

## Marine biodiversity in the Mediterranean in the era of global warming

Charles-François BOUDOURESQUE<sup>1</sup>\*, Aurélie BLANFUNE<sup>1</sup>, Thomas CHANGEUX<sup>1</sup>, Gérard PERGENT<sup>2</sup>,  
Michèle PERRET-BOUDOURESQUE<sup>1</sup>, Sandrine RUITTON<sup>1</sup> and Thierry THIBAUT<sup>1</sup>

**Abstract:** The Mediterranean is a semi-enclosed temperate to locally warm sea. It is a hotspot of species, functional and ecosystem diversity, characterized by a high rate of endemism and a number of unique ecosystems. Between 12,000 and 17,000 marine species have been reported in the Mediterranean. Only one species is totally extinct and less than ten are extinct in the Mediterranean but still present elsewhere. In contrast, many species are functionally and/or regionally extinct. The progressive arrival of a thousand non-native species has in fact considerably increased the  $\epsilon$  species diversity of the Mediterranean, contrary to the naive beliefs of some environmentalists. Several of the emblematic ecosystems of the Mediterranean (e.g. the dune-beach-*banquette* ecosystem, the *Lithophyllum byssoides* algal rim, the seagrass *Posidonia oceanica* meadow, the reef fucalean forests and the coralligenous) are currently in decline. Finally, the functioning of ecosystems (relative abundance of key species, carbon and nutrient flows, food webs, and interactions between ecosystems) has been profoundly altered. The causes of this impact on biodiversity are various; the three major causes are coastal development, overfishing, and biological invasions. Global warming is beginning to play a role, which will increase significantly over the course of the 21<sup>st</sup> century, but it is currently far behind other human-induced causes. The concern over the growing and irreversible effects of global warming is totally justified; but the underestimation of other threats derives from issues which may be political or related to human perceptions and science funding, and which are discussed here.

**Keywords :** *biodiversity, biological invasions, global warming, overfishing*

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1) Aix-Marseille University, Université de Toulon, MIO (Mediterranean Institute of Oceanography), CNRS, IRD, Campus of Luminy, 13288 Marseille, France  
2) Università di Corsica Pasquale Paoli, Laboratoire Sciences Pour l’Environnement, UMR 6134 SPE, Corti, Corsica, France

\*Corresponding author: Charles-François Boudouresque  
Tel: + 33-486090574  
Fax: + 33-486090643  
E-mail: [charles.boudouresque@mio.osupytheas.fr](mailto:charles.boudouresque@mio.osupytheas.fr)

## 1. Introduction

The Mediterranean is an east-west semi-enclosed sea, the largest in the world ocean (COLL *et al.*, 2010), 3,800 km long (from the Alboran Sea to the Levantine basin) and up to 900 km wide, with a surface area of ~2.5 million km<sup>2</sup>. It communicates with the Atlantic Ocean, through the narrow (14 km) Straits of Gibraltar, and with the Black Sea. Since 1869, the Mediterranean has also communicated with the Red Sea, *via* the man-made 193 km long Suez Canal (NICOLE, 1870; POR, 1978; BOUDOURESQUE, 1999). The Mediterranean is for the most part a temperate sea, i.e. a sea where the winter sea surface temperature (SST) ranges between 10 and 20°C; however, the westernmost part of the Levantine basin, with winter SST close to or over 20°C, can be regarded as subtropical (LÜNING, 1990; LEONI *et al.*, 2021; TMEDNET, 2021). It has been compared to a miniature ocean and studying it can shed light on issues concerning the global ocean (LEJEUSNE *et al.*, 2010).

Due to the northwards push of Africa, the communication between the Mediterranean and the Atlantic Ocean was closed between 5.7 and 5.3 million years ago. The Mediterranean, which has a water deficit due to its dry climate and the insufficient flow of tributary rivers, then partially dried up (the Messinian crisis) (GARCIA-CASTELLANOS *et al.*, 2009; MILLOT and TAUPIER-LETAGE, 2005; DANOVARO and BOERO, 2019). This resulted in the disappearance of most of its flora and fauna; after the opening of the Straits of Gibraltar and the refilling of the Mediterranean, this sea was predictably repopulated by species originating from the Atlantic (BOUDOURESQUE, 2004; LEJEUSNE *et al.*, 2010).

During the Pleistocene climatic glacial cycles, North-Atlantic species periodically shifted their latitudinal ranges, northwards (interglacial epi-

sodes) or southwards (glacial episodes), allowing species of warm and cold affinities, respectively, to enter the Mediterranean *via* the Gibraltar Straits. Once in the Mediterranean, because of reduced opportunities for north-south migration in response to changing sea temperatures, populations of these species were subject to higher evolutionary pressures. In addition, the Alboran Sea, at the entrance to the Mediterranean, acts as a buffer reducing gene flow, and the 46,000 km of Mediterranean coasts are highly compartmentalised into relatively isolated sectors. This mechanism can account for the high rate of endemism in the Mediterranean, the sea functioning as a 'species factory' or a 'diversity pump' from the Atlantic, as coined by Carlo Nike Bianchi (BIANCHI, 1996; BIANCHI and MORRI, 2000; BOUDOURESQUE, 2004; LEJEUSNE *et al.*, 2010; BIANCHI *et al.*, 2012a).

## 2. The concept of biodiversity

'Biodiversity' is today a term that has gained popular currency, widely used not only by scientists but also by political leaders, government officials, conservationists, environmentalists ('greens') and the public at large. However, the modern scientific concept of biodiversity is sometimes worlds away from its popular definition, as used in the environmentalist's jargon. For the latter, biodiversity is synonymous with species richness, which in fact represents a rather limited part of the species diversity concept, itself a relatively small part of the biodiversity concept. Finally, the term 'biodiversity' is now often used to reflect a concern for the natural environment, nature conservation and species extinctions, without any real relation to the scientific concept to which it properly refers.

For many managers, politicians and 'greens', species richness held sacred. The more species there are in a habitat or an area, the more

important that habitat or area is and the more it deserves to be protected. This belief is incorrect for several reasons (SALA and KNOWLTON, 2006; BOUDOURESQUE, 2014; BOUDOURESQUE *et al.*, 2017a). (i) Many habitats are relatively poor in species (at least for certain 'noble' taxa favoured by environmentalists and NGOs - e.g. flowering plants, mammals), while having high heritage value; this is the case for belts of terrestrial halophilic vegetation on rock, *sansouïres* (mud-flats subject to sea inundation, colonized by salicorniae of the genus *Arthrocnemum*), beach-dune systems and coastal lagoons. (ii) The species richness is very dependent on the scale (see below): point diversity (scale of the sample),  $\alpha$  species diversity (scale of the ecosystem in a region),  $\gamma$  species diversity (all the ecosystems of a region), and  $\epsilon$  species diversity (all the ecosystems of a vast biogeographical region, such as the Mediterranean Sea). It is important to note that the species diversity in a given habitat may be high at one scale (e.g. point diversity) and low at another (e.g.  $\alpha$  species diversity), or the opposite (see examples *in* BOUDOURESQUE *et al.*, 2017a). Furthermore, the same human impact (e.g. pollution, biological invasion) can increase the  $\alpha$  species diversity in one ecosystem (e.g. a coastal sandy bottom) and reduce it in another (e.g. a *Posidonia oceanica* seagrass meadow). (iii) In most cases, non-extreme disturbances, e.g. pollution, do not reduce species diversity, but increase it (CONNELL, 1978; MOLINO and SABATIER, 2001; SALA and KNOWLTON, 2006; OURGAUD *et al.*, 2013, 2015). In a 11,000-m<sup>2</sup> bathing area close to the commercial port of Barcelona (Catalonia, Spain), a marina and the outfall of a sewage treatment plant, a high  $\gamma$  species diversity was observed (517 taxa), including heritage value species such as the fan mussel *Pinna nobilis* and the dusky grouper *Epinephelus marginatus* (PONTES *et al.*, 2021). In

a seagrass *Zostera noltei* meadow, artificial detritus increased point diversity of invertebrates (COSTA *et al.*, 2021). (iv) For a given ecosystem, the right species diversity is its 'natural' value, either high or low. It is therefore inappropriate to think that a decline in the number of species is a negative effect, while an increase would be positive, as some authors claim (see e.g. GRIBBEN and WRIGHT, 2006; WRIGHT and GRIBBEN, 2008; ANTON *et al.*, 2019). In fact, both the decline and the increase in species richness, relative to the 'natural' value, are negative effects.

Biodiversity means the variety of life, encompassing levels of complexity from within species to across ecosystems, and includes five dimensions (SALA and KNOWLTON, 2006; GAERTNER *et al.*, 2010; BOUDOURESQUE, 2014; BOUDOURESQUE *et al.*, 2017a). (i) Evolutionary scale, i.e. diversity within species (genetic diversity), diversity between species, diversity between taxa higher than species (genera, families, orders, classes, phyla, kingdoms, etc.) and phylogenetic diversity (mean phylogenetic distance between taxa; FAITH, 1992; WARWICK and CLARCK, 1995, 2001). (ii) Functional scale, i.e. diversity in the functional role of species, functional groups and guilds within ecosystems, e.g. photosynthetic or chemosynthetic primary producers, diazotrophic species, filter-feeders, suspension-feeders. (iii) Organizational scale, i.e. diversity between patches, communities, ecosystems, landscapes/seascapes, including beta-diversity. (iv) Spatial scale, from local and regional to global (RAMADE, 1994; GRAY, 2000). As far as the species diversity is concerned (evolutionary scale), it can be considered at the scale of a sample (point diversity), of an ecosystem within a region ( $\alpha$  diversity), of all the ecosystems of a region ( $\gamma$  diversity) and of all the ecosystems of a large biogeographical province ( $\epsilon$  diversity). The spatial (geographical) scale matters a great deal for biodiversity

estimates (WARWICK, 1998; WILLIS and WHITTAKER, 2002). (v) Finally (heterogeneity scale), biodiversity includes the proportional distribution of the individuals among the species, the so-called heterogeneity diversity, abundance diversity or evenness (SHANNON and WEAVER, 1949; PIELOU, 1975; HEIP *et al.*, 1998; GRAY, 2000). Like other measures of biodiversity, heterogeneity diversity is sensitive to spatial scale (FRASCHETTI *et al.*, 2006).

Biodiversity is, *par excellence*, a multidimensional concept. The choice with regard to the meaning (qualitative or quantitative, compositional or functional, scale, etc.) depends primarily on one's goals and interests. Biodiversity can therefore be measured in different and complementary ways and thus involves the use of at least 200 different metrics (SALA and KNOWLTON, 2006; BOUDOURESQUE, 2014; BOUDOURESQUE *et al.*, 2017a). This complexity of meanings, scale and units makes it impossible to assess the state of biodiversity using a single measure or index.

### 3. Biodiversity of the Mediterranean Sea

The Mediterranean Sea is a hotspot of  $\epsilon$  species diversity; the number of reported species has been estimated to range between 12,000 and 17,000 species (BOUDOURESQUE, 2003, 2004; COLL *et al.*, 2010; BIANCHI *et al.*, 2012a; CONIDES and PAPACONSTANTINO, 2020). It is also a hotspot in the terrestrial realm (BLONDEL and MÉDAIL, 2009). Mediterranean taxa represent 17% of the earth's marine species diversity for brown algae (Phaeophyceae) (BOUDOURESQUE, 2004), 10% for Hydraria (GRAVILI *et al.*, 2013) and Porifera (GRENIER *et al.*, 2018) and 8% for seagrasses (GERAKARIS *et al.*, 2019). The point species diversity can also be very high in coastal habitats (BELLAN-SANTINI, 1962, 1968): up to 109 species of macroalgae in a 400 cm<sup>2</sup> sample in a photophilous reef habitat at 10 m depth (Port-Cros Island,

Provence) (COPPEJANS and BOUDOURESQUE, 1975).

At the end of the Messinian crises, 5.3 Ma ago, the Mediterranean was mostly repopulated by species originating in the Atlantic Ocean. It is therefore not surprising that, several million years later, the majority of species, ~50%, are common with those of the Atlantic (PÈRES and PICARD, 1964; GIACCONE and GERACI, 1989; BOUDOURESQUE, 2004; BIANCHI *et al.*, 2012b). Endemic species represent more than 30% of Mediterranean species, as a result of the 'Mediterranean species factory' (see above) (LEJEUSNE *et al.*, 2010; BIANCHI *et al.*, 2012a). This percentage is constantly increasing, at the expense of that of the Atlantic species, which is actually an artifact; when molecular studies are carried out on species that are believed to be common to the Atlantic and the Mediterranean, they generally result in the conclusion of the existence of distinct cryptic species in the Mediterranean and the Atlantic. For example, the Atlantic sea anemone *Actinia equina* is replaced in the Mediterranean by *A. mediterranea* (MONTEIRO *et al.*, 1997); the Atlantic red alga *Radicilingua thysanorhizans* is replaced in the Mediterranean by *R. mediterranea* (WOLF *et al.*, 2021); the Mediterranean red alga *Botryocladia chiajeana* is replaced in the Atlantic by *B. macaronesica* (AFONSO-CARRILLO *et al.*, 2006). The most iconic endemic species in the Mediterranean are the seagrass *Posidonia oceanica* (Fig. 1), the fan mussel *Pinna nobilis*, the precious red coral *Corallium rubrum*, and the orange stony coral *Astroides calycularis*, although the two latter also occur on the neighbouring Atlantic coasts (DEN HARTOG, 1970; ZIBROWIUS *et al.*, 1984; BASSO *et al.*, 2015; ROUANET *et al.*, 2015; PRADA *et al.*, 2019; LEDOUX *et al.*, 2021). Finally, non-indigenous species (NIS) represent almost 10% of Mediterranean species (BOUDOURESQUE and VERLAQUE, 2002;

ZENETOS *et al.*, 2005; GALIL, 2008; ZENETOS and GALANIDI, 2020). Most of them are definitely or probably introduced, i.e. naturalized: new generations in the non-native area, the Mediterranean, are born without human assistance, thus constituting self-sustaining populations (BOUDOURESQUE and VERLAQUE, 2002a, 2012). In the eastern Mediterranean, the Suez Canal, inaugurated in 1869, and widened and deepened several times since, is the main vector of NISs (NICOLE, 1870; POR, 1978; BOUDOURESQUE, 1999; GALIL *et al.*, 2015). In the western Mediterranean, by contrast, aquaculture is the main vector: escaped reared species and especially species accompanying the reared species (e.g. epibionta and parasites) (VERLAQUE *et al.*, 2007; GRIGORAKIS and RIGOS, 2011; BOUDOURESQUE *et al.*, 2020). Other vectors are the fouling on ship hulls (BOUDOURESQUE and VERLAQUE, 2002b; PETROCELLI *et al.*, 2019), ballast waters (DAVID *et al.*, 2007), the aquarium trade (MEINESZ and HESSE, 1991; MEINESZ and BOUDOURESQUE, 1996) and packaging material used for shipment of seafood (RUITTON *et al.*, 2021).

About fifty ecosystems have been described in the Mediterranean (PÉRÈS and PICARD, 1964; PÉRÈS, 1967; RODRIGUES, 1982; BOUDOURESQUE, 1984; BIANCHI and MORRI, 2001; BEVILACQUA *et al.*, 2021). Their delineation and number differ from one author to another, but this question is outside the scope of this article. They are distributed from the supralittoral zone, above mean sea level, to the abyssal zone, whose maximum depth is, in the Mediterranean, 5,267 m. Some ecosystems straddle several zones, such as the Dune-Beach-*Banquette* ecosystem (supralittoral and midlittoral) and the coralligenous ecosystem (infralittoral and circalittoral).

Some Mediterranean ecosystems are unique, endemic to this sea. Below, we list a few of them, going from the supralittoral zone to the abyssal



Fig. 1 The front of a *Posidonia oceanica* meadow, with plagiotropic rhizomes (creeping) and bundles of leaves (shoots). Port-Cros Island (eastern Provence, France). Photo © Sandrine Ruitton.

zone. (i) The Dune-Beach-*Banquette* ecosystem (DBB) differs from worldwide beach-dune systems by the presence and the overwhelming role of the *banquette*, a thick (up to 2 m) layer of dead *Posidonia oceanica* leaves cast ashore by storms and covering the beach (Fig. 2). In addition to feeding local food webs, these leaves are in part exported to the dune and the foredune, where they constitute the main source of nitrogen. The remaining leaves of the *banquette* return to the sea during storm episodes and play a pivotal role in coastal food webs (GAUCI *et al.*, 2005; DEIDUN *et al.*, 2007; CARDONA and GARCÍA, 2008; DEIDUN *et al.*, 2009; BOUDOURESQUE *et al.*, 2012; SIMEONE *et al.*, 2013; BOUDOURESQUE *et al.*, 2017b). (ii) The *Lithophyllum byssoides* algal rim is a bioconstruction built by a calcareous red alga a few centimetres above the mean sea level, in the midlittoral zone of rocky and relatively shady habitats, under semi-exposed and exposed conditions (Fig. 3). It can reach 2 m in width and its upper surface is flat, hence the name *trottoir* (after a French word meaning sidewalk) which is usually given to it. *Trottoir* occur in exposed and shady habitats. Their construction requires



**Fig. 2** A *banquette* of cast ashore dead *Posidonia oceanica* leaves on a beach. The figure (MPB and her dog Diego) shows the scale. In the background, the dune with the European beachgrass *Ammophila arenaria* and the backdune with a *Juniperus phoenicea* forest. Beach of Barcaghju, Capicorsu, Corsica. Photo © Charles-François Boudouresque.

periods of relative stability of the sea level for several centuries (PÉRÈS and PICARD, 1964; LABOREL *et al.*, 1983; BIANCONI *et al.*, 1987; LABOREL, 1987; FAIVRE *et al.*, 2013; INGROSSO *et al.*, 2018; BEVILACQUA *et al.*, 2021; FAIVRE *et al.*, 2021). (iii) The *Posidonia oceanica* seagrass meadow extends from the sea level down to 30–40 m depth, in sandy and reef habitats of the infralittoral zone (Fig. 4). It is a hotspot of  $\alpha$  species diversity and provides many ecosystem services (e.g. high primary production, carbon sequestration, sand factory, protection of beaches against erosion, export of dead leaves to all other Mediterranean ecosystems, spawning area, nursery). Dead leaves are exported towards all the Mediterranean ecosystems, from the supralittoral and midlittoral DBB to deep bathyal canyons, where they constitute a valuable food resource (Fig. 5) (MOLINIER and PICARD, 1952; MAZZELLA *et al.*, 1992; MATEO *et al.*, 2006; BOUDOURESQUE *et al.*, 2012, 2016; PAOLI



**Fig. 3** The *Lithophyllum byssoides* algal rim (*trottoir*) of Punta Palazzu (western Corsica) in the early 1980s. Photo © Jean-Georges Harmelin, courtesy of the author.

*et al.*, 2018; MONNIER *et al.*, 2020; RIGO *et al.*, 2021). (iv) The reef fuclean forests are built by erect large and long-lived brown algae (Fucales, Phaeophyceae, kingdom stramenopiles) belonging to the genera *Sargassum* and *Cystoseira sensu lato*, such as *Ericaria brachycarpa* and *Gongolaria montagnei*. They dwell on reefs of the infralittoral zone (THIBAUT *et al.*, 2017; BEVILACQUA *et al.*, 2021; SANT and BALLESTEROS, 2021a). (v) The coralligenous ecosystem is a bi-construction built by calcareous red algae and calcified metazoans (cnidarians, bryozoans, molluscs, etc.). In addition, gorgonians (*Paramuricea clavata*, *Eunicella* spp.), the precious red coral *Corallium rubrum* below overhangs, the Fucales *Gongolaria zosteroides* and *Sargassum* spp., build a mixed animal and seaweed forest (Fig. 6).



Fig. 4 A *Posidonia oceanica* seagrass meadow. Bagaud Island, Port-Cros Archipelago Marine Protected Area (MPA), eastern Provence. Photo © Sandrine Ruitton.



Fig. 6 A coralligenous ecosystem, 20 m depth, at La Ciotat (western Provence, France). Photo © Sandrine Ruitton.

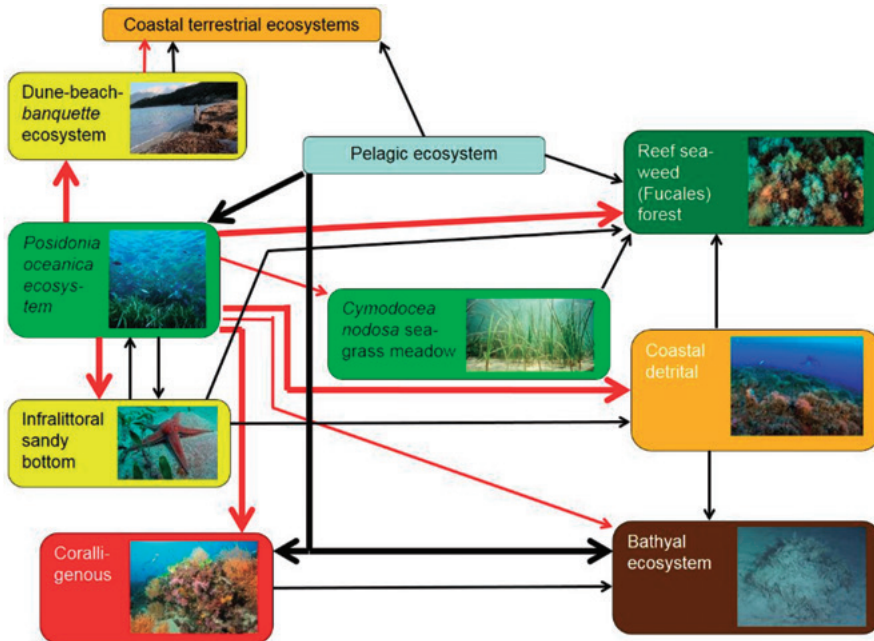


Fig. 5 Interactions (flow of carbon and nutrients) between some Mediterranean coastal ecosystems. The *Posidonia oceanica* ecosystem interacts, via the export of dead leaves (red arrows), with all coastal ecosystems. Black arrows: other flows. Width of the arrows: high, medium or low flows. Original figure © Charles-François Boudouresque.

Gorgonians, red coral and Fucales are long-lived species. This ecosystem dwells in the lower infralittoral zone and in the circalittoral zone (BALLESTEROS, 2006; RUITTON *et al.*, 2014; CAPDEVILA *et al.*, 2016; BOUDOURESQUE *et al.*, 2017c; CAPDEVILA LANZACO, 2017; BEVILACQUA *et al.*, 2021; SANT and BALLESTEROS, 2021b).

Other ecosystems, although not unique to the Mediterranean Sea, deserve special attention, such as the vermetid platforms (GORDÓ-VILASECA *et al.*, 2021) and the *Zostera marina* seagrass meadows (BOUDOURESQUE *et al.*, 2009; PERGENT *et al.*, 2012).

Two main features characterize the functioning of the Mediterranean ecosystems: the extreme oligotrophy of Mediterranean waters and the scarcity of native macro-herbivores. The oligotrophy results from the drought which characterizes part of the Mediterranean catchment area (the south and the east) and from the weak contributions of the tributary rivers. The Nile was once the main tributary river. Since the construction of the Aswan dam in 1970, the Nile has almost dried up before reaching the Mediterranean. It is therefore the Rhône River which is today the main provider of water and nutrients (SADAoui *et al.*, 2016). The nitrogen deficit is partly compensated by diazotrophic bacteria (capable of fixing dinitrogen N<sub>2</sub> into a biologically useful form, ammonia), both in the pelagic ecosystem and in the seagrass *Posidonia oceanica* ecosystem (BÉTHOUX and COPIN-MONTÉGUT, 1986; BÉTHOUX *et al.*, 1992; GARCÍA-MARTÍNEZ *et al.*, 2005; BOUDOURESQUE *et al.*, 2006; GARCIA *et al.*, 2006). Macro-herbivore species are few in ecosystems belonging to supralittoral, midlittoral, infralittoral and circalittoral zones, i.e. the zone which houses primary producers. The most conspicuous are the teleost fish *Sarpa sarpa* and *Sparisoma cretense* (the latter mainly in the eastern Mediterranean, but currently spreading

in the western basin) and the sea urchins *Paracentrotus lividus* and *Arbacia lixula* (MAGGIORE *et al.*, 1987; VERLAQUE, 1990; VERGÉS *et al.*, 2009; ASTRUCH *et al.*, 2016; TSIRINTANIS *et al.*, 2018; BOUDOURESQUE and VERLAQUE, 2020; ESPOSITO *et al.*, 2021). The giant limpet *Patella ferruginea*, in the midlittoral of the western basin, should also be taken into account (GUERRA-GARCÍA *et al.*, 2004; COPPA *et al.*, 2011). *Sarpa sarpa*, *Sparisoma cretense* and *Paracentrotus lividus* are browsers: they pick plants from above, like terrestrial large herbivores. *Arbacia lixula* and *P. ferruginea* are grazers: they scrape benthic organisms from the side, like a bulldozer; as a result, they engulf both plants and metazoans, which is the case of *A. lixula*, the isotopic signature of which is that of a predator (WANGENSTEEN *et al.*, 2011). The role of omnivorous fish, such as *Diplodus vulgaris*, *Coris julis* and *Thalassoma pavo*, should also be taken into account, as they either consume macroalgae or cut them off them when feeding on invertebrates (PAPADAKIS *et al.*, 2021). Overall, in most undisturbed coastal benthic ecosystems, the detritus-feeder path, or the suspension-feeder and filter-feeder paths, are the dominant pathways in the ecosystem functioning (BOUDOURESQUE *et al.*, 2005a, 2017a).

## 4. Threats to Mediterranean biodiversity

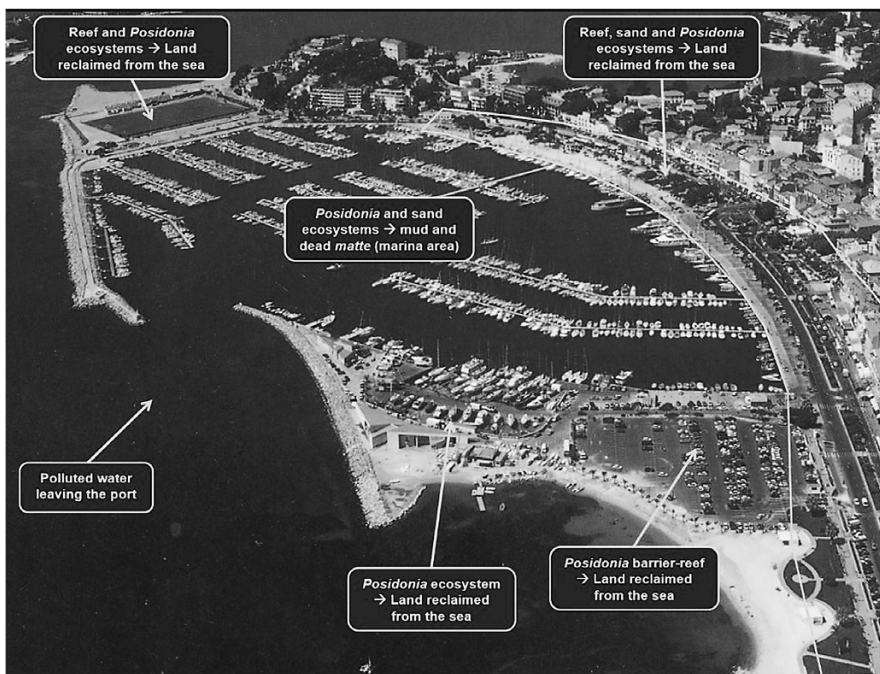
### 4.1. Stressors

A variety of stressors threaten Mediterranean biodiversity (GIAKOUMI *et al.*, 2015; HOLON *et al.*, 2015, 2018; RUITTON *et al.*, 2020; BEVILACQUA *et al.*, 2021; GAGLIOTI and RADLO, 2021); one way to assess their respective severity is to determine their degree of reversibility (Table 1) (BOUDOURESQUE *et al.*, 2005a; MEINESZ, 2021). (i) Coastal development. The impact is direct when land is reclaimed from the sea, for example Nice airport (French Riviera), or in ports and



**Table 1** Time needed for recovery, after the end of the forcing disturbance. +: yes; ±: yes or no; -: no. From BOUDOURESQUE *et al.* (2005a), updated.

Disturbance	Human origin?	Natural origin?	Recovery (years: y)	Key references
Domestic pollution (soft substrates)	+	-	< 1-10 y	BELLAN <i>et al.</i> , 1999
Artisanal fishing (fish abundance)	+	-	< 5-10 y	RAMOS, 1992; ROBERTS <i>et al.</i> , 2001
Oil spill	+	-	< 10 y	RAFFIN <i>et al.</i> , 1991; BOUDOURESQUE <i>et al.</i> , 2019a
Disease of marine species	±	+	> 10 y	MOSES and BONEM, 2001
Loss of long-lived species	+	±	10-100 y	SOLTAN <i>et al.</i> , 2001
Coastal development	+	-	Millenia	MEINESZ <i>et al.</i> , 1991
Over-fishing (genetic change)	+	-	Millenia?	CONOVER, 2000; LAW, 2000; KENCHINGTON <i>et al.</i> , 2003; OLSEN <i>et al.</i> , 2004
Climate warming	+	+	Glacial cycle?	ZWIERS and WEAVER, 2000; BARNETT <i>et al.</i> , 2001
Biological invasions	+	-	Irreversible	CLOUT, 1998; BRIGHT, 1998
Species neo-extinction	+	-	Irreversible	CARLTON, 1993; POWLES <i>et al.</i> , 2000



**Fig. 7** Coastal development: the city and marina of Bandol (Provence, France). Land reclaimed from the sea and marina area, with ecosystems possibly formerly occurring there.

marinas (Fig. 7). It is also indirect, due to the resulting pollution and turbidity (MEINESZ *et al.*, 1991; MEINESZ, 2021). (ii) Biological invasions. Invasive species deeply alter the functioning of host ecosystems. The most concerning species are the seaweeds *Caulerpa cylindracea*, *C. taxifolia*, *Womersleyella setacea* and *Rugulopteryx okamuræ* and the teleosts *Siganus luridus*, *S. rivulatus* and *Pterois miles* (BOUDOURESQUE *et al.*, 1995; VERGÈS *et al.*, 2014; GIOVOS *et al.*, 2018; RUITTON *et al.*, 2021). (iii) Overfishing. Most fish stocks are overexploited worldwide, which has resulted in a decline in catches, despite the considerable increase in fishing effort (WATSON and PAULY, 2001; PAULY *et al.*, 2003; CHASSOT *et al.*, 2010). The same occurs in the Mediterranean, where 90 % of fish stocks are overexploited and depleted (COLLOCA *et al.*, 2017; CONIDES and PAPAConstantinou, 2020; AKBARI *et al.*, 2021). In addition, catch, as reported by FAO, is widely underestimated (PAULY and ZELLER, 2016); Illegal, Unreported and Unregulated (IUU) fishing can be responsible for catches equal to or much greater than those from official professional fishing, such as in Sicily (Italy) (FALAUTANO *et al.*, 2018); recreational fishing can represent considerable catches in the most touristic regions in the world, such as the Mediterranean (BOUDOURESQUE *et al.*, 2005b; LLORET and FONT, 2013, LLORET *et al.*, 2019); trawling is responsible for havoc in coastal ecosystems, in particular the seagrass *Posidonia oceanica* meadows (BOUDOURESQUE *et al.*, 2012; PERGENT *et al.*, 2013; SALA *et al.*, 2021); to harvest the borer mollusc *Lithophaga lithophaga*, divers break the rock with special sledgehammers, in Apulia (southern Italy) and in some other Mediterranean areas, which results in the devastation of the reef fucallean forests (FANELLI *et al.*, 1994; FRASCHETTI *et al.*, 2001; GUIDETTI *et al.*, 2004); fishing with explosives (dynamite)

was widely practiced, and is still practiced in a few areas (FAGET, 2015); finally, lost fishing gear continues to fish and harm benthic ecosystems (RUITTON *et al.*, 2019a). (iv) Pollution. It comes from atmospheric fallout, tributary rivers channeling water from the catchment area, discharges from coastal towns and aquaculture (MIRACLE, 1994; ROMAÑA and GUILLAUD, 1995; PERGENT-MARTINI *et al.*, 2006; PERGENT *et al.*, 2011; RICHIR *et al.*, 2015; BOUDOURESQUE *et al.*, 2020). Along the northern Mediterranean coast, thanks to the binding directives from the European Union (EU), applied willingly or unwillingly by States, pollution has been considerably reduced since the 1980s; most sewage water today passes through sewage treatment plants, with some positive consequences (DE LOS SANTOS *et al.*, 2019). However, at the scale of the entire Mediterranean, 50% of wastewater remains untreated (MEOLA and WEBSTER, 2019). (v) Other stressors should be taken into account, e.g. seawater warming (BIANCHI *et al.*, 2013; RIVETTI *et al.*, 2014; SHALTOUT and OMSTEDT, 2014; GUY-HAIM *et al.*, 2016a, 2016b; RIVETTI *et al.*, 2017; HOEGH-GULDBERG *et al.*, 2019), the rise in sea level (VACCHI *et al.*, 2017; PERGENT *et al.*, 2019), water acidification (TEIXIDÓ *et al.*, 2018; BARRUFFO *et al.*, 2021) and macro- and microlitter (DEUDERO and ALOMAR, 2015; ASENSIO-MONTESINOS *et al.*, 2019; ANGIOLILLO *et al.*, 2021); their actual role, in relation to the stressors mentioned above, will be discussed later.

When assessing the respective importance of stressors, it is important to consider what the target is: humans? Or marine life? The general public often confuses the two targets (MEINESZ, 2021). Pollution has by definition an impact on the target 'humans'; by contrast, the impact of contamination on the target 'marine life' is very diverse, and in some cases it may be slight. Regarding the target 'marine life', it is important to

distinguish the scale of the individual from that of the population and that of the ecosystem: stress on the individual may not have an impact on the population and even less on the ecosystem. Many authors confuse an impact on the individual (which is stressed), a very real and documented impact, with an impact on biodiversity or the ecosystem, an impact generally not demonstrated (see e.g. LIONETTO *et al.*, 2021). The paradigm example is that of *Homo sapiens*: millennia of wars, pandemics and pollution have stressed or killed hundreds of millions of people, but have not even slowed the proliferation of *Homo sapiens*.

#### 4.2. Threats to species diversity

Only one species is definitely extinct, the great auk *Pinguinus impennis*; it was present in the Mediterranean and northern Atlantic, was depicted by man in the Cosquer Cave, near Marseilles, 18 000–19 000 years ago, and became extinct in 1844 (CLOTTE and COURTIN, 1994; PLANHOL, 2004; BRUGAL, 2021). Several species have never been recorded for more than 70 years, up to 150 years, e.g. the brown algae *Compsonea minutum* and *Ectocarpus siliculosus* var. *subulatus* (CFB, AB and TT, unpublished data); as these are species that are difficult to distinguish, of uncertain status, their extinction is just a hypothesis. Some species are considered as extinct in the Mediterranean, but still occur in other areas, e.g. the Atlantic Ocean. This is the case of the hydroid *Tricyclusa singularis* (BOERO and BONSDORFF, 2007), the whales *Eubalaena glacialis* and *Eschrichtius robustus* (RODRIGUES *et al.*, 2018) and the harbour porpoise *Phocaena phocaena* (BEAUBRUN, 1995; FONTAINE, 2016). In contrast with the relatively low number of extinct or possibly extinct taxa, a much higher number of species are functionally or regionally extinct. The monk seal

*Monachus monachus* is extinct in the western Mediterranean Basin (MARCHESSAUX, 1989; BOUDOURESQUE, 2003; VOULTSIADOU *et al.*, 2012). Regional and functional extinctions are common in brown algae of the order Fucales (Table 2) (THIBAUT *et al.*, 2005; BLANFUNE *et al.*, 2013, 2016a; THIBAUT *et al.*, 2016, 2017; BLANFUNE *et al.*, 2019).

For the general public, environmentalists, managers and journalists, biodiversity often means 'How many species?', which is incorrect, and the erosion of biodiversity means 'How many extinct species?' Environmental NGOs often publish ambiguous or exaggerated press releases which the press in turn exaggerates. It must be said that some of the general public and politicians are only sensitive to the cataclysmic news, whereas true and therefore more complex information goes unnoticed, even when it may actually be more of a concern in the long run than more dramatic news. Information such as 'Over 40 years, 50% of species have seriously declined' becomes 'In 40 years, 50% of species have become extinct'. The following anecdote illustrates this (BOUDOURESQUE, 2021). Recently, following such a press release of this kind, a French television journalist called the first author (CFB): 'I am putting together a program on the erosion of biodiversity in the Mediterranean; I am missing some important information: what is the percentage of recently extinct species? 20%? 30%? 40%?' The author tried to explain to her that very few species had disappeared in the Mediterranean and that, on the contrary, human impact had considerably increased the number of species. He did not have time to explain to her that biodiversity is not, for the most part, 'How many species?', and that the erosion of biodiversity is as much 'more species' than 'less species'; she told him 'I was misled in thinking you were an ecologist' and hung up on me with barely a

**Table 2** Current status of species of Fucales (Phaeophyceae, Stramenopiles) in French Mediterranean regions. RE: regionally extinct. FE: functionally extinct. -: naturally absent. +: unchanged status or no dramatic decline. md: missing data. Data from THIBAUT *et al.* (2005), BLANFUNÉ *et al.* (2013), THIBAUT *et al.* (2014, 2015), BLANFUNÉ *et al.* (2016a), THIBAUT *et al.* (2016) and BLANFUNÉ *et al.* (2019).

Accepted name	Synonym	French Catalonia	Western Provence	Eastern Provence	French Riviera and Monaco	Corsica
<i>Carpodesmia caespitosa</i>	<i>Cystoseira caespitosa</i>	FE	md	md	-	md
<i>Cystoseira compressa</i>		+	md	md	+	md
<i>Cystoseira foeniculacea</i>		RE	md	md	FE	md
<i>Cystoseira jabukae</i>		-	-	-	+	+
<i>Ericaria amentacea</i>	<i>Cystoseira amentacea</i>	-	+	+	+	+
<i>Ericaria brachycarpa</i>	<i>Cystoseira brachycarpa</i>	-	md	md	FE	md
<i>Ericaria crinita</i>	<i>Cystoseira crinita</i>	RE	FE	+	FE	+
<i>Ericaria funkii</i>	<i>Cystoseira funkii</i>	RE	md	md	-	md
<i>Ericaria mediterranea</i>	<i>Cystoseira mediterranea</i>	+	-	-	-	-
<i>Ericaria zosteroides</i>	<i>Cystoseira zosteroides</i>	FE	md	md	+	md
<i>Gongolaria barbata</i>	<i>Cystoseira barbata</i>	RE	md	md	FE	md
<i>Gongolaria elegans</i>	<i>Cystoseira elegans</i>	FE	md	md	RE	md
<i>Gongolaria montagnei</i>	<i>Cystoseira spinosa</i>	RE	md	md	FE	md
<i>Gongolaria sauvageauana</i>	<i>Cystoseira sauvageauana</i>	RE	md	md	FE	md
<i>Gongolaria squarrosa</i>	<i>Cystoseira squarrosa</i>	-	md	md	RE	md
<i>Sargassum acinarium</i>		RE	RE	FE	FE	+
<i>Sargassum hornschurchii</i>		RE	RE	FE	RE	RE
<i>Sargassum vulgare</i>		RE	FE	+	FE	+

goodbye - and chose 30%! Similar anecdotes were reported by PAVÉ (2019) and CHEINET (2020). Unfortunately, some scientists play a role in the propagation of cataclysmic forecasts, which subsequently prove to be erroneous. EHRlich and EHRlich (1981) wrote, in an influential book, that 50% of the species present in 1980 would have become extinct by 2000, which obviously did not happen.

#### 4.3. Threats to ecosystems

Regarding threats to ecosystems, we focus here on five iconic ecosystems in the

Mediterranean: the dune-beach-*banquette* ecosystem (DBB), the *Lithophyllum byssoides* algal rim, the seagrass *Posidonia oceanica* meadow, the reef fucalean forest and the coralligenous ecosystem. Deep ecosystems also merit consideration (FANELLI *et al.*, 2021).

(i) The DBB ecosystem (Fig. 2) is mainly threatened by the decline of *P. oceanica* meadows in front of the beaches, which protect beaches from erosion by waves and swell, and by the destruction of the dunes (urbanization, roads, trampling), which prevents the back and forth movements of the sand essential for the

equilibrium of the beach. It is also threatened by the removal of the *banquette* of cast ashore dead leaves of *P. oceanica* by ill-informed local authorities, which results in further beach erosion (CANCEMI and BURON, 2008; SIMEONE, 2008; BOUDOURESQUE *et al.*, 2012; SIMEONE and DE FALCO, 2013; BOUDOURESQUE *et al.*, 2017b; ROIG-MUNAR *et al.*, 2019).

(ii) The *Lithophyllum byssoides* algal rim (Fig. 3) is a slow growing bioconstruction; its formation corresponds to cold climate episodes, when the polar ice sheets stop melting and Alpine glaciers advance, more or less stabilizing the sea level (FAIVRE *et al.*, 2013). By the end of the LIA (Little Ice Age; mid-19th century), the sea level had resumed its rise. This rise was at first slow ( $0.4 \text{ mm y}^{-1}$ ), but, due to the human-induced amplification of climate warming, resulting in the melting of polar ice sheets and of mountain glaciers together with the thermal expansion of the seawater, the sea-level rise steadily accelerated. It is now too fast, so that *L. byssoides* rims have begun to be submerged throughout the Mediterranean. The ecosystem engineer species *L. byssoides* then dies and is covered by infralittoral species such as soft red algae and articulated corallines (e.g. *Corallina caespitosa*). Subsequently, the dead, 'subfossil' algal rim is bioeroded by endolithic photosynthetic and heterotrophic borers, and by grazers. (Fig. 8) (THIBAUT *et al.*, 2013; BLANFUNE *et al.*, 2016b; BOUDOURESQUE *et al.*, 2021a; FAIVRE *et al.*, 2021).

(iii) The seagrass *P. oceanica* meadow is mainly threatened by coastal development (ports, marinas, land reclaimed from the sea; Fig. 7), pollution (water quality, including from fish farms), trawling and anchoring of large yachts and cruise ships (SANCHEZ-LIZASO *et al.*, 1990; BOUDOURESQUE *et al.*, 2009, 2012; ALAMI *et al.*, 2014; GIAKOURI *et al.*, 2015; ABADIE *et al.*, 2016; DETER *et al.*, 2017; BOUDOURESQUE *et al.*, 2020;



Fig. 8 A dead, highly eroded, *Lithophyllum byssoides* rim, in 2014, at Punta Palazzu, Scàndula Nature Reserve, Corsica. Photo © Thierry Thibaut.

BLANCO-MURILLO *et al.*, 2022). Noise is an unexpected further cause of *P. oceanica* meadow alteration (SOLÉ *et al.*, 2021). At least along the northern EU coasts of the Mediterranean, the importance of pollution as a cause of *P. oceanica* decline is diminishing (JACKSON *et al.*, 2006). In some Mediterranean areas (e.g. Italian Liguria, French Riviera, Sardinia, Marseilles and Barcelona areas), the decline of *P. oceanica* has been conspicuous (MONTEFALCONE *et al.*, 2007; BOUDOURESQUE *et al.*, 2009; BURGOS *et al.*, 2017; DI MURO *et al.*, 2018); however, this is not the case for most of the Mediterranean, e.g. Provence (LERICHE *et al.*, 2006), Corsica (PASQUALINI, 1997; BONACORSI *et al.*, 2013) and Sicily; the decline may therefore have been

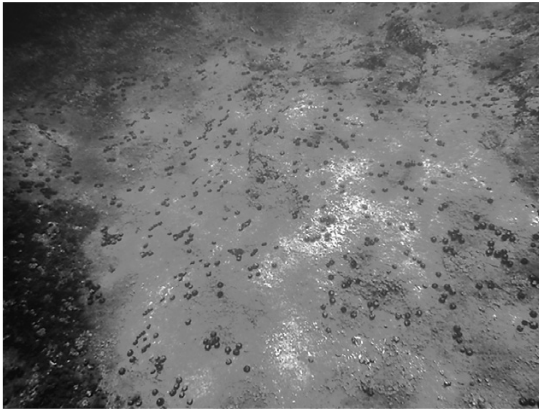


Fig. 9 A barren ground with the sea urchin *Paracentrotus lividus*, in an area formerly occupied by a fucal forest and ravaged by overfishing. Montenegro, 5–6 m depth. Photo © Thierry Thibaut.

overestimated (BOUDOURESQUE *et al.*, 2009; PERGENT-MARTINI *et al.*, 2013; BOUDOURESQUE *et al.*, 2021b). The estimates indicating that between 13% and 50% of the overall area of *P. oceanica* was lost during the last 50 years (MARBÀ *et al.*, 2014), and that the loss was about 6.9% per year, although possible at a very local scale, are totally unrealistic at Mediterranean-wide scale; less than 10%, maybe 5%, over the last 50 years, is probably a more realistic estimate (BOUDOURESQUE *et al.*, 2009, 2021b); a decline of 10% in total seagrass area by 1900 has been suggested (DUNIC *et al.*, 2021). In addition, the natural recolonization of *P. oceanica*, when stressors have ceased to work, has been observed in many areas (BOUDOURESQUE *et al.*, 2021b; BLANCO-MURILLO *et al.*, 2022); on the scale of the Mediterranean, the seagrass recolonization is conspicuous, the seagrass area returning to the supposed values of the 1920s (DUNIC *et al.*, 2021). As far as future sea water warming is concerned, it should cause a withdrawal, at the limit of the range area, in the warmest regions of the Levantine Basin, e.g. in Turkey, and an ad-

vance in the currently too cold regions of the northern Mediterranean. In the regions between the two, the effects are complex, e.g. an increase in the density of the shoots and a decrease in the width of the leaves (PANSINI *et al.*, 2021). In addition, the increase in temperature causes a decline in the primary production (PI) and rise of the deep lower limit, where PI is a limiting factor; the rise of the lower limit has been actually observed in Turkey (MAYOT *et al.*, 2005; MEINESZ, 2021).

(iv) The reef fucal forest is mainly threatened by the overgrazing of the sea urchins *Paracentrotus lividus* and *Arbacia lixula*; their proliferation results for the most from the overfishing of their fish predators; the forest is then replaced by a barren ground, which constitutes an alternative stable state in a regime shift context (Fig. 9) (SALA and ZABALA, 1996; BONAVIRI *et al.*, 2011; COMA *et al.*, 2011; FRASCHETTI *et al.*, 2011; AGNETTA *et al.*, 2015; LING *et al.*, 2015; BLANFUNE *et al.*, 2016a, 2016c; BOUDOURESQUE and VERLAQUE, 2020; BEVILACQUA *et al.*, 2021). In the eastern Mediterranean, the invasive rabbit fish *Siganus luridus* and *S. rivulatus* are responsible for the extirpation of the fucal forests (SALA *et al.*, 2011). The destruction of habitats due to coastal development has also played a role (FRASCHETTI *et al.*, 2011; THIBAUT *et al.*, 2015; ORFANIDIS *et al.*, 2021). Warming was suggested by ORLANDO-BONACA *et al.* (2021) in the northern Adriatic and by FALACE *et al.* (2021) in Sicily (Italy). Pollution, put forward in the 1970s–1980s, could have been overestimated as a cause of decline (BOUDOURESQUE, 2003; MANGIALAJO *et al.*, 2008; THIBAUT *et al.*, 2014). Natural recovery has been recorded in the northern Adriatic Sea (IVEŠA and DEVESCOVI, 2014).

(v) The coralligenous ecosystem is threatened by heat waves, which cause mass mortality of gorgonians, precious red coral, sponges and

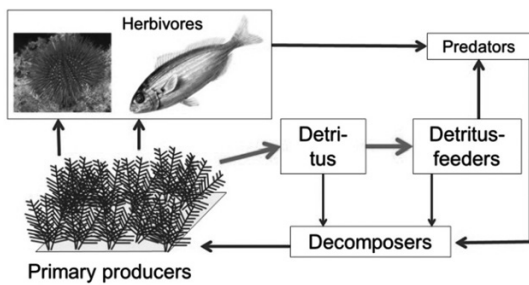


Fig. 10 A simplified sketch of food-webs in undisturbed Mediterranean marine benthic ecosystems. Here, a reef fuclean forest. Herbivores are the sea urchin *Paracentrotus lividus* and the teleost *Sarpa salpa*. The intensity of the flow is proportional to the width of the arrow between functional compartments (widest arrow: the main path). From BOUDOURESQUE *et al.* (2017a).

other metazoans (CERRANO *et al.*, 2000; PEREZ *et al.*, 2000; LINARES *et al.*, 2008a; BOUDOURESQUE *et al.*, 2017c; VERDURA *et al.*, 2019; CHIMIENTI *et al.*, 2021; GARRABOU *et al.*, 2021). There are synergistic effects between invasive species (e.g. the red alga *Womersleyella setacea*) and the warming, resulting in the drastic decline of crustose coralline algae (CEBRIAN *et al.*, 2021). The coralligenous is also threatened by over-frequentation by divers (LINARES *et al.*, 2008b; CASOLI *et al.*, 2017) and by fishing gear which uproot gorgonians, erect sponges and the Fucales *Sargassum* spp. and *Ericaria zosteroides* (THIBAUT *et al.*, 2016; GENNARO *et al.*, 2020; AZZOLA *et al.*, 2021; FERRIGNO *et al.*, 2021).

In addition to the five above-mentioned ecosystems, it is worth emphasizing the severe threats to ecosystems such as the vermetid platforms (GORDÓ-VILASECA *et al.*, 2021).

Undisturbed Mediterranean benthic ecosystems are characterized by a low level of herbivory; as a result, the food web is usually driven by the detritus-feeders rather than by the herbivores. Most macrophytes have not developed

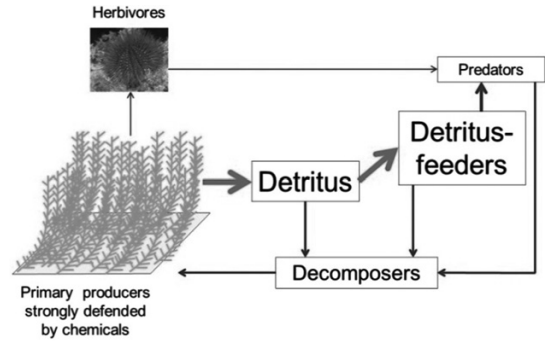


Fig. 11 A simplified sketch of a food-web in a Mediterranean benthic ecosystem, in the presence of non-palatable primary producers, here *Caulerpa taxifolia*. The possible increase in the DOC (Dissolved Organic Carbon) release towards the pelagic ecosystem is not considered here. The herbivore is *Paracentrotus lividus*. The intensity of the flow is proportional to the width of the arrow between functional compartments (widest arrow: the main path). From BOUDOURESQUE *et al.* (2017a).

chemical defences against herbivores (Fig. 10).

(i) In the north-western Mediterranean, the dramatic arrival of strongly defended and poorly palatable invasive species, such as *Caulerpa taxifolia* (Chlorobionta), *Asparagopsis armata*, *Lophocladia lallemandii* and *Womersleyella setacea* (Rhodobionta; kingdom Archaeplastida), has profoundly changed the functioning of the ecosystems, with a further reduction of the flow running through the herbivores being expected (Fig. 11; BOUDOURESQUE *et al.*, 1996, 2005a; RUITTON *et al.*, 2006; DEUDERO *et al.*, 2011; TOMAS *et al.*, 2011a, 2011b; BOUDOURESQUE *et al.*, 2017a).

(ii) In contrast, in the eastern Mediterranean, the arrival of voracious herbivorous teleosts (*Siganus luridus* and *S. rivulatus*) from the Red Sea, *via* the Suez Canal, has strongly intensified the herbivore pressure (Fig. 12) (GOLANI, 2002; GOLANI *et al.*, 2002; BOUDOURESQUE *et al.*, 2005a;

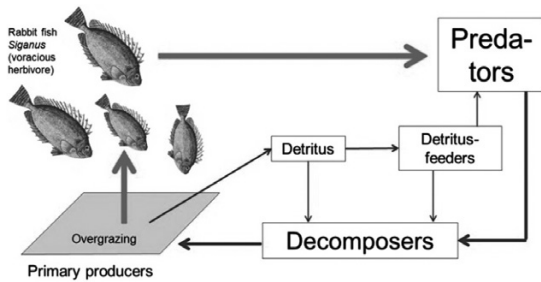


Fig. 12 A simplified sketch of a food-web in a Mediterranean benthic ecosystem, in the presence of herbivorous fish of the genus *Siganus* (eastern Mediterranean), here, a barren-ground. The intensity of the flow is proportional to the width of the arrow between functional compartments. widest arrow: the main path. From BOUDOURESQUE *et al.* (2017a).

AZZURO *et al.*, 2007; SHAKMAN *et al.*, 2009; BOUDOURESQUE, 2017a; CORALLES *et al.*, 2017; GALIL, 2017; DRAMAN, 2018). The arrival in the Levantine Basin of the voracious sea urchin, *Diadema setosum*, has further enhanced the herbivore compartment (YOKES and GALIL, 2006; KATSANEVAKIS *et al.*, 2014). The turnover of primary production is then faster than through the detritus-feeders, which has resulted in an increase in the secondary production of large carnivorous teleosts (GALIL, 2007). This has resulted in an impressive regime shift, from ecosystems dominated by canopy-forming primary producers and under bottom-up control, such as Fucales, to an Alternative Stable State (ASS) dominated by encrusting calcified coralines (red algae) and sometimes also characterized by sea urchin overgrazing (barren ground), with top-down control (SALA *et al.*, 2011, 2012).

(iii) Finally, in coastal lagoons harbouring shellfish farm facilities, on natural and artificial hard substrates, the dominance (species richness, cover, biomass) of macrophytes intro-

duced from the cold-temperate northern Pacific Ocean is overwhelming. In Thau Lagoon (Southern France), they represent 32% of the gamma species diversity, 97–99% and 48–95% of the spring and autumn biomass, respectively, and 100% of the cover (Fig. 13) (BOUDOURESQUE *et al.*, 2011). Similar observations have been reported in other Mediterranean lagoons, e.g. the Venice Lagoon (northern Adriatic Sea, Italy) (OCCHIPINTI-AMBROGI, 2000; SFRISO, A. and D. CUIEL, 2007; MARCHINI *et al.*, 2015) and Tunisian lagoons (OUNIFI BEN AMOR *et al.*, 2019).

## 5. Changing scapegoats

The general public, journalists, who often have literary rather than a scientific culture, and policy makers, need scapegoats, clearly identified enemies, and simplifications. These 'enemies' have evolved over time, and it is often the oversimplifying media that has shaped them. Even today, whether in a working-class district in the north of Marseilles, such as Estaque, or in a district inhabited by well-educated people, in London, a street survey, on the main threats to marine biodiversity collects the same answers, the order of which may vary: pollution, oil spills and climate change.

In the years 1950s-1960s, the world became aware of the serious consequences of the hundreds of atmospheric nuclear weapon tests carried out by the USA and the Soviets; a huge cloud of radioactive particles circled the northern hemisphere, with massive fallout on land and sea (SANCHEZ-CABEZA *et al.*, 2002; AOYAMA *et al.*, 2006). It was the Moscow Partial Nuclear Test Ban Treaty in 1963 that put an end to these atmospheric tests. It has taken several decades for the radioactive cloud to disappear, with radioactive fallout ending up in the soil and at sea (CALMET *et al.*, 1988). This radioactivity has had serious consequences for human health, although



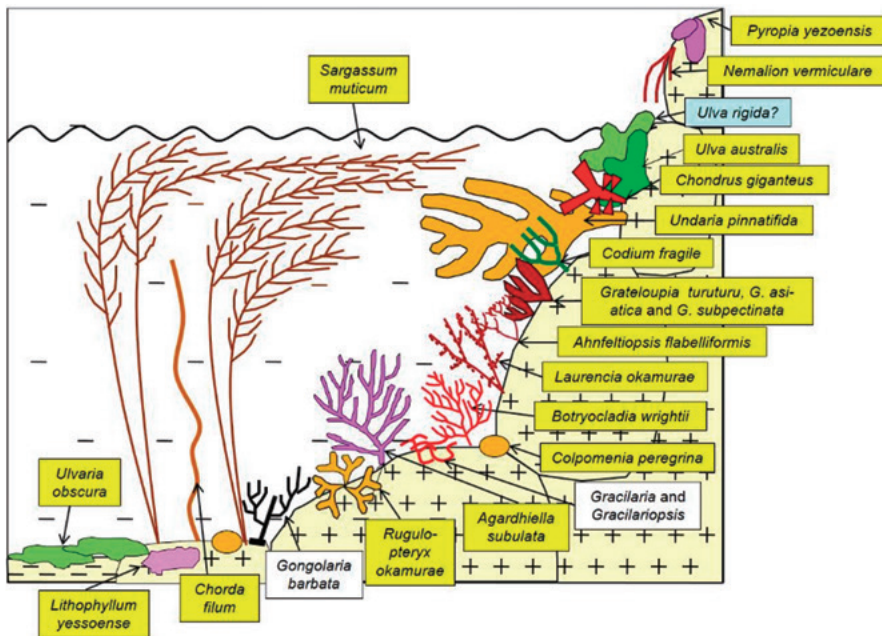


Fig. 13 A sketch of the dominant macrophytes on shallow (down to 1 m depth) rocky substrates of Thau Lagoon (Occitania, France) in spring. Most of these taxa (yellow boxes) are native to the northwestern Pacific Ocean. Blue box: a cryptogenic species, i.e. a species possibly introduced, but the native area of which is unknown. From BOUDOURESQUE *et al.* (2011), adapted.

little was known at the time. In the 1960s, any exceptional climatic event was attributed to nuclear tests: floods, storms, drought, etc.

In the 1970s-1980s, the general public became aware of the dangers of pollution. In those days, rivers (Rhône, Po, Ebro, etc.) had become open sewers; the large coastal cities (Marseilles, Barcelona, Naples, etc.) discharged their sewage into the sea without treatment. In Marseilles, it was in Cortiou, in the heart of what is now the Calanques National Park, that a colossal sewer dumped sewage. Pollution, in particular contamination by metals such as mercury and cadmium, has had serious consequences for human health. Organic pollution has also been responsible for profound changes in ecosystems; at Cortiou, in Marseilles, the halos of completely destroyed,

deeply modified, modified and sub-normal benthic stands around the outfall have been accurately described (BELLAN-SANTINI, 1966; COGNETTI and COGNETTI, 1992; BELLAN *et al.*, 1999). At that time, pollution was considered the main cause of all environmental issues, e.g. the decline of edible sea urchins (while pollution actually favors them - BOUDOURESQUE and VERLAQUE, 2020), the decline of *Posidonia oceanica* meadows (while pollution is far from being the main cause - BOUDOURESQUE *et al.*, 2009, 2012), the decline of the Fucale *Ericaria amentacea* (while actually it did not significantly decline - THIBAUT *et al.*, 2014), and the collapse of fish stocks (while overfishing is the main cause, in the Mediterranean as everywhere in the world - PAULY, 1988; GRÉMILLET, 2019).

Today, it is global warming that has become the 'one-size-fits-all' explanation for everything that is happening. It is indisputable that global warming, induced and accentuated by anthropogenic emissions of greenhouse gases, constitutes a severe threat to terrestrial and marine biodiversity; this threat is direct (increase in temperature, acidification of the ocean) but also indirect (rise in sea level) (NEUKOM *et al.*, 2019). Heat waves have been responsible for spectacular mass mortality of a variety of marine taxa, e.g. gorgonians, and the frequency and severity of mortality events are steadily increasing. In addition, species of warm affinities, formerly confined to, or more abundant in the warm waters of the south and east of the Mediterranean, such as the sea urchin *Arbacia lixula*, the teleost *Sparisoma cretense*, the sea turtle *Caretta caretta* and the seagrass *Cymodocea nodosa*, increase in abundance and/or extend their range northwards and westwards, resulting in the 'meridionalization' of the sea (FRANCOUR *et al.*, 1994; BIANCHI and MORRI, 2004; LEJEUSNE *et al.*, 2010; BIANCHI *et al.*, 2013; ASTRUCH *et al.*, 2016; BIANCHI *et al.*, 2018; ENCARNAÇÃO *et al.*, 2019; SBRAGAGLIA *et al.*, 2020; TUNCER *et al.*, 2020; ESPOSITO *et al.*, 2021; GIRARD *et al.*, 2021; MARX *et al.*, 2021; MEINESZ, 2021). Acidification potentially threatens calcified species, which represent a sixth of the Mediterranean species  $\epsilon$  diversity (MEINESZ, 2021), although its current and/or future impact seems complex, taxon-specific and controversial (BAGGINI *et al.*, 2014; FOO *et al.*, 2018; HALL-SPENCER *et al.*, 2018; KUMAR *et al.*, 2018; TEIXIDÓ *et al.*, 2018; MECCA *et al.*, 2020). But global warming cannot explain everything, from storms to collapsing marine resources and pelagic zooplankton functional diversity (see BENEDETTI *et al.*, 2018), and can be a scapegoat for other currently more severe human-related impacts.

Unexpectedly for the general public, at the start of the 21<sup>st</sup> century, by far the main impact on species diversity is the overexploitation of resources, in particular overfishing (PARSONS *et al.*, 1984; PAULY *et al.*, 2002; GRÉMILLET, 2019). Biological invasions (including host shift of parasites and pathogens) and coastal development, with irreversible destruction of coastal habitats, are also major drivers of change. Pollution comes almost second to last and warming last (Fig. 14) (MAXWELL *et al.*, 2016). In France (Occitania, Provence, French Riviera and Corsica), the total (100%) and irreversible destruction of coastal habitats concerns 5,300 ha, while the area provisionally and reversibly altered by more than 50% by pollution from wastewater treatment plants does not exceed 100 ha (MEINESZ, 2021). (i) If the Fucale *Sargassum vulgare* is regionally extinct in French Catalonia and functionally extinct in Western Provence and the French Riviera (Table 2; Thibaut *et al.*, 2005, 2015, 2016), this is obviously not due to warming, since it is a species of warm affinities, which would be expected to be in expansion, but to other reasons, such as overfishing and the resulting overgrazing. (ii) If the abundance of the invasive green alga *Caulerpa cylindracea* fluctuates strongly from one year to another, it is due to inter-annual variations in precipitation, wind speed and temperature; but, unexpectedly for some, the peaks of abundance do not correspond to the highest temperatures, but to the lowest temperatures (RAVAGLIOLI *et al.*, 2022). (iii) If the vermetid reefs in Israel (Levantine Basin) cannot resist the sea level rise, it is not due to the warming, the main ecosystem engineer *Dendropoma anguliferum* being a species of warm affinities, but to its local functional extinction and the tremendous grazing of invasive *Siganus* teleosts (RILOV *et al.*, 2021). (iv) If the dusky grouper *Epinephelus marginatus* is back in the

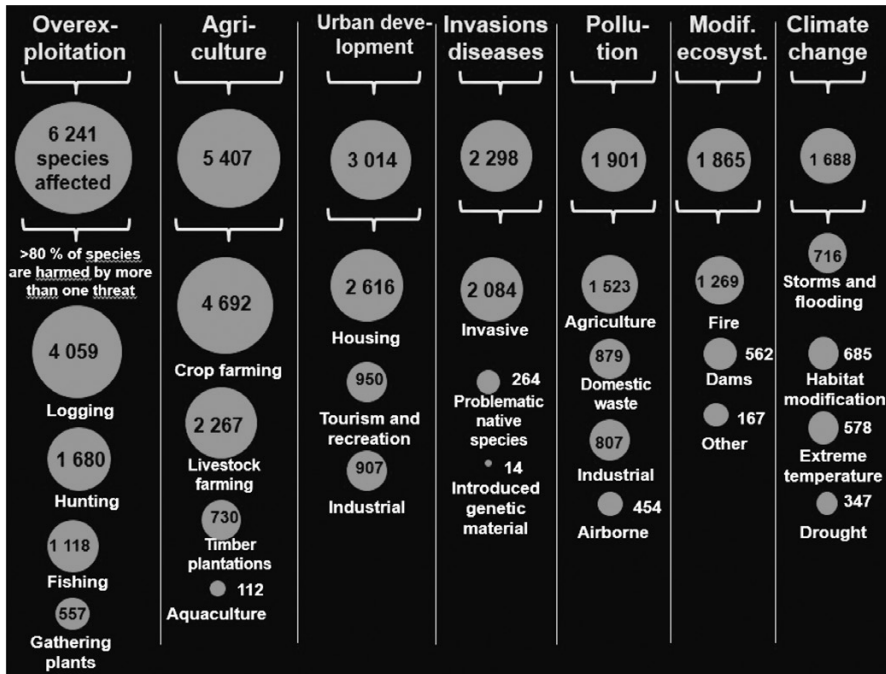


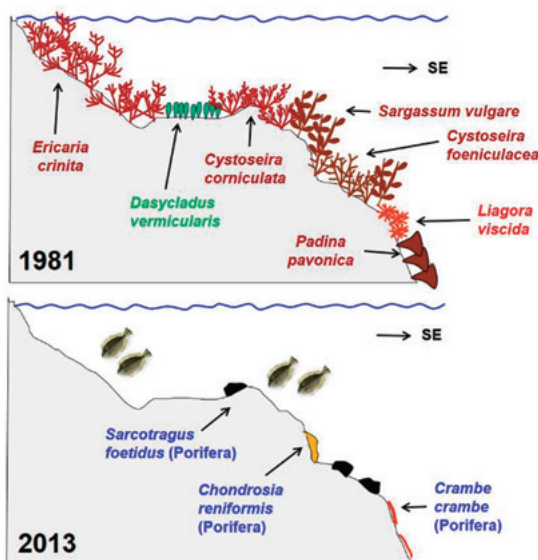
Fig. 14 Threats to species, according to the IUCN red list of threatened species. The values in the circles, or beside the circles, indicate the number of species affected by a stressor. From MAXWELL *et al.* (2016), adapted and redrawn (Charles-François Boudouresque).

northwestern Mediterranean, with even reproductive aggregations, it is less because of the sea warming, as naively claimed by DURAND (2018) and in an interested way by spearfishers, than thanks to the establishment of efficient MPAs; interestingly, the dusky grouper was very common in Provence during the cold episode of the 1950s (BOUDOURESQUE *et al.*, 2005b; HARMELIN-VIVIEN *et al.*, 2007; HARMELIN *et al.*, 2010; RUITTON *et al.*, 2019b). (v) If the number of introduced species is on the increase in the Mediterranean, this not solely due to the warming, which 'pushes' the Red Sea species range area, once introduced, westwards and northwards, but also and mainly to the vectors of introduction, first the Suez Canal and its enlargement, and second the farming of molluscs

from the northeastern Pacific (Japan and Korea); unexpectedly, by the 1980s, the percentage of newly introduced species from cold native areas has increased, at the expense of species native to tropical areas (BOUDOURESQUE *et al.*, 2010) (Table 3). At Kos Island (Greece, eastern Mediterranean), BIANCHI *et al.* (2014) compared benthic data collected in 1981 and in 2013, by the same persons and using the same method. During this 30+ year period, increases in Sea Surface Temperature (SST, +1–2°C), human pressure (resorts and hotels, 15 to 163 beds km<sup>-2</sup>), and NISs (e.g. rabbitfish *Siganus rivulatus* and *S. luridus*) were observed. Huge changes occurred in rocky reef habitats; the once flourishing fucalean forests (*Cystoseira* spp., *Ericaria crinita*, *Sargassum vulgare*) had disappeared in

**Table 3** Biogeographical affinities, in their native area, of the seaweed introduced to the Mediterranean. Tropical: annual SST minimum > 20°C. Temperate: annual SST minimum between 10°C and 20°C. Cold: annual SST minimum < 10°C. See LÜNING (1990) for definitions and SST maps. From BOUDOURESQUE and VERLAQUE (2010).

Period	Number of introduced species	Native area of introduced species		
		Cold areas (North and South)	Temperate areas (North and South)	Tropical areas
1800–1940	21	4.3 (20%)	7.7 (37%)	9.0 (43%)
1941–1980	39	7.7 (20%)	14.0 (36%)	17.3 (44%)
1981–2008	48	16.2 (35%)	17.9 (39%)	11.9 (26%)



**Fig. 15** Schematic profile of a reef slope down to about 7 m depth at Kos Island (Greece), illustrating the impressive change between 1981 (top) and 2013 (bottom). Names of brown algae (Phaeophyceae) are in brown, green algae (Chlorobionta) in green, red algae (Rhodobionta) in red and sponges (Porifera, Metazoa) in blue. The invasive fish is *Siganus luridus*. From BIANCHI *et al.* (2014), redrawn by Charles-François Boudouresque.

favour of sponges and wide bare substratum areas (Fig. 15). These changes can be seen as a synergistic action between biological invasions,

SST warming and human impact. More realistically, they show the crushing, by NISs (especially overgrazing rabbitfish), of the other stressors, including warming.

A general poleward range expansion of species of warm affinities is expected and has actually been recorded. The corresponding shrinkage in the Mediterranean range of some cold affinity species has been recorded, e.g. the mysid crustacean *Hemimysis speluncola*, which is being replaced by *H. margalefi* (CHEVALDONNÉ and LEJEUSNE, 2003). However, this is not yet observed for most species, e.g. the seagrass *Zostera marina* and the teleost *Sprattus sprattus* (BOUDOURESQUE *et al.*, 2009; PERGENT *et al.*, 2012; SARAUX *et al.*, 2019).

## 6. Discussion and conclusion

The concern about the growing and irreversible effects of global warming is totally justified (HOEGH-GULDBERG *et al.*, 2019); as also the effects of pollution, although in decline. But the underestimation of other threats is based on reasons which may be political or related to human perceptions, in some cases to science funding, and which are discussed hereafter. The general public and policymakers are above all sensitive to what can be seen (e.g. television reports). The (exaggerated?) importance accorded to oil spills

is an illustration of this (BOUDOURESQUE *et al.*, 2019a; MEINESZ, 2021). There is a *doxa* (consensual discourse) from which it is difficult to deviate (HUET, 2018a, 2018b).

Let us consider the blatant exaggerations first. WAYCOTT *et al.* (2009) stressed the worldwide acceleration of seagrass decline from 1% per year before 1940, 1–7% per year between 1940 and 1990 to 7% per year since 1990. Although the authors clearly warned that these estimates were based on data available at the time, from a limited number of regions of the world ocean, and reported the geographical and historical bias in their dataset, some later authors cited this article without reference to these caveats. This article, which is the most widely cited in the seagrass world literature, as simplified by further authors, typically announces the apocalypse. In the Mediterranean, MARBÀ *et al.* (2014) claimed that between 13% and 50% of the *Posidonia oceanica* seagrass extent appears to be lost, and that 6.9% of the potential *P. oceanica* vegetation has been lost annually over the last 50 years. Yet, a very simple mathematical model which any student could perform indicates that, if these estimates and predictions were correct, there would be hardly any seagrass meadows left in the world today, and no *P. oceanica* meadow left in the Mediterranean, which is clearly not the case (BOUDOURESQUE *et al.*, 2009, 2012; CALVO *et al.*, 2020; BOUDOURESQUE *et al.*, 2021b). The physicist John Holdren wrote in 1978 that it is conceivable that before 2020, a CO<sub>2</sub>/climate-induced famine could kill as many as a billion people (*in* EHRlich and EHRlich, 1981); this apparently has not happened.

The positive side of these exaggerations must also be taken into account. They may have helped alert the general public and decision-makers to the risks. We can also consider that, if the forecasts did not come true, it is precisely

thanks to these alerts. Moreover, it is easy, long afterwards, to mock erroneous forecasts: this is a risk intrinsic to any forecast, and our conclusions in the present paper will not avoid this risk.

As BOERO (2015) and DUARTE *et al.* (2015) suggested, it is easier to publish in high IF (Impact Factor) journals if you announce the apocalypse than if you describe moderate changes. Deviation from the current mainstream is poorly accepted by journals: you can publish anything if you write that seagrasses are in steep decline and that global warming or acidification are involved; you need a rock solid argument to go against the grain. One of the authors of this article (CFB) has experienced this difficulty twice, when he showed, on the basis of accurate data, that (i) the regression of seagrasses (all species combined) in the Mediterranean was much more moderate than announced (BOUDOURESQUE *et al.*, 2009), and that (ii) in a bay of mainland France (Saint-Cyr, Provence), despite urbanization, pollution, the construction of harbours, etc., the regression of *Posidonia oceanica* had been much less significant than expected (LERICHE *et al.*, 2006). One of the reviewers wrote: '*Even if your data is reliable, you can't write this! It would be too good news for the developers who are building all along the coast!*'

Secondly, for the marine environment, there are no pressure groups comparable to amateur ornithologists, or to natural history societies (botanists, entomologists, bat specialists, etc.), capable of bringing the problems before public opinion and before the authorities. Seabirds, sea turtles and marine mammals are the exception that proves the rule: the pressure groups that support them constitute the extension of a terrestrial 'culture'. The authorities are first and foremost sensitive to what we are talking about (in the media in particular). The (sometimes

exaggerated) importance given to the protection of certain marine mammals is an illustration of this. Even respectable NGOs such as WWF and IUCN, dominated by ornithologists and mammalogists and (it must be noted), sometimes promoting a simplistic vision of biodiversity (e.g. how many marine mammals, on the increase or on the decline?), have more or less completely forgotten the marine environment and its real biodiversity, which is far from being limited to seabirds, sea turtles and marine mammals. It is quite astonishing that some marine species, 1,000 to 10,000 times rarer than terrestrial protected species, which have disappeared from a number of regions and are on the brink of extinction elsewhere, like a marine equivalent of the giant panda, do not benefit from any legal protection status in most of the 21 Mediterranean countries. The cases of the brown algae (Fucales, Stramenopiles) *Sargassum acinarium* and *S. hornschuchii* exemplify this situation, almost to the point of caricature; this is what THIBAUT *et al.* (2016) referred to as 'the *Sargassum conundrum*'. Despite the bulk of scientific data concerning some marine species, on the brink of extinction, but unfortunately not relating to sea birds, sea turtles and sea mammals, the IUCN Red List places them in the 'trash category' of 'Data Deficient (DD)' (BOUDOURESQUE, 2002; BOUDOURESQUE and BIANCHI, 2013; VERLAQUE *et al.*, 2019). The media generally play a negative role, as shown by COMPAS *et al.* (2007) on an MPA project in Australia; they give priority to the opponents, who, even when they do not dispute the project, criticize the 'lack of consultation' (even if it has lasted for years) and the location of the NTZ (No Take Zone within the MPA).

Thirdly, public sensitivity is selective. Some species are lovable in themselves, at least nowadays: dolphins, seals, grouper. Others are much

less so: sharks, annelids, etc. (LAUREC, 1997; FAGET, 2020; ALESSANDRI, 2021). The breathtaking beauty of the orange stony coral *Astroides calycularis* can explain why it is listed in the annexes of the Bern and Barcelona conventions, while actually far from being threatened (LEDoux *et al.*, 2021). This sensitivity also varies from one region to another: seals attract more sympathy in the countries of southern Europe, where they are rare or absent, than in the North, where they are sometimes considered as invasive (LAUREC, 1997). The public can be self-interested, even hypocritical: they sometimes designate as 'ecology' and 'biodiversity' the simple defence of a privilege of enjoyment and/or the search for the payment of damages; this syndrome is called NIMBY (Not In My Backyard) (GOBERT, 2015; MEINESZ, 2021). Research effort is also selective: vertebrates, which barely represent 3% of species, are the subject of 69% of publications devoted to conservation (CLARK and MAY, 2002). Some 46% of the EU 'Life' funded projects dealt with bird species, versus 8% concerning invertebrates, at least functionally as important as birds and more than 100 times more numerous, and less than 0.01% macroalgae (MAMMIDES, 2019). On a larger scientific scale, in the era of biodiversity launched by the Rio summit in 1992, many scientists consider that the concept of biodiversity has been 'stolen', diverted from its true meaning, by some sort of 'merchants', who openly pursue commercial objectives or belong to disciplines other than ecology. Contrary to what the general public believes, the bulk of funding goes to researchers who do not have extensive knowledge (or none at all) of biology and ecology, but who put forward techniques or concepts, for example modelling, which are appealing to decision-makers (BOERO, 2010, 2015). As stressed by BOERO (2016), '*the risk of reductionism is to produce a lot of knowledge*

*about nothing, and that of holism is to produce a little knowledge about everything*'. A balance between taxonomy and disciplines such as modeling and genetics, both essential, is necessary (GUIDETTI *et al.*, 2014).

Fourthly, for many policymakers, the destruction of the seabed due to coastal urbanization is too simple a cause. A basic calculation makes it possible to determine the lost surface area. We know the depth of the corresponding habitats, and the ecosystems that occupied them, or most likely occupied them. Policymakers often prefer complexity (sometimes simply flamboyant), perhaps because complexity allows for wait-and-see, or a 'headlong rush' into scientific research (MEINESZ, 2021).

Fifth, a perverse effect of a 'total-warming' approach is that we somehow feel helpless in the face of a planetary phenomenon that would require an international response and that irresponsible lunatics in Australia, Brazil, the US and elsewhere continue to deny. What can the individual human actually do? It is then convenient for some managers and policymakers to attribute everything to climate change, and not to causes closer to home, against which it would be possible to intervene, e.g. overfishing, biological invasions and coastal development, but to which one does not wish to draw attention. When they are lucky enough to have a universal scapegoat, some policy makers take advantage of it!

Finally, Marine Protected Areas (MPAs) are a powerful response to biodiversity erosion and to adaptation to warming, in the Mediterranean Sea as everywhere in the world. As stressed by Daniel Pauly (pers. comm.), from the University of British Columbia (Vancouver, Canada), depleted populations of overfished areas cannot evolve in response to warming, in contrast to healthy populations thriving within MPAs. MPAs are therefore the best tool and response

to climate warming. Unfortunately, most Mediterranean MPAs are paper parks (fictitious protected areas: lines on an official map without park wardens, management plans, scientific council or even a park director) or mist parks (protected areas intended to fulfill the international commitments of countries; they are often immense, have a real existence - director, premises, officials -, but do not implement any real management measures involving, where necessary, constraints for some of the users) (MEINESZ and BLANFUNE, 2015; BOUDOURESQUE *et al.*, 2017b, 2019b, 2021a).

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