occur in the case of an increment of the present day warming of Mediterranean waters (BETHOUX et al., 1990; BIANCHI and MORRI, 1993; FRANCOUR et al., 1994; BETHOUX and GENTILI, 1996, 1998; BIANCHI, 1997; BETHOUX *et al.*, 1998).

Conclusions

The Mediterranean Sea, probably thanks to the narrowness of its communication with the Atlantic, to its east-west orientation and to its geological history, constitutes one of the major hot spots of marine species diversity. Also for historical reasons, a very few biota from the former Tethys Sea, which extended from the Caribbean to South-East Asia, were preserved. However, one of these Tethys relicts, namely the seagrass *Posidonia oceanica,* plays a major role in the modern Mediterranean of which it is emblematic.

The fauna and flora of the Mediterranean are mainly of Atlantic origin. They encompass a rather high number of endemics, most of them being relatively recent (neo-endemics). The Mediterranean harbours a large variety of communities, as a function of depth, substrate, mean irradiance, water movement and the annual range of temperature. Some of these communities are unique, giving the Mediterranean its touch of originality, e.g. the *Posidonia oceanica* meadow, the coralligenous community, the *Lithophyllum byssoides* rim and the *Neogoniolithon brassica-florida* algal reefs.

In contrast to the terrestrial environment, in particular Mediterranean islands, where many species have become extinct during the last 10 000 years, no marine species seems, at the moment, to have totally disappeared from the Mediterranean. However, some of them are critically endangered, like the monk seal *Monachus monachus* and the

giant limpet *Patella ferruginea*. In addition, many other species drama-
tically declined during the twentieth century. Unfortunately, recent data
are more or less totally lacking for most Mediterranean species, so that
it is impossible to assess the status of their populations. They could
prove to be vulnerable, on the brink of extinction, without a previous alert
making it possible to intervene in good time, or even extinct. The
possibility that many species extinctions have escaped the investigators'
notice ("cryptic extinctions") has been emphasized by CARLTON (1993).

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