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Ecosystem dynamics and trophic cascades in shallow rocky reefs under different protection regimes.
A case study from the Mediterranean marine protected area of Tavolara-Punta Coda Cavallo

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Abstract

Marine Protected Areas (MPAs) are largely considered effective management tools to foster the recovery of overexploited population. The broad question underlying this analysis is whether MPAs can be effective in reversing negative ecosystem-wide consequences of excessive fishing pressure on sea urchin predators (*e.g., Diplodus* spp.) in shallow rocky reefs. Indeed, when their populations are depleted by overfishing, they fail to exert a control upon sea urchins, which are allowed to thrive and grow in density. In many Mediterranean sites, this has resulted into excessive grazing pressure of sea urchins on erect macroalgal species, ultimately causing the depletion of underwater forests and the ensuing loss of ecosystem services. This cause-effect chain linking predators, sea urchins and macroalgae is an example of trophic cascade. In this work, we analyse the effects of protection on populations of sea urchin predators in the MPA of Tavolara – Punta Coda Cavallo (Sardinia, Italy), from 2005 to 2021. Overall, our results highlight rather rapid and long-lasting effects of full protection on density, biomass and size of the analysed species. Partially protected zones did not differ from unprotected ones when data were expressed in terms of density, while some small but statistically significant difference was observed when biomass data were used. Estimated mortality rates for commercially important species are significatively higher in unprotected zones than in fully protected ones, further confirming the efficacy of protection. In the analysed reserve, predator densities reached under full protection regime are considered sufficient to control sea urchin populations. Hence, there are chances for positive effects of protection to extend to macroalgal forests, although further field research is needed to support this hypothesis.

Sommario

Le aree marine protette (AMP) sono ampiamente considerate degli strumenti di gestione efficaci nel supportare il recupero di popolazioni sovrasfruttate. La questione fondamentale da cui prende le mosse questa analisi è la valutazione del potenziale delle AMP nel riparare le conseguenze negative su scala ecosistemica dell'eccessiva pressione di pesca sui predatori dei ricci (es., *Diplodus* spp.) nei fondali marini rocciosi superficiali. Se sovrasfruttate da operazioni di pesca, queste popolazioni non riescono più ad esercitare un controllo di predazione efficace sulle popolazioni di riccio di mare, a cui viene quindi concesso di espandersi. In molti siti nel mar Mediterraneo, questo processo ha condotto ad una eccessiva pressione di pascolo da parte dei ricci su alcune specie di alghe erette, causando così una riduzione delle foreste sottomarine e la conseguente perdita di servizi ecosistemici. Questa catena di relazioni causa-effetto che unisce predatori, ricci di mare e alghe è un esempio di cascata trofica. In questo lavoro analizziamo gli effetti della protezione sui predatori dei ricci di mare nell'AMP di Tavolara – Punta Coda Cavallo (Sardegna), dal 2005 al 2021. Nel complesso, i risultati evidenziano come la protezione integrale abbia consentito una ripresa piuttosto rapida e dagli effetti duraturi delle popolazioni prese in esame, in termini di densità, biomassa e taglie. Le zone a protezione parziale, invece, non presentano differenze sostanziali rispetto alle aree non protette in termini di densità, mentre alcune differenze piccole ma statisticamente significative sono osservabili in termini di biomassa. I tassi di mortalità stimati per le specie ad alto valore commerciale risultano molto maggiori nelle aree non protette rispetto a quelle a protezione integrale, confermando ulteriormente l'efficacia della protezione. Nella AMP analizzata, le densità di predatori raggiunte in regime di protezione integrale sono considerate sufficienti a garantire il controllo delle popolazioni di riccio di mare. C'è quindi la possibilità che gli effetti positivi della protezione si estendano alle foreste di macroalghe, sebbene ulteriori analisi sperimentali siano richieste per confermare questa ipotesi.

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List of Acronyms

MPA   Marine Protected Area

TMPA   Tavolara – Punta Coda Cavallo Marine Protected Area

UVC   Underwater Visual Census

INTRODUCTION

The world's oceans are vital organs to the Earth system. Not only they teem with life, holding 80% of biodiversity on this planet (European Union, 2021) but they also support the existence other life forms on land. The humankind itself highly relies on oceans, exploiting its climate regulatory actions, the nutritional sources it provides and the income it guarantees. Despite its ecological, social and economic importance, oceans health is nowadays jeopardised by several well-known anthropic stressors, such as pollution, rise in seawater temperature provoked by climate change, acidification and overfishing. Global fisheries production has multiplied almost 12 times over the last seven decades to reach 213 million tonnes in 2019 (FAO, 2022b), causing 35% of fish stocks globally to be fished beyond sustainable levels (FAO, 2022a). This situation calls for urgent conservation action, that is reflected in international guidelines and targets, such as UN Sustainable Development Goal 14 (life below water) and the goal of protecting at least 30% of the world's oceans by 2030, set during UN COP15.

In the Mediterranean Sea, the situation is even more compromised due to centuries of intense exploitation of fishery resources. In 2018, 75% of stocks were fished beyond biologically sustainable levels (FAO, 2020), with only 0.23% of Mediterranean Sea falling under integral protection regimes (Claudet et al., 2020).

One of the most valuable and yet threatened ecosystems in the Mediterranean basin is that of macroalgal forests growing on temperate rocky reefs, which is included in the European red list of endangered habitats (European Commission, 2016). Flourishing macroalgal beds are characteristic of healthy rocky reefs providing a wide array of ecosystem functions (*e.g.*, food source, refuge, spawning and nursery grounds) that are of paramount importance to all taxa living in this habitat. Unfortunately, the long-term viability of forests is currently threatened and, in several Mediterranean sites, macroalgal-dominated patches are being replaced by bare rocky beds (known as "barrens") or by less complex algal assemblages, with negative repercussions on the whole ecosystem. Often, creation and maintenance of barrens are ascribable to excessive grazing pressure exerted by herbivores – chiefly sea urchins – feeding upon macroalgae. In turn, high densities of sea urchins are caused by the scarcity of their predators in the ecosystems, whose populations are depleted because of overfishing. Mechanisms of this kind, linking multiple levels of the trophic chain with cause-effect relationships are called trophic cascades. In this context, it appears evident

that overfishing can cause major ecological alterations, affecting not only populations of target species but also lower interconnected trophic levels. Therefore, preserving and recovering stocks of sea urchin predators (*e.g.*, through the establishment of marine protected areas) may be crucial for maintaining or restoring healthy ecosystem states, with beneficial effects extending down to the level of primary producers.

The aim of this work is exploring whether and under what management conditions marine protected areas have the potential of recovering sea urchin predator populations depleted by overfishing. We do so by analysing the temporal evolution of some key fish species inhabiting shallow rocky reefs of the marine protected area of Tavolara – Punta Coda Cavallo (Sardinia, Italy) and by comparing estimates of mortality rates between protected and unprotected areas. Our assessment involves statistical analyses of exceptionally long high-quality time series, covering a period of 17 years (from 2005 to 2021). Data were kindly provided by researchers Paolo Guidetti, Antonio di Franco and their research team.

To the best of our knowledge, no previous study has followed the evolution of protection effects in this reserve for longer than three years. With this work, therefore, we also provide an updated dynamic picture of the state of shallow rocky reefs in this reserve.

Chapter 1 introduces shallow rocky reefs ecosystems, outlining current threats to macroalgal forests and focussing on the predators-urchins-algae trophic cascade. Chapter 2 gives an overview of existing evidence of ecosystem restoration in protected Mediterranean rocky reefs and presents the case study of Tavolara – Punta Coda Cavallo marine protected area (TMPA). Chapter 3 quantifies the significance of the effects of protection on density and biomass of fish species applying the statistical techniques of multiple linear regressions and ANCOVA, while in Chapter 4 different protection regimes are compared in light of fish mortality estimates. Finally, future perspectives for expanding this work are discussed.

Statistical analyses and graphs presented in this work were obtained through the software R (R Core Team, 2022), while maps were drawn in ESRI ArcGIS®.

1. Shallow Mediterranean rocky reef ecosystems

1.1 Structure and dynamics

In the Mediterranean Sea, rocky beds hold a fundamental role in guaranteeing coastal ecosystems functioning. More than half of the Mediterranean coasts consists of rocky formations (Furlani et al., 2014) which support the existence of a great variety of habitats, including horizontal or sloped platforms, plunging cliffs, macroalgal forests, submarine caves and other kinds of bioconstructions (Bevilacqua et al., 2021). These very heterogeneous structures provide home and resources to a wide array of benthic, demersal and pelagic species, making Mediterranean rocky reefs a highly diverse and dynamic system.

The spatial distribution of assemblages in this ecosystem varies according to many parameters, such as light and food availability, water movement, water temperature and human disturbance intensity. Remarkable differences in terms of dominant benthic organisms can be observed between the intertidal and the sublittoral zones of the continental shelf, where the former is the portion comprised between high and low tide marks and the latter is the portion below the intertidal zone down to the edge of the continental shelf (*A Dictionary of Environment and Conservation*, 2007).

The intertidal zone is only periodically submerged, hence colonising organisms show a certain tolerance to desiccation and hydrodynamic disturbances. In a microtidal sea such as the Mediterranean, with a vertical tidal range of about 40 cm (Furlani et al., 2014) this fringe is typically very narrow. Its upper part is dominated by barnacles and littorinids while deeper intertidal areas may host erect, encrusting and red turf algae (Bevilacqua et al., 2021) (see Section 1.3.1 for a description of these three types of macroalgae). The shallower sublittoral areas are usually algal dominated. Here, stands of brown algae of the order Fucales are typically present down to approximatively 2 m depth, although in the best-preserved sites they can extend further to the deeper zones, where other orders such as Sphacelariales and Dictyotales (brown algae), Gigartinales and Bryopsidales (green and red algae respectively) may be found as well (Bevilacqua et al., 2021).

The presence of prosperous macroalgal beds in sublittoral zones is often symptomatic of a rocky reef ecosystem in a good state (Guidetti, 2006b; Sala et al., 2012; Thibaut et al., 2017) and is generally associated with high primary production of macroalgae (see Section 1.3.1), ecosystem complexity and biological diversity (Pinna et al., 2020). Indeed, macroalgal beds can provide nursery, refuge and resources to many vertebrate and invertebrate species (Blanfuné et al., 2016; Thiriet et al., 2016) contributing from the bottom of the trophic chain to the dynamism and functionality of the entire ecosystem. However, it is well known that, in temperate rocky reefs, macroalgal forests often alternate in space and time with patches of less complex habitats dominated by turf-forming or encrusting algae, which lend to shallow Mediterranean rocky reefs a typical mosaic-like structure. Crusts-dominated zones and denuded rocky beds are typically called "barrens" in the literature, with reference to their lower biological complexity with respect to forests. (Bulleri et al., 2002; Guidetti, 2006b; Sala et al., 1998; Thiriet et al., 2016). Barrens represent an extremely degraded state of macroalgal forests and turf-dominated beds (Figure 1.1), where ecosystem complexity, primary production and biodiversity reach very low levels (Pinna et al., 2020; Sala et al., 1998). Mechanisms underlying the shift between forests and barrens, as well as its ecosystem-wide implications are at the heart of this work and will be extensively discussed in Sections 1.2. and 1.3.
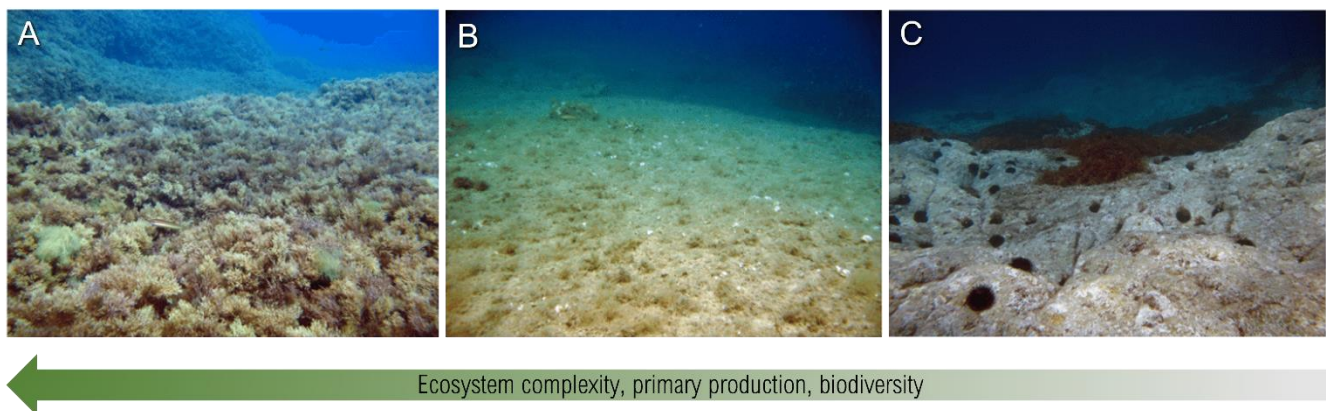
Figure 1.1: Possible alternative configurations of shallow Mediterranean rocky reefs, with different levels of ecosystem complexity, primary production and biodiversity. **A.** Macroalgal forests, **B.** Seabed dominated by turf-forming algae, **C.** barren ground. *Photo credits:* Thiriet et al. (2016).

1.2 THREATS TO MACROALGAL FORESTS AND FUTURE CHALLENGES

In the last decades, a general decline in forests-forming macroalgae – such as Fucoids – has been registered throughout Mediterranean shallow rocky reefs. The degradation is ascribable to many different stressors. Their combined action has driven the decision of the European Commission to

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include Mediterranean macroalgal forests within the European Red List of Habitat, classifying their status as "endangered" (European Commission, 2016). In this section, we summarize the most relevant stressors leading to the degradation of macroalgal forests, whose last stage is represented by barren grounds. We do not claim to be exhaustive, as cause-effect relationships in ecosystem processes are often highly complex and not easily generalisable. It is important to underline that stressors are not always constantly present, or do not necessarily act simultaneously: therefore, restoration and management actions, to be successful, need to be site-specific. Restoration and management will be discussed in Section 2.1.

1.2.1 POLLUTION AND COASTAL DEVELOPMENT

Coastal zones of the Mediterranean basin are heavily burdened by increasing urbanisation patterns and over-intrusive, unsustainable touristic models, which result into several sources of marine pollution. Indeed, near-coasts marine communities receive contaminated water inputs from various origins, such as agricultural and industrial activities, urban runoff and civil sewages. Pollution can profoundly alter shallow rocky reefs communities in various ways. Inorganic pollutants can accumulate into macroalgae and fish tissues and be transmitted to upper levels along the trophic chain at ever-greater concentrations (*i.e.*, biomagnification). In many Mediterranean sites, both organic and inorganic pollution represent a threat for several macroalgal species of the order Fucales. In particular, Sales et al. (2011) demonstrated that high levels of inorganic pollutants (*e.g.*, heavy metals) can reduce survival and growth of some species of the genus *Cystoseira*. Furthermore, de Caralt et al., (2020) showed that low but constant concentrations of both organic (*e.g.*, nitrates) and inorganic pollutants can have negligible effects on adults of *Cystoseira crinita* but cause severe adverse effects on survival and growth of recruits, ultimately jeopardising long-term population viability.

A further consequence of pollution on macroalgal forests can be mediated by sea urchins. The sea urchin *Paracentrotus lividus* can withstand high concentrations of heavy metals and as discussed in Section 1.3.2, its development can be enhanced by the presence of organic pollutants in the water column (Klaoudatos et al., 2022), which can be absorbed by its porous spines. This characteristic lends *P. lividus* the possibility of resisting also in situations where primary production of macroalgae is low (Thibaut et al., 2017). Altogether, these factors potentially cause *P. lividus* to thrive despite - or thanks to - water pollution and increase its grazing damages on already scarce macroalgae.

1.2.2 BIOINVASIONS

The number of non-indigenous species introduced either intentionally or accidentally in Mediterranean waters has been continuously increasing in the last decades (Bevilacqua et al., 2021) and some of them have become invasive, to the detriment of several ecosystems. This is the case of the herbivorous rabbitfish *Siganus luridus* and *Siganus rivulatus*¸which have entered the Mediterranean basin through the Suez Canal in the first half of the last century and, since then, have been expanding towards western areas (Gianni et al., 2017; Sala et al., 2011). As discussed in Section 1.3.2, in Mediterranean shallow rocky reefs these species are progressively replacing the native salema *Sarpa salpa* or they co-occur with it, in both cases enhancing herbivory pressure on macroalgae. *Siganus* fish graze with higher intensity with respect to *S. salpa* and seem able to induce strong algal losses alone, to the extent of creating barrens (Sala et al., 2012). Rabbitfish-created barrens have been observed by Sala et al. (2011) along the Mediterranean coasts of Turkey. During their field experiments, sea urchins were not detected, showing that barrens can also be created and maintained by other herbivores. Authors also suggest that a targeted fishery on *Siganus* fish may reduce their pressure upon algae.

Invasive alien species are present in the algal compartment as well. An outstanding example is the erect algae *Caulerpa cylindracea*, which shows a high invasive potential to the detriment of native species. There seems to be a reciprocal facilitative relationship between *C. cylindracea* and algal turfs: *C. cylindracea* often establishes following erect macroalgae regression and can co-occur with some turf-forming species, which provide a suitable substrate for the anchoring of *C. cylindracea*. The latter, in turn, was found to favour the permanence of turf algae and to prevent the re-growth of native erect species (Piazzi et al., 2016). Therefore, *C. cylindracea* appears to stabilise temporary deviations, due to environmental disturbances, from complex assemblages to some degraded forms, thus hampering the restoration of macroalgal canopies.

C. cylindracea also produces metabolites that are toxic for some native species. *Sarpa salpa*, *Diplodus sargus* and *Diplodus vulgaris* feed on this algae despite its toxicity, experiencing, as a result, some physiological alterations such as an increase in mortality and a decrease in reproductive potential (Bevilacqua et al., 2021). As already recalled, a decrease in fish predators of sea urchins can lead to further algal decline.

1.2.3 CLIMATE CHANGE

The Mediterranean region has been defined as a primary hot spot for climate change (Pastor et al., 2020), implying that climate change impacts are more pronounced in this region than elsewhere: indeed, seawater temperature is projected to rise 3-6 times faster than in global oceans (Bevilacqua et al., 2021). It is estimated by Pastor et al. (2020) that seawater in Eastern Mediterranean regions rose with a trend of +0.040 °C/y between 1982 and 2016, faster than in Western and Central ones - whose warming rates were +0.035 °C/y and +0.031 °C/y respectively.
The Mediterranean Sea is also a biodiversity hotspot, being home to 4-18% of world's marine biodiversity (United Nations, 2017): taking this into account, it appears evident that the extent of ecosystem value losses due to climate change is potentially very large.

Shallow Mediterranean coastal zones hosting stands of erect macroalgae (see Section 1.3.1) are among the most sensitive Mediterranean ecosystems to climate change effects, as observed by European Commission, (2016). Seawater temperature rise can reduce recruitment success of some canopy-forming species of the genus *Cystoseira*, such as *C. compressa*. Ocean acidification, due to the uptake of carbon dioxide from the atmosphere, was found to worsen the issue by favouring the establishment of other carbon-limited competitors such as turf algae, thus preventing overgrowth by erect species (Monserrat et al., 2022). Increasing sea water temperatures can also enhance sea urchin growth, reproduction and grazing intensity upon algae (Roma et al., 2021), thus further increasing the destructive action of sea urchins towards algal forests.
Water warming has effects on higher levels of the trophic chain as well. For instance, in Mediterranean Sea, it was found to induce a general, assemblage-wide, decline in fish larval stage duration, up to 25% (Raventos et al., 2021). The longer the time spent by fish in the larval stage, the higher their probability of settling further from the spawning area and thus the connectivity across metapopulations. Larval stage duration is indeed used as a proxy for the dispersal potential of species (Giacalone et al., 2022): its reduction implies that fish populations are likely to be increasingly isolated as water warms.

Climate change is a global phenomenon that clearly requires international policy-making effort to be stemmed. However, while working on global-scale solutions, it is important not to overlook conservation and restoration actions of a more local nature, as they have the great potential of preserving or even increasing the biological richness of marine and terrestrial ecosystems.

1.2.4 OVERFISHING

Since ancient times, fisheries in the Mediterranean basin have been crucial for sustaining local populations. Unfortunately, the economic and nutritional reliance on marine resources has led to an overexploitation of fish populations: it was estimated that, as of 2018, in the Mediterranean and Black Sea area 75% of stocks were fished beyond biologically sustainable levels (FAO, 2020). [1]

Both recreational and professional fisheries are particularly detrimental to fish populations as they selectively target large-sized individuals, namely those with the highest reproductive potential (Giakoumi et al., 2012; Guidetti et al., 2014). However, overfishing not only affects target species but also all the other trophic groups indirectly. For this reason, it is recognised as one of the major causes of alterations on an ecosystem scale (Sala, 2004).

One of the most significative examples of fishing-induced ecosystem alterations in Mediterranean shallow rocky reefs is the formation of barrens in areas that were previously dominated by erect macroalgal stands forming underwater forests (Guidetti, 2006b). As already stated, in the last decades, losses of these forests have been reported for multiple sites throughout the Mediterranean Sea. Despite several stressors can trigger the formation of barrens, many studies postulate the existence of a trophic cascade mechanism (Guidetti, 2006a; Sala et al., 1998 and references therein; Thibaut et al., 2005), according to which intense fishing upon predators of herbivores can cause an increase in herbivores densities – mainly sea urchins – which ultimately leads to a decline in macroalgal stands. Among the main herbivores which graze on erect macroalgae a key role is played by the sea urchins *Paracentrotus lividus* and *Arbacia lixula*, while among predators of grazers in shallow rocky reefs, a prominent role is played by *Diplodus* spp., *Coris julis* and *Thalassoma pavo*. *Diplodus* fish have a high commercial value and appear in both recreational and professional fishing catches (Thibaut et al., 2005), while the two wrasses (*C. julis* and *T.pavo*) are mainly exploited for recreational purposes (Froese & Pauly, 2023; Milazzo et al., 2016). Thus, overfishing of these species affects the formation of barrens through the trophic cascade fish-urchins-algae. The next section explores the features and dynamics of this trophic cascade.

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[1] According to FAO, unsustainable fishing levels are those exceeding the Maximum Sustainable Yield (MSY) threshold, defined as *"The greatest average amount of catch that can be harvested in the long-term from a stock under constant and current environmental conditions without affecting the long-term productivity of the stock"* (FAO term portal, accessed 25/03/2023 - https://www.fao.org/faoterm/en/?defaultCollId=21).

1.3 TROPHIC CASCADE FISH-URCHINS-ALGAE

One of the most relevant factors driving the loss of algal cover in the Mediterranean shallow sublittoral zone is the intense grazing activity of some herbivorous species, when present at high densities (Sala et al., 1998; Blanfuné et al., 2016; Thiriet et al., 2016). Among the several species of herbivores in rocky reefs, sea urchins are recognised to be the most effective grazers in triggering barren formation (Guidetti, 2006b; Thibaut et al., 2017), despite other species such as the native fish *Sarpa salpa* and the non-indigenous *Siganus* spp. can exert significant additional grazing pressure (E. Di Franco et al., 2021). In many cases, in the Mediterranean Sea, the expansion of sea urchins has been ascribed to a scarce predatory pressure upon them (Guidetti, 2006b; Sala et al., 1998; Thibaut et al., 2005), thus validating the trophic cascade hypothesis. According to this hypothesis, a decrease in fish that predates on urchins – due, for instance, to overfishing – may increase sea urchin density, which in turn may result into the over-consumption of macroalgae (Giakoumi et al., 2012). On these bases, predators of sea urchins (*e.g.*, *Diplodus* spp. and the wrasses *Coris julis* and *Thalassoma pavo*) can play a key role in regulating ecosystem dynamics by mediating the grazing pressure of sea urchins. Thus, the factors that drive the dynamics of predator populations influence the dynamics of algal cover of the Mediterranean shallow sublittoral zone and related barren formation. To explain such dynamics therefore, it is essential investigating the drivers of predator populations. The first aim of this work is indeed analysing such drivers in a specific context of Sardinia - Western Mediterranean (see Chapter 2).

Given the very complex network of relationships connecting species in this ecosystem, the analysis of the barren formation requires focusing on key factors that, through cause-effect relationships, determine the bulk of impacts. In the next sub-sections, therefore, we will zoom in on those species which chiefly participate in the trophic cascade, categorising them into three trophic groups: primary producers, focussing only on macroalgae, consumers and sea urchin predators (Figure 1.2).
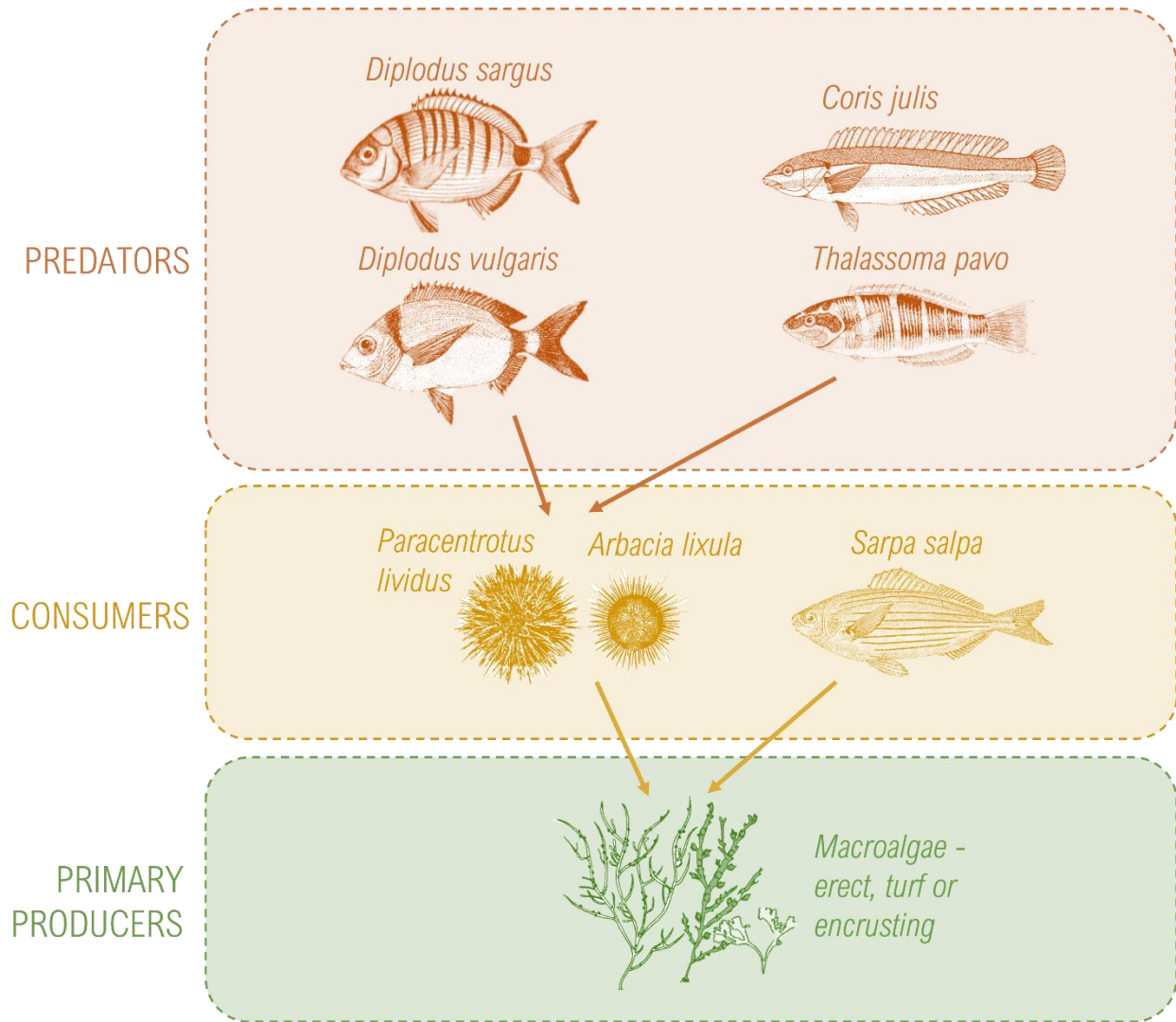
Figure 1.2: Scheme of the simplified trophic web considered in this work for shallow Mediterranean rocky reefs. Arrows leave from the feeder and end on the resource. Seabreams and wrasses, when present at adequate densities, can control sea urchin populations through predation, thus preventing their overgrazing on macroalgae. Herbivory of *Diplodus* fish has been neglected as they are not considered able to induce barrens formation alone.

1.3.1 PRIMARY PRODUCERS - MACROALGAE

The systematic classification of macroalgae is based on the pigments that are involved in the photosynthesis. Therefore, four groups are identified: Rhodophyta, Ochrophyta, Chlorophyta and Cyanophyta. However, to analyse the trophic cascade, a morpho-functional classification is more appropriate since, rather than analysing the biological characteristics of each species, we are primarily interested in understanding how the architectural structure of algal communities ultimately influences processes on an ecosystem scale.

It is worth noticing that a formal, agreed-upon morphological definition of algal types is missing in

the literature, despite it would allow for more consistent and meaningful comparisons among studies. Despite that, for the sake of this work, we will stick to the categories (even if not always precisely defined, see Connell et al., 2014) used by several researchers to analyse the dynamics of barrens, notably: encrusting algae, turf-forming algae and erect algae. These categories are described in the next sub-sections.

ENCRUSTING ALGAE

Encrusting algae – or crusts - are characterised by a hard structure and a crustose holdfast, allowing adherence to the substrate. Their vertical development is limited (about 3 cm) as well as their structural complexity (Steneck & Dethier, 1994). These algae have a lower nutritional value with respect to the other two types (Filbee-Dexter & Scheibling, 2014).

Some representatives of this group, which includes both calcareous and non-calcareous organisms, are *Mesophyllum lichenoides*, *Lithophyllum spp.* and *Peyssonnelia spp.* (Figure 1.3). Encrusting algae tend to predominate in areas subject to intense disturbance (*e.g.*, from sand scouring or intense grazing activity) (Dethier, 1994) such as barrens. Reproduction of encrusting algae has been reported to occur continuously throughout the year by propagules recruitment (Airoldi, 2000 and references therein).
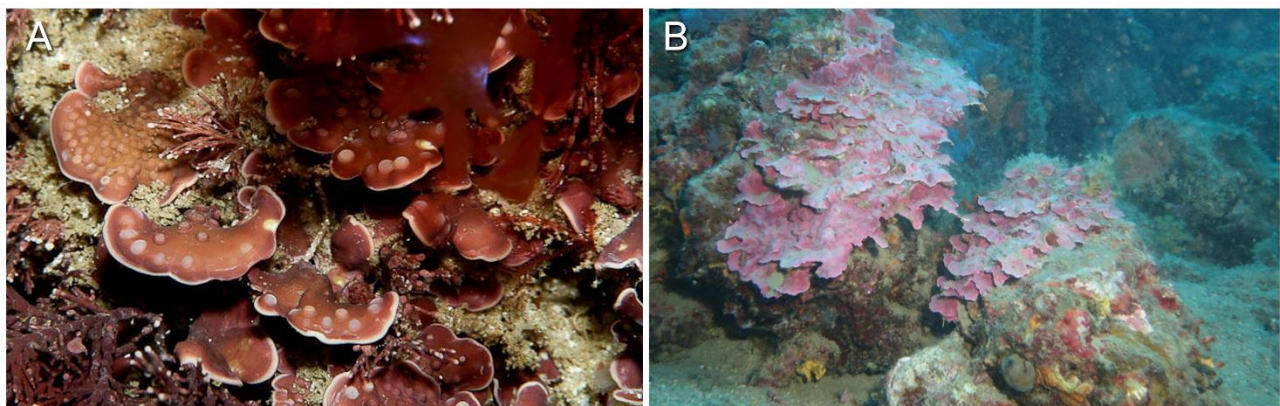
Figure 1.3: Examples of encrusting algae. **A**. *Mesophyllum lichenoides*, **B**. *Lithophyllum stictiforme*.
Photo credits: A. F.Gully www.doris.ffessm.fr, B. F.Rindi https://doi.org/10.3897/italianbotanist.13.81812

TURF-FORMING ALGAE

This group includes species of foliose (*e.g.*, *Acetabularia acetabulum* - Figure 1.4 A) filamentous (*e.g*, *Polysiphonia* spp - Figure 1.4 B , and *Sphacelaria* spp.), and coarsely branched algae (*e.g.*, *Laurencia obtusa*). These algae are characterised by the formation of horizontal mats with limited vertical extension, not exceeding 15 cm (Connell et al., 2014), but often reaching smaller sizes. Turf-

dominated bottoms present an intermediate level of habitat complexity between beds dominated by erect algae and barren grounds, dominated by encrusting organisms (Thiriet et al., 2016). To present knowledge, unlike encrusting and erect algae, their reproduction is vegetative with rather high lateral expansion rates (Airoldi, 2000).
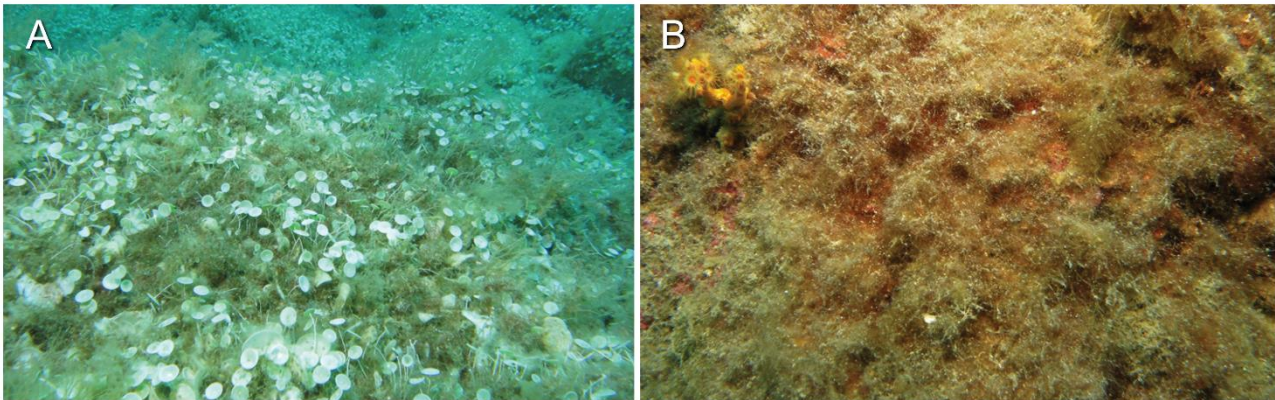
Figure 1.4: Examples of turf-forming algae. **A**. *Acetabularia acetabulum*, **B**. *Polysiphonia setacea*. *Photo credits: . F.Rindi https://doi.org/10.3897/italianbotanist.13.81812*

ERECT ALGAE

These organisms are characterised by higher biomass and structural complexity with respect to the other two types. Erect algae, like encrusting ones, mostly reproduce by recruitment of propagules (Airoldi, 2000). As already mentioned, dominant species of erect macroalgae in many Mediterranean shallow rocky reefs are those belonging to the order Fucales, such as *Cystoseira* spp. and *Sargassum* spp. (Figure 1.5). These species can form luxurious canopies up to 1 m high (Thiriet et al., 2016) and 20-40 cm wide and, despite being smaller than Laminariales (*i.e.*, their counterparts in oceanic temperate forests), they display similar structural complexity (Bevilacqua et al., 2021). Thanks to their articulated three-dimensional structure, Fucales provide fundamental ecosystem functions and services, ensuring a suitable habitat to several algal and animal species. In light of their role as ecosystem engineers (Blanfuné et al., 2016; Sales et al., 2011) many ecologists and biologists have expressed their concern regarding the long-term decline to which the whole genus seems to be doomed, in the Mediterranean Sea (Bianchi et al., 2014; Blanfuné et al., 2016; Gatti et al., 2017; Thibaut et al., 2005) and worldwide (Beck & Airoldi, 2007 and references therein; Valdazo et al., 2017). Indeed, all species belonging to the genus *Cystoseira* (except for *C. compressa*) have been declared as protected during the Barcelona convention for the protection of Mediterranean, in 2010. The reduction of Fucales has been attributed to several stressors (Section 1.2), among which excessive

grazing activity (Thibaut et al., 2005; Thiriet et al., 2016), further highlighting the need of a thorough comprehension of the mechanisms regulating herbivores populations.

The competition dynamics among the three algal types are very case dependent and not easily predictable, with many known and possibly unknown factors determining dominance. However, we can recognise some general patterns. First of all, there is evidence that encrusting algae, once established, are able to exert an inhibitory action in the settling of their erect competitors, even in the absence of herbivory (Bulleri et al., 2002), somehow stabilising the barren configuration in time (Guidetti, 2006b). Furthermore, according to the results obtained by Airoldi (2000), encrusting organisms seem to be the first colonisers of patches of bare rock, cleared by physical or biological disturbances such as storms and herbivory. Turf algae can in principle expand laterally on crusts-dominated patches but cannot completely replace them, as encrusting organisms appear to have high tolerance to overgrowth by turfs (Airoldi, 2000). These considerations seem to enforce the hypothesis that hysteresis mechanisms (i.e., lacking reversibility, see Section 2.1) underlie the formation of crusts-dominated barren patches, even though further studies on their formation and stabilisation are needed to consolidate the theory.
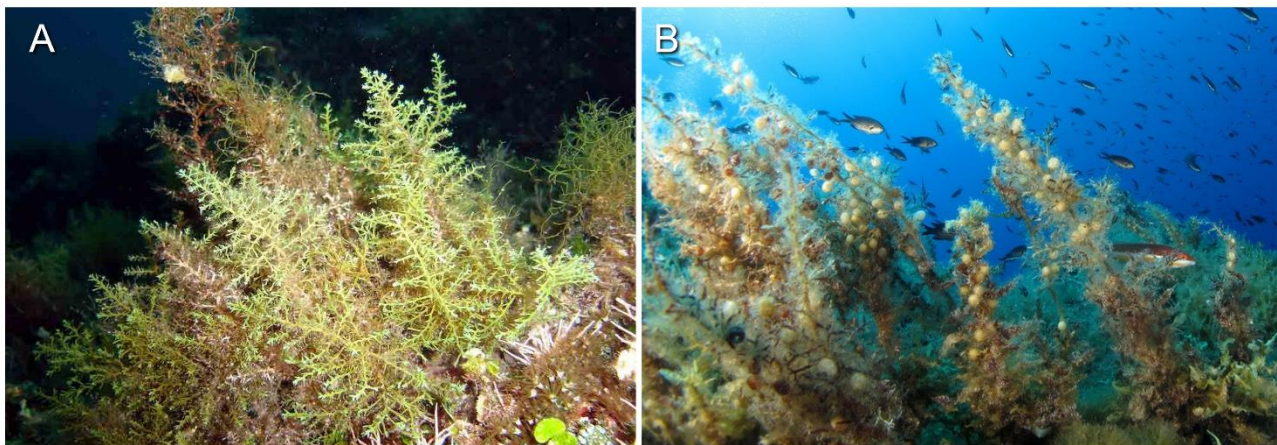
Figure 1.5: Examples of erect algae of the order Fucales. **A.** *Cystoseira mediterranea*, **B.** *Sargassum vulgaris.*
Photo credits: https://www.biologiamarina.org

1.3.2 CONSUMERS

Among macroalgae consumers, in the Mediterranean Sea, there are several species of vertebrates and invertebrates. As already mentioned, sea urchins are the most active grazers in the Mediterranean Sea, often driving the shift from macroalgal communities to barrens (Guidetti, 2006a). The most widespread and abundant grazers in shallow Mediterranean rocky ecosystems are the two co-

occurring species of urchins, notably *Paracentrotus lividus* and *Arbacia lixula* (Gianguzza & Bonaviri, 2013; Guidetti, 2006a). In addition, despite the grazing activity of herbivorous fish is generally considered less impactful than that of sea urchins (Hereu et al., 2008), it has been observed that some grazers can give a substantial contribution in shaping the distribution of macroalgal assemblages (Sala and Boudouresque, 1997; Ruitton et al., 2000; Vergés et al., 2009). Notably, the diet of the sparid fish *Sarpa salpa* can be in large part composed of those macrophytes that have been experiencing a decline in the last decades, such as *Cystoseira spp.* (Vergés et al., 2009), thus making the role of this fish non-negligible. In the next paragraphs, some key features of the three herbivores *P. lividus*, *A. lixula* and *S. salpa* will be outlined, to give better insights on those actors occupying the intermediate level of the trophic chain which can ultimately cascade to barrens.

THE SEA URCHINS PARACENTROTUS LIVIDUS AND ARBACIA LIXULA

Paracentrotus lividus (Figure 1.6 A) and *Arbacia lixula* (Figure 1.6 B) the latter recognised as a thermophilic species (Gianguzza & Bonaviri, 2013; Guidetti, 2006a) are two co-occurring sea urchins in Mediterranean shallow rocky habitats (Agnetta et al., 2013). *P. lividus* exists in different shades (*e.g.*, black-purple, dark brown, red-brown) and its test diameter - namely the diameter without spines - reaches a maximum of 7-8 cm; *A. lixula* is instead darker and smaller, with test diameters up to 5 cm (Boudouresque & Verlaque, 2013; Gianguzza & Bonaviri, 2013). Because of the rise in sea water temperature that has been occurring in the last decades (Pastor et al., 2020), the thermophilic *A. lixula* has massively widened its distribution since the 1960s: to give the gist of the extent of its expansion, a study in the Scandola marine protected area (Corsica, France) reports a ten-fold increase in the abundance of *A. lixula* over a nine years time interval, from 1983 to 1992 (Francour et al., 1994).

Both sea urchins reproduce continuously with one or two annual peaks, whose temporal occurrence can be significantly different among locations (Boudouresque & Verlaque, 2013; Gianguzza & Bonaviri, 2013).

Despite sharing the same habitats, the two species display important dissimilarities in terms of behaviour, life history traits and resources use. Both urchins are present down to approximatively 20 m depth, even though *A. lixula* shows a preference for shallower waters, due to its thermophily and higher structural resistance (Ruitton et al., 2000). Resistance not only allows for better tolerance of water turbulence in shallow zones but also makes *A. lixula* less subject to attacks by predators (Boudouresque & Verlaque, 2013). *P. lividus* instead, defends itself from predation adopting

different strategies, such as hiding in crevices and interstices, when available, and using them as a refuge. This is known as "cryptic behaviour" and is typical of sea urchins that are less than 3-5 cm in test diameter. Above this diameter, commonly referred to as "escape size", sea urchins are usually much less targeted by predators and can therefore abandon this behaviour (Bonaviri et al., 2011).

P. lividus shows high ability in penetrating zones dominated by erect algae, while the movement of *A. lixula* seem to be impaired by them. This feature is reflected by the feeding habits of the two species. Indeed, *P. lividus* browses and feeds mainly on erect algae rather than encrusting ones, while the opposite is true for *A. lixula*, which reaches high densities only in barrens and prefers encrusting organisms even when erect algae are present (Agnetta et al., 2013; Gianguzza & Bonaviri, 2013; Klaoudatos et al., 2022). Besides preferences on algal types, the two urchins differ also in terms of trophic position: both urchins are omnivorous, with a tendency to carnivory for *A. lixula* and to herbivory for *P. lividus*. The latter isalso capable of capturing drift algae floating in the water column and to absorb particulate organic matter (Boudouresque & Verlaque, 2013). For this reason, *P. lividus* does not seem to be negatively affected by organic pollution, which, to the contrary, has been shown to enhance its growth rate (Klaoudatos et al., 2022).

Overall, considering the differences in behaviours, trophic position and use of resources such as space and food, researchers could reasonably state that the two species do not generally compete (Agnetta et al., 2013; Boudouresque & Verlaque, 2013). Regarding barrens formation, they seem to produce a combined effect: on the one hand, *P. lividus*, with its superior movement ability, may introduce itself into macroalgal-dominated zones and consume algal canopies, thus creating clear patches that are subsequently colonised by encrusting algae. On the other hand, *A. lixula* finds in barren patches its preferred conditions and may therefore give a substantial contribution to its maintenance through grazing. This is of course a simplified scheme, but it is one of the possible scenarios explaining formation and temporal persistence of barrens. In this context, the role of sea urchin predators can be determinant in regulating not only urchins' abundance but also their grazing activity. Indeed, the sole presence of predators can inhibit urchins' grazing (Hereu et al., 2008), reducing their feeding range to about one meter around their shelters (Sala & Boudouresque, 1997).

THE HERBIVOROUS FISH SARPA SALPA

Sarpa salpa, commonly known as "Salema" (Figure 1.6 C), is a sparid fish inhabiting shallow waters of both rocky and seagrass beds (Raventos et al., 2009; Vergés et al., 2009). It is a protandrous

hermaphrodite species, meaning that individuals are born as males and, at a given point in their lifespan, they develop female gonadic tissue (Criscoli et al., 2006). Male size is typically between 15 and 30 cm while females are bigger, ranging from 30 to 45 cm in size. It has been observed that individuals tend to travel into schools of rather homogeneous size (Raventos et al., 2009).

S. salpa is the only strictly herbivorous fish in the Mediterranean Sea (Guidetti & Sala, 2007; Vergés et al., 2009). Consistently with its habitat choices, its diet composition broadly varies over space and time. S. salpa largely grazes on *Posidonia oceanica* meadows - being responsible for up to 70% of total leaf consumption - and on beds occupied by other macrophytes, such as *Caulerpa* spp. or *Cystoseira* spp. (Marco-Méndez et al., 2016) but it is also able to scrape encrusting algae from rocky bottoms (Ruitton et al., 2000).

The high variability in *S. salpa* feeding habits makes it difficult to generalise its contribution to the depletion of macroalgal forests. Some studies (*e.g.,* Guidetti, 2006b; Sala et al., 2012) point out that *S. salpa* is unlikely to induce strong algal declines alone, while some others claim that its effects on macroalgal forests have been overlooked in the last decades (Gianni et al., 2017; Ruitton et al., 2000; Vergés et al., 2009) and that this species could play a major role in driving the decline of macroalgal forests. Notwithstanding, there is enough consensus in the literature upon the fact that *S. salpa* is being replaced by the tropical herbivorous rabbitfish *Siganus* spp. in the easternmost Mediterranean regions, due to the rise in sea water temperature. (Gianni et al., 2017; Santana-Garcon et al., 2023). There is evidence that these species, able to graze with sufficient intensity to cause the formation of barrens, are progressively expanding westwards (Sala et al., 2012; Santana-Garcon et al., 2023), thus representing a cause of concern at the Mediterranean scale. These considerations emphasise the need of carefully monitoring the combined effects of all these grazers on the current and future status of Mediterranean macroalgal forests.
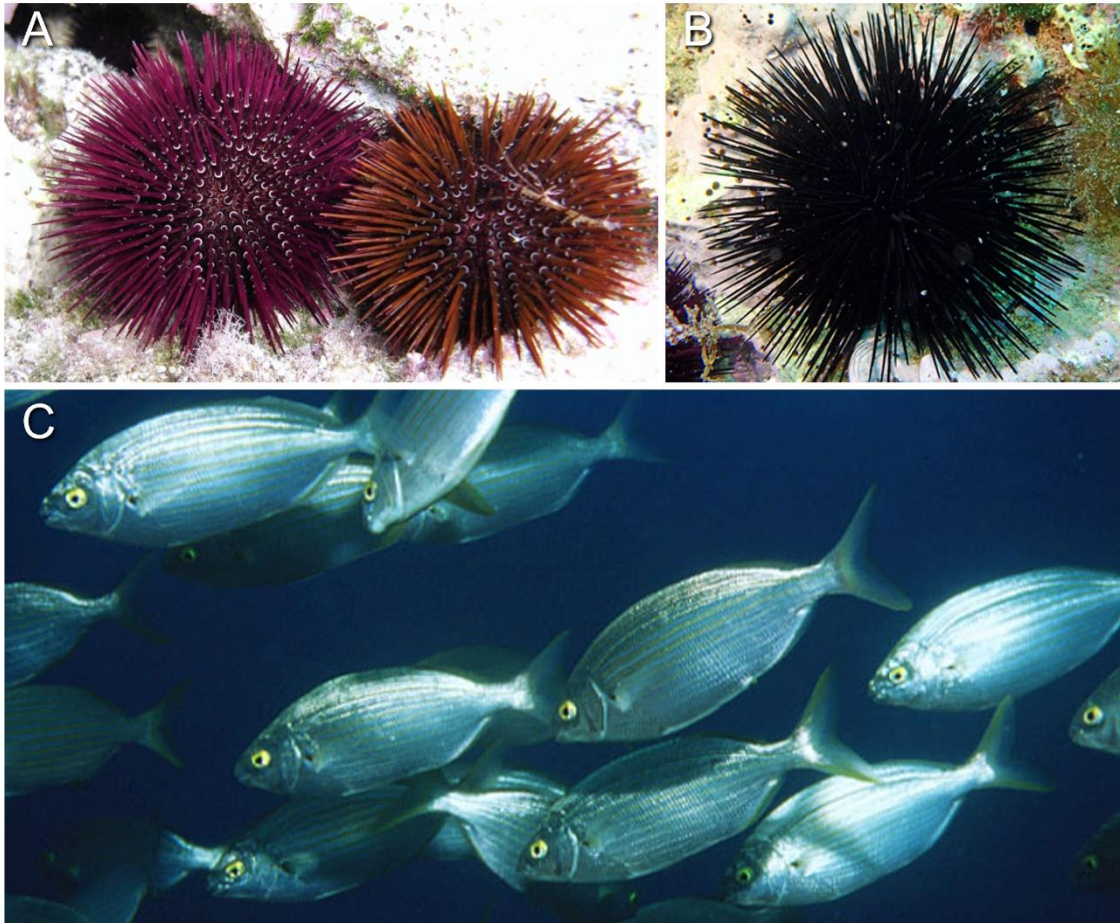
Figure 1.6: Consumers of macroalgae. **A**. two individuals of *Paracentrotus lividus* in different shades. **B**. *Arbacia lixula*. **C**. individuals of *Sarpa salpa* showing a schooling behaviour.
Photo credits: A. www.marinespecies.org B. www.european-marine-life.org C. www.fishbase.se

1.3.3 SEA URCHIN PREDATORS

In the Mediterranean Sea, several species of crabs, gastropods, lobsters and starfish are able to prey upon sea urchins. Nevertheless, only the seabreams *Diplodus sargus* and *Diplodus vulgaris* and, to a lesser extent, the two wrasses *Coris julis* and *Thalassoma pavo* feed on sea urchins with adequate intensity to control their populations (Guidetti, 2006b). Studying the dynamics of these predators' populations and understanding how they respond to protection is of paramount importance to determine which management measures can be put in place to try to recover depleted fish populations and, by way of consequence, macroalgal beds: this is indeed the focus of much of the present work, which uses a marine protected area in Sardinia (Western Mediterranean) as experimental ground. In the next paragraphs, the most relevant biological and behavioural traits of

the above-mentioned species are summarised, in order to provide the necessary information to interpret the results presented in the following chapters.

THE SEABREAMS DIPLODUS SARGUS AND DIPLODUS VULGARIS

The white seabream *Diplodus sargus* (Figure 1.7 A) and the two-banded seabream *Diplodus vulgaris* (Figure 1.7 B) are two species belonging to the family *Sparidae*, very widespread in the Mediterranean sea. They can reach about 40 cm length - although large sizes are less frequent for *D. vulgaris* (Gordoa & Molì, 1997) - and make up a large share of total fish biomass in shallow rocky habitats (Sala & Ballesteros, 1997). Both species can live on rocky, sandy or artificial substrates down to depths of about 50 m for *D.* sargus and 30 m for *D. vulgaris* (Sala & Ballesteros, 1997). They are highly residential, with *D. vulgaris* using a smaller home range than *D. sargus* (Abecasis et al., 2009). A review of several studies on *D. sargus* made by Giacalone et al., (2022) reports that home ranges for this species can span from 0.5 to 393 ha. According to the authors, the reason for this high variability is ascribable to the differentiation in the types of habitats used by *D. sargus* for its various activities (e.g., algal dominated grounds are employed for foraging while holes and crevices are used for nocturnal resting or as a refuge from predators). Therefore, *D. sargus* may adjust its home range based on how far it can retrieve food or safe places.

Reproduction of the two sparids occurs continuously, with peaks in spring for *D. sargus* (Giacalone et al., 2022) and in winter for *D. vulgaris* (Gonçalves & Erzini, 2000). Larvae of the two species can be advected for several kilometres – up to 100 km - over about four weeks (Giacalone et al., 2022; Raventos et al., 2021), before settling to a favourable environment, that for *D. sargus* seems to be mostly in shallow waters (Giacalone et al., 2022). For these species, connectivity among metapopulations is mostly guaranteed by larval dispersal rather than adult movement, since the former occurs on a much larger spatial scale than the latter (Giacalone et al., 2022).

A fundamental characteristic of *D. sargus* is its protandric hermaphroditism, with sex reversal from male to female taking place at about 20-25 cm in size (Giacalone et al., 2022). Large individuals of *D. sargus*, namely those that are chiefly targeted by fishery, are more likely to be big reproductive females: this is an important characteristic to consider when designing protection strategies and releasing fishing permits.

Protandry is a shared feature with other species of the genus *Diplodus*. Indeed, it is reported also for *D. vulgaris*, although it does not seem to be the rule for all individuals. A study from Gonçalves &

Erzini, 2000 on the south-west coast of Portugal reports hermaphroditism for only 2.9% of the total (N=420) caught individuals.

D. sargus and *D. vulgaris* are among the few fish species that, when present at adequate densities (see Section 2.1), are able to control sea urchin populations size (Guidetti, 2006b) through their predatory activity on both adult and juvenile individuals (i.e., top-down control). *D. sargus* preferentially feeds on the sea urchin *Paracentrotus lividus* rather than on *Arbacia lixula* (Guidetti, 2006a) and successfully attacks individuals that are less than 5 cm in test diameter, while *D. vulgaris* typically preys on smaller individuals, with a test diameter not exceeding 3 cm (Boudouresque & Verlaque, 2013). When sea urchins are beyond these diameters, seabreams have a hard time in attacking and crushing them. Furthermore, large-sized *Diplodus* individuals have been found to be more successful predators than small-sized ones, in that they can prey on urchins of a wider size range (Giakoumi et al., 2017). Considering that large-size fish are much more frequent in marine protected areas than in fished ones, it appears evident that regulating fishing intensities can allow *Diplodus* fish to reach bigger sizes, thus being more effective in controlling sea urchin populations and, indirectly, their grazing pressure.

Other than sea urchins, the two *Diplodus* also feed on molluscs, small crustaceans as well as on some algae, reason for which they are considered omnivorous species (Osman & Mahmoud, 2009; Sala & Ballesteros, 1997),. Although the two *Diplodus* can also graze on some algae, they are not generally considered direct responsible of barrens formation (Sala et al., 2011). In fact, it is rather the lack of these two seabreams in overfished area that, as already mentioned, can cause the over-expansion of urchins' population, which ultimately leads to a decline in macroalgal forests.

From a study made by Sala & Ballesteros, (1997) in the North-western Mediterranean, it emerges that, although there is a significant similarity in dietary composition between *D. sargus* and *D. vulgaris*, the two species do not seem to compete for food or, more broadly, resources. This happens because the two seabreams exploit the habitat differently, namely *D. vulgaris* was found to exploit deeper zones with respect to *D. sargus*. This is a case of "niche complementarity", meaning that different species can co-occur even if their diets overlap, provided that there is a certain degree of habitat separation among them, or time shift in resources use.

THE WRASSES CORIS JULIS AND THALASSOMA PAVO

The rainbow wrasse *Coris julis* (Figure 1.7 C)and the ornate wrasse *Thalassoma pavo* (Figure 1.7 D) are two very common fish in the Mediterranean Sea down to about 60 m depth, belonging to the family

Labridae (Milazzo et al., 2016). They chiefly live in seagrass beds and rocky habitats, although it is possible to find *C. julis* also on sandy beds (Guidetti & D'Ambrosio, 2004).

The two wrasses are summer spawners and protogynous hermaphroditism (*i.e.*, sex change from female to male) has been reported for both (Sara et al., 2005; Škeljo et al., 2012). In *C. julis*, sex reversal happens in individuals about 4 years old (Škeljo et al., 2012) while no information about sex reversal age was found for *T. pavo*.

Fundamental characteristic of these wrasses is their thermal preference, which strongly affects their local habitat choice as well as their large-scale distribution. The ornate wrasse *T. pavo* is a thermophilic species, while the rainbow wrasse *C. julis* is a cold-water one. On steep bottoms, a certain segregation between the two species based on water temperature is typically observed, with *C. julis* inhabiting deeper and colder waters and *T. pavo* occupying shallower and warmer ones. On gentle-sloping bottoms, the two species tend to co-exist (Milazzo et al., 2016).

Until the 1980s, *T. pavo* used to be confined to the south-eastern coasts of the Mediterranean Sea. On the contrary, *C. julis* was rather homogeneously distributed throughout the basin (Guidetti & D'Ambrosio, 2004). Due to the progressive warming of Mediterranean waters, however, the distribution patterns of these species are rapidly changing. There is evidence that the ornate wrasse *T. pavo* has been moving northward, since previously cold zones are becoming ever warmer and suitable to host thermophilic species, while *C. julis* is moving towards deeper areas in search for cooler habitats (Milazzo et al., 2016; Sara et al., 2005). *T. pavo* is one of the Mediterranean species which has been expanding with the highest rates, namely 66 km/y in the period 1980-1995 according to Sorte et al., 2010. Some simulations (see Milazzo et al., 2016) based on the projected seawater temperature rise confirm the current trends and predict:

i.   for *T. pavo*, a further expansion towards northern and western sectors, as well as the conquest of deeper habitats in the warmer eastern and southern coasts.
ii.   for *C. julis*, an overall restriction of distribution to the shrinking coldest regions and further displacement towards deeper areas.

The responsiveness of *C. julis* and *T. pavo* to seawater temperature rise has drawn the attention of scientists. Indeed, the two species have been considered marine "sentinel species" of climate change and have been included in the recently published "ClimateFish" database (Azzurro et al., 2022), a collaborative project for tracking Mediterranean ecosystem changes through the temporal trajectories of temperature-sensitive species.

The local partitioning between the two wrasses observed for the spatial dimension seem to be present also on the dietary one. Indeed, *T. pavo* feeds preferentially on gammarids, crustaceans, decapods and sipunculids, whereas the diet of *C. julis* diet is composed mainly of *Alvania* spp. and Paguroidae (Sinopoli et al., 2017). To a lesser extent, both wrasses feed also on juvenile sea urchins that are typically less than 1 cm in test diameter (Guidetti, 2006b; Milazzo et al., 2016). Despite not feeding on sea urchins as much as *Diplodus* spp. do, *C. julis* and *T. pavo* still give an important contribution to the control of sea urchin populations operated from the predator level of the trophic chain.
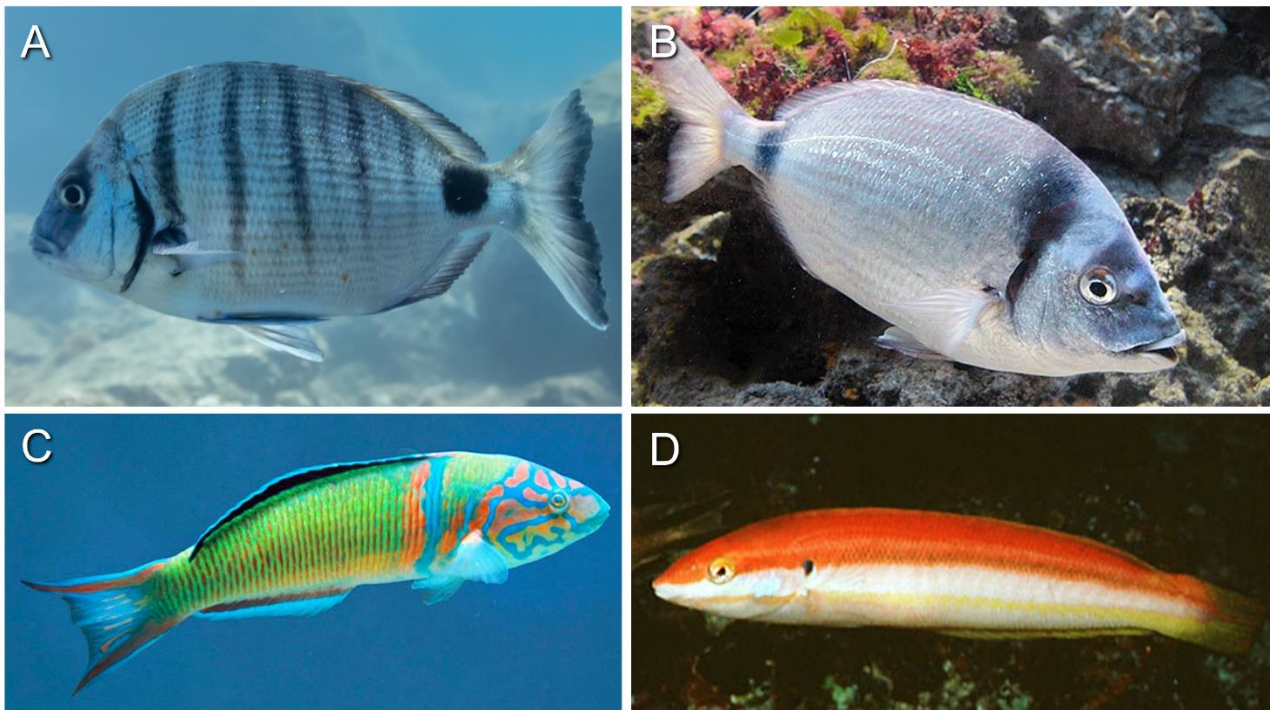
Figure 1.7: Sea urchins' predators: **A**. the white seabream *Diplodus sargus*, **B**. the two-banded seabream *Diplodus vulgaris*, **C**. Male of the ornate wrasse *Thalassoma pavo*, **D**. Female of the rainbow wrasse *Coris julis*. Photo credits:A. D.Delso. B,C. www.monaconatureencyclopedia.com D. www.fishbase.se

On the basis of the considerations above, it appears evident that preserving and recovering stocks of these species (*e.g.*, through the establishment of marine protected areas) may be crucial for attaining healthy ecosystem states, with beneficial effects extending down to the level of primary producers.

Figure 1.8 provides a schematic representation of the process together with potential recovery strategy.

The focus of the next chapters will therefore be put on the dynamics of five fish species inhabiting shallow Mediterranean rocky reefs (four urchins' predators and one herbivore) and their response to protection in the Mediterranean MPAs.
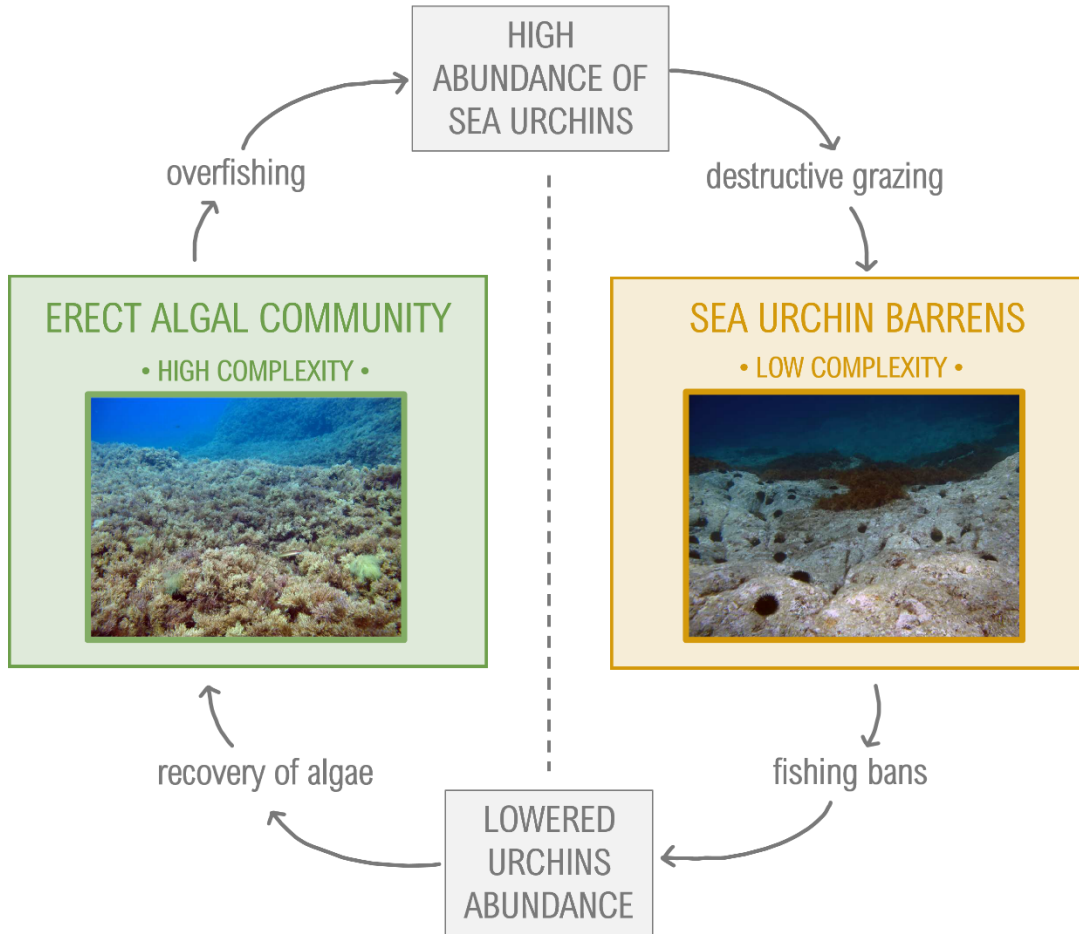
Figure 1.8: Schematic representation of overfishing-induced barrens formation and potential recovery through fishing bans. Adapted from Sala et al. (1998).
Photo credits: Thiriet et al. (2016).

2. Marine protected areas in the Mediterranean Sea: a case study in Sardinia, Italy

The establishment of Marine Protected Areas (MPAs), namely portions of sea where human activities, such as fishing, are regulated or banned, is widely considered an effective management tool to support ecosystem-wide recovery (E. Di Franco et al., 2021). MPAs typically allow an increase in mean size, density, biomass and reproductive potential of targeted fish, as well as potential spillover of fish individuals from fully protected areas towards adjacent partially protected or fished areas[2] (Giakoumi et al., 2017; Guidetti & Sala, 2007). These recovery signs are usually grouped under the umbrella term "reserve effect".

In the Mediterranean region, in 2020, 6 % of the sea surface was designated as MPA. However, only 0.23% of the Mediterranean Sea fell under full protection (no-take and no-access areas) and for only 18% of MPA surface a management plan was implemented (Claudet et al., 2020). In light of recent international commitments of European Union and United Nations to protect 30% of European seas and global oceans respectively by 2030, effort is still needed towards the institution of new MPAs and the transformation of "paper reserves" into effective ones.

In this chapter, we provide evidence about the role of MPAs in preserving and recovering macroalgal forests in shallow Mediterranean rocky reefs and introduce the case study of the Mediterranean MPA of Tavolara – Punta Coda Cavallo (Sardinia, Italy), with the aim of providing the background to the analysis presented in Chapters 3 and 4.

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[2] However, it is to be noticed that, while increases in size, biomass and density may be rather rapid (Halpern & Warner, 2002), spillover of individuals outside MPAs boundaries might take longer, as fish populations need to establish density-dependent dynamics (typical of healthy populations) before it occurs (Di Lorenzo et al., 2016).

2.1 THE ROLE OF MARINE PROTECTED AREAS IN THE CONSERVATION AND RESTORATION OF MACROALGAL FORESTS

The existence of macroalgal forests in Mediterranean rocky reefs is of paramount importance to the well-being of the whole ecosystem: they provide nursery grounds, food and shelter to many species and reduce the disturbance provoked by wave action (Blanfuné et al., 2016). Section 1.2 hints at the main causes of forests deterioration and leaves an open question about actions that might be undertaken to contain algal decline. The establishment of MPAs is a management tool that has been used worldwide to restore ecosystem quality. Although MPAs cannot directly tackle the effects of changes happening on a global scale (*e.g.*, climate change, ocean acidification) (Gianni et al., 2013), they were shown to be effective in supporting the local recovery of previously overfished populations, especially if their extension is large enough to encompass the species' home range (Giakoumi et al., 2017).

In the context of Mediterranean rocky reefs, MPAs may be crucial allies in preserving and restoring predatory relationships upon sea urchins and, indirectly, macroalgal forests health (E. Di Franco et al., 2021; Filbee-Dexter & Scheibling, 2014; Giakoumi et al., 2019; Guidetti et al., 2014). Although the status of macroalgal forests and chances of their recovery in the Mediterranean Sea have been poorly studied (Gianni et al., 2013; Tamburello et al., 2022), recent evidence points in this direction. A study conducted by Di Franco et al. (2021) on MPAs at a Mediterranean scale reports a significative positive effect of protection on erect canopy-forming macroalgae of the genus *Cystoseira*, with higher covering of these species found inside protected locations. Two other regional studies referring to the Mediterranean basin found greater biomass of sea urchins predators inside MPAs than outside (Giakoumi et al., 2017; Guidetti et al., 2014) . In particular, Giakoumi et al. (2017) found that biomass of *Diplodus sargus* and *Diplodus vulgaris*, two major sea urchin predators, was on average 2.8 and 1.4 times higher in MPAs than in control areas and that density of sea urchins was significantly lower inside MPAs. Notoriously, MPAs allow the existence of large-sized fish individuals, which are instead the most targeted by fishery in unprotected zones. Large sea breams are much more efficient predators than small-sized ones as they can feed on urchins belonging to a wider size-spectrum and, consequently, they can limit excessive grazing pressure more successfully (Giakoumi et al., 2017).

It is to be noticed that, however, marine reserves can be effective in enhancing trophic cascade mechanisms - such as the one linking sea urchin predators and erect macroalgae - only if predators' density is high enough to control sea urchin population. Guidetti & Sala (2007) defined a critical

threshold for *Diplodus* fish (about 15 adult sea breams/ 100 m²) below which their predatory pressure upon sea urchins is too weak to impose a top-down control, whose effects propagate to macroalgal forests. Reaching these densities in MPAs can take several years. Indeed, there are studies accounting for situations where this threshold density has not been reached, both within and outside reserves (see Giakoumi et al., 2012; Sala et al., 2012). In these cases, it is important to understand what factors are hampering the restoration of carnivores' populations and, if necessary, re-design management strategies.

Furthermore, recovery pathways are seldom linear. It is hypothesised that the barren configuration can undergo hysteresis mechanisms, meaning that barrens may persist through time due to self-reinforcing mechanisms, even though initial conditions are restored (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015; Melis et al., 2019; Pinna et al., 2020). Several mechanisms seem to act as barren stabilisers, such as the increase in the grazing activity of the sea urchin *Arbacia lixula* after barrens are formed, or the decrease in density of sea urchin predators, due to unsuitable habitat conditions (Pinna et al., 2020). Competition dynamics among algal types, such as inhibitory actions of crusts and turfs to the re-growth of erect competitors, can also hinder forests recovery (Bulleri et al., 2002; Monserrat et al., 2022). Last but not least, human-induced stressors, such as pollution and climate change, may further reduce the resilience of macroalgal forests and stabilise the barren state (see Section 1.2).

If the hysteresis hypothesis were verified, we could regard barrens and macroalgal forests as two alternative stable states of shallow temperate rocky reef (eco)systems. The transition between the two states could therefore be considered as a discontinuous phase shift, meaning that thresholds of some state variables (*e.g.*, sea urchin or predator density) for forward shift (forest to barren) are different from thresholds needed to attain backshift (Filbee-Dexter & Scheibling, 2014) (see Figure 2.1 for a graphical representation of this concept). At this regard, Ling et al. (2015) found that the density of sea urchins that causes the shift to barrens may be about one order of magnitude higher than the one that allows recovery. Consequently, if forward shift happens at a urchin density of 7-8 individuals/m², as hypothesised by Guidetti & Sala, (2007), the backshift may happen when densities as low as 0.7-0.8 individuals/m² are attained.
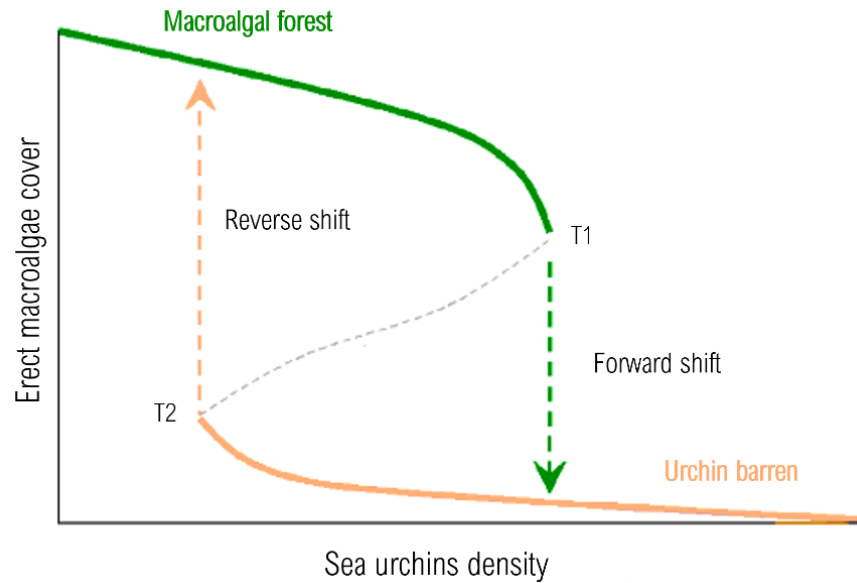
Figure 2.1: In this example, sea urchins density is considered as a state variable. When erect macroalgal forest approaches threshold T1, any small disturbance can trigger the forward shift to barren state. To attain a backshift towards forest state, an urchins density T2 < T1 has to be reached; the extent of the difference between T2 and T1 indicates the strength of the hysteresis mechanism. Adapted from **Filbee-Dexter & Scheibling, (2014)**.

Despite increasing evidence for the existence of self-reinforcing mechanisms in barrens, there is no agreement among researchers about whether to consider barrens and forests two alternative stable states (Filbee-Dexter & Scheibling, 2014).

Potential self-reinforcing mechanisms, coupled with limited dispersal ability of some forest-forming algae (*e.g.*, *Cystoseira* spp.) may hamper the natural recovery of macroalgal forests in the Mediterranean Sea (Gianni et al., 2013; Tamburello et al., 2022). Thus, memory of past disturbances might be maintained even within MPAs, making it difficult for ecosystems to approach restoration pathways. However, the reported cases of natural (*i.e.*, spontaneous) recoveries of forests have been documented inside MPAs boundaries (Gianni et al., 2013), most likely due to favourable conditions and reduced herbivory pressure in these areas. As already mentioned, evidence for these events for the Mediterranean Sea, despite encouraging (see, for instance, Sala et al., (2012) and Bonaviri et al., (2009) - Medes islands and Ustica), is still limited. A likely explanation lies in the inherent difficulty of carrying out monitoring campaigns lasting for sufficient long time spans to detect possible changes in forest cover. Economic and research efforts in this direction are fundamental, especially in the context of global changes we are witnessing. Given the hindrances to natural recovery, a prospective interesting research field is that of human-induced forest recoveries, through transplantations or seeding. Ecosystems in MPAs where forests presence was historically recorded

may be on the path of recovery and benefit from an artificial re-introduction of native canopy-forming species (Gianni et al., 2013; Tamburello et al., 2022).

Overall, from the literature it emerges that MPAs are crucial management tools for preserving existing forests and creating the right conditions for natural or human-facilitated recoveries. Yet, there are still knowledge gaps to be filled concerning mechanisms that promote recovery, as well as the temporal scale on which they occur.

2.2 THE MARINE PROTECTED AREA OF TAVOLARA – PUNTA CODA CAVALLO

2.2.1 Description, structure and enforcement

The Marine Protected Area (MPA) of Tavolara – Punta Coda Cavallo (40°53'06.2"N, 9°42'57.6"E, Table 2.1), named TMPA hereafter, is located in northeast Sardinia (Italy). It was selected as a candidate MPA by law 979 of December 31, 1982 and designated in 1997 by ministerial decree. Since 2006, it was declared Site of Community Interest (SCI) as part of the Natura 2000 network. It comprises 76 km of coastline and covers 15,357 ha of sea. Tourism, with a strong seasonal component, is an integral part of the economy of the area and has shaped its urban development throughout the years. In TMPA, coasts are mostly granitic, except for Capo Figari promontory and the Tavolara Island, consisting of limestone or dolomite slabs (Guidetti & D'Ambrosio, 2004). Seabed at TMPA hosts a great variety of habitats including coralligenous assemblages, sandbanks, rocky reefs, *Posidonia oceanica* meadows, photophilic algal stands (mostly in shallow nearshore areas) and emisciaphilic assemblages (Rovere et al., 2013). The parallel existence of high natural capital and significative anthropic pressure due to tourism (Micheli & Niccolini, 2013) stresses the need for a major protection effort in this area.

As several other MPAs, TMPA is divided into sub-areas characterised by different levels of protection. Fully protected zones are surrounded by buffer areas, with the main purpose of filtering anthropic disturbances coming from outside the reserve. Ordered according to the stringency of constraints, the protection zones are characterised as follows (Figure 2.2):

i. Zone A – fully protected (529 ha): access is allowed only to MPA staff, police authorities (*e.g.*, coast guard) and researchers for monitoring or scientific purposes. Swimming, navigation, anchoring and any kind on fishing activity are forbidden.

ii. Zone B – general reserve (3,113 ha): artisanal fishing is allowed but only if performed with techniques that do not damage the sea-bottom (trawling is forbidden) and is restricted to professional fishermen residing in coastal villages comprised in the MPA. The TMPA management authority regulates daily catches through permits. Navigation at low speed is also allowed.

iii. Zone C – partial reserve (11,715 ha): professional and recreational fishing are allowed but regulated through permits, with gear not damaging the sea bottom. Navigation at low speed is permitted. Differently from outside MPA boundaries, spearfishing is not allowed.

Outside TMPA, all kinds of legal fishing activities in accordance with the Italian law are permitted, including spearfishing. In this work, we refer to "zones A" or "fully/integrally protected zones" interchangeably, while "partially protected" or "buffer zones" indicate zones B and C.
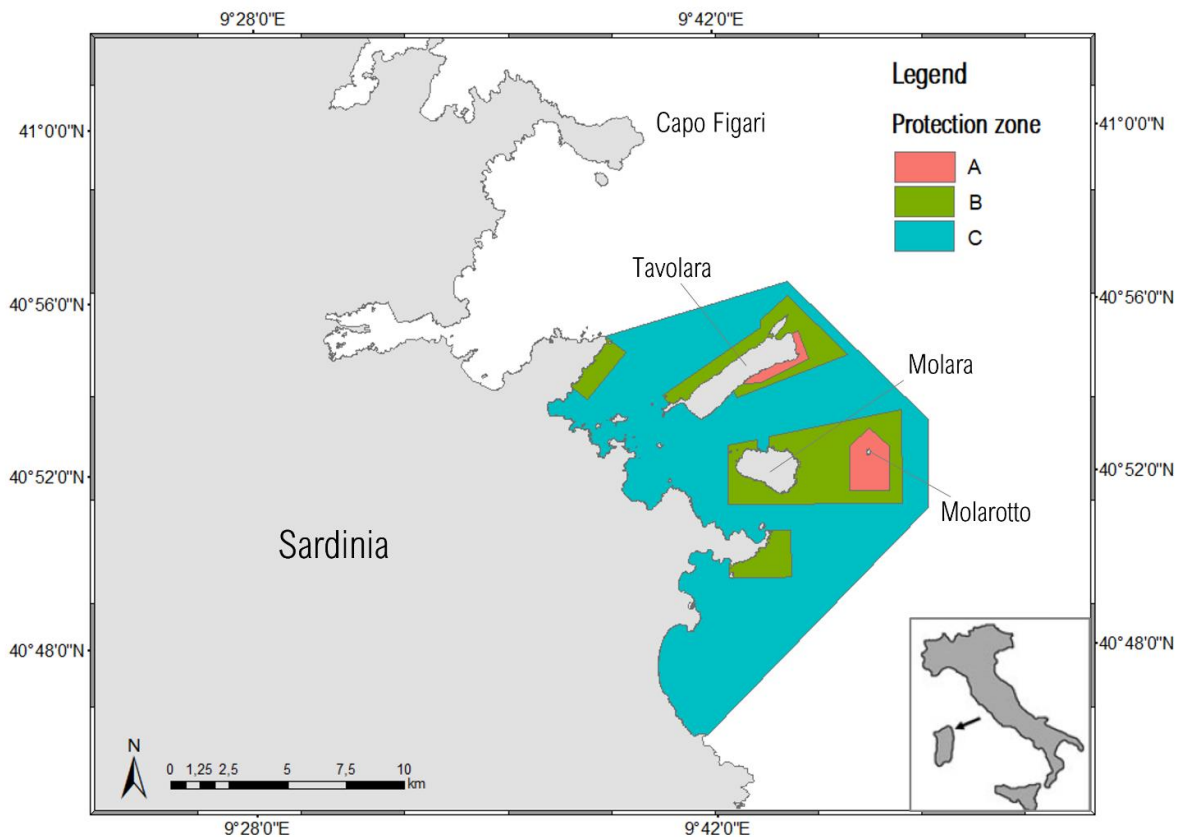
Figure 2.2: Zonation at Tavolara – Punta Coda Cavallo Marine Protected Area.
Created using Esri ArcGIS software (http://www.esri.com/software/arcgis).

At TMPA, where fishing is allowed, gillnets and longlines are the most employed gear (A. Di Franco et al., 2009). Gillnets (Figure 2.3 A) are long rectangular walls of netting kept opened by floats, where fish, with lengths largely dependent upon mesh size, remain entangled. Longlines (Figure 2.3 B) consist instead of a main string with connected branch lines, each having a hook at the free end. (FAO, 2021). For both fishing techniques, concerns have been raised regarding the high level of by-catch that they can generate (FAO, 2021), resulting into a depletion of fish stocks that is not even justified by food provisioning purposes.

Despite non numerous, some significant episodes of illegal fishery have been reported by the TMPA authority, consisting mostly in spearfishing inside the reserve, typically carried out at night-time. Furthermore, authorised fishers complain of systematic incursions of small fishing boats belonging to fishermen non residing in TMPA's municipalities.

At TMPA, staff does not have sanctioning power but does supervise the area. When noticing illegal activities, they report it to the coast guard, which holds police status. However, according to the enforcement analysis of TMPA made by Hogg et al., (2021), the coast guard often does not react to MPA supervisory warnings. The authors report that MPA staff is in further difficulty because of the short duration of their contracts (about eight months), which also hampers governance and long-term planning for the reserve. Overall, in spite of some management difficulties, enforcement at TMPA has been classified as "medium" by Guidetti et al. (2008) and "high" by Sala et al. (2012). It is important to underline that TMPA has not been effectively enforced before 2003-2004, as operational surveillance was lacking in the first years following establishment: this has been taken into account to allow a correct interpretation of ecological data concerning some fish species at TMPA, which will be presented in the next chapters.

Table 2.1: Characteristics of Tavolara – Punta Coda Cavallo Marine Protected Area.

Location	NE Sardinia (40°53'06.2"N, 9°42'57.6"E)
Total surface	15,357 ha
Zone A surface	529 ha (3.4%)
Zone B surface	3,113 ha (20.3%)
Zone C surface	11,715 ha (76.3%)
Year of establishment	1997
Year of effective enforcement	2003-2004
Enforcement level	Medium-high
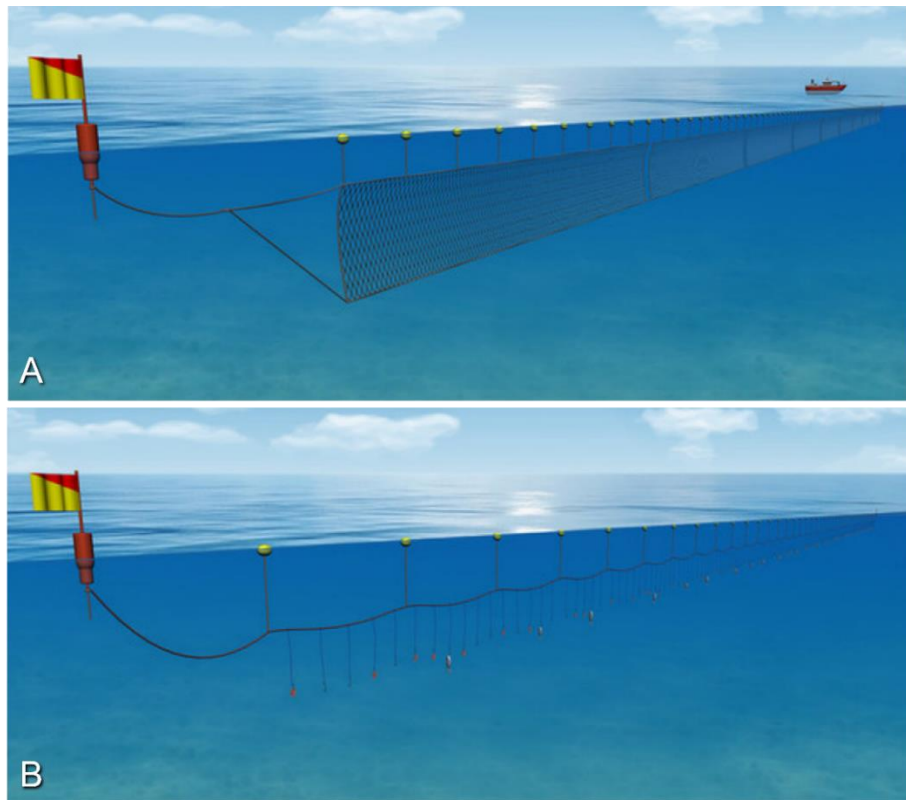
Figure 2.3: Schematic representation of the most used fishing gear at Tavolara – Punta Coda Cavallo Marine Protected Area. **A.** Gillnets, **B.** Longlines.
Images credits: FAO, (2021).

2.2.2 EXISTING EVIDENCE ON EFFECTIVENESS

Past experimental evidence indicates that TMPA has achieved good biological performances in terms of fish assemblages, despite high levels of anthropogenic pressure ascribable to tourism (Micheli & Niccolini, 2013). In a Mediterranean-wide assessment of protection efficacy, Sala et al. (2012) found that TMPA in 2008 ranked highest in terms of total fish biomass among twelve surveyed MPAs. Little is instead known about the state of benthic communities, macroalgal forests included. We know by Fraschetti et al. (2022) that in 26 Mediterranean MPAs they examined, including TMPA, forests were generally in poor conditions, but no specific information was provided at the level of single reserves.

To the best of our knowledge, assessments of the effects of protection at TMPA following its establishment (1997) are based on field data gathered before 2008. Concerning this specific topic, A. Di Franco et al., (2009) analysed data relative to the period 2005-2007 – hence, about two to four years after effective enforcement - and found a positive response to protection at TMPA on biomass and size of fish assemblages, although differences among protection zones were undetectable when data were expressed in terms of density. Furthermore, no variations in biomass and size were detected between partially protected zones (B and C) and between partially and unprotected ones. These results were confirmed by Sahyoun et al. (2013), in an analysis of data acquired in 2007 and 2008.

Virtually no information was instead found with respect to the conditions of TMPA before its establishment. From a methodological perspective, baseline knowledge would be a great advantage in tracking potential ecosystem changes through time. However, some studies referring to the time lapse between enforcement and effective protection are available, somehow depicting TMPA situation before real chances of recovery were provided. In particular, Murenu et al. (2004) carried out the first reserve assessment on rocky reefs after formal establishment and, unsurprisingly, found no differences in 2002 between fully protected zones and unprotected control sites in terms of total fish density. Reinforcing these results, a more detailed study by Guidetti et al. (2008) observed no protection effects at TMPA, both in terms of density and biomass in the years 2002-2003. The analysis also unpacks data at single species and trophic group levels, providing valuable baseline information about rocky reefs ecosystem at TMPA. This knowledge has been of paramount importance to contextualise recent data about five fish species at TMPA and to allow their correct interpretation (see Chapter 3).

Overall, considering the evidence provided by these two studies, we can reasonably and confidently conclude that the lack of actual enforcement at TMPA before 2002-2003 (A. Di Franco et al., 2009) has resulted into the absence of macroscopic protection effects, at least before 2003. We have learned from the above-mentioned studies (A. Di Franco et al., 2009; Sahyoun et al., 2013) that the situation has probably evolved and protection has become a significant explanatory factor at least for fish densities and sizes.

However, it is important to consider that, to date, no studies following the temporal development of the reserve for more than three consecutive years are available. With the present work, we attempt to fill this gap providing a dynamic picture of TMPA's evolution from 2005 to 2021, through the analysis of five key fish species of sea urchin predators inhabiting shallow Mediterranean rocky reefs.

This has been done *via* both quantitative and qualitative analyses (see Chapters 3 and 4) on high-quality datasets whose composition is explained in a dedicated section of the next chapter.

3. Effects of protection on shallow rocky reefs at Tavolara – Punta Coda Cavallo

In Chapter 1, we outlined the main characteristics of shallow Mediterranean rocky reef ecosystems, along with the anthropic threats they are facing. Among them, overfishing is particularly detrimental because it can activate trophic cascade mechanisms that can alter the structure of the whole community. As we have seen, a prominent example is the cause-effect chain linking overfishing of sea urchin predators leading to an increase in key grazers (sea urchins) populations, causing in turn the depletion of macroalgal forests (Figure 1.8). In light of the potential role of these fish in driving community-wide changes, it is fundamental to assess whether and under what conditions they can benefit from relaxation of fishing pressure. To do this, we quantitatively analysed the response to different levels of protection of the four main sea urchin predators (*Diplodus sargus*, *Diplodus vulgaris*, *Coris julis*, *Thalassoma pavo*) inhabiting shallow rocky reefs at Tavolara – Punta Coda Cavallo Marine Protected Area (TMPA), over a period of 17 years (2005-2021). The analysis is also extended to the herbivorous fish *Sarpa salpa*, which is very abundant in the study area. In Sections 3.1 and 3.2, we present the data collection methodology and its statistical treatment, while Section 3.3 is devoted to the exposition of gained insights on the effects of protection and their discussion.

3.1 Data collection and structure

3.1.1 Underwater Visual Censuses and sampling design

Researchers often have difficulties in keeping track of marine ecosystem changes over time due to the absence of sufficiently long time series of observations, or the lack of methodological consistency across samplings. The analysis presented hereafter are based on an exceptionally long time series (17 years) of Underwater Visual Census (UVC) data, acquired with outstanding consistency and regularity throughout the years.

UVC is the most widely used technique for the assessment of fish density and size in shallow subtidal reefs (Edgar et al., 2004). It involves the immersion of a trained operator (Figure 3.1) who swims at constant speed on a path of given length, recording the number of encountered fish of each species and classifying them into size classes. At TMPA, UVCs were carried out along strip transects 25 m long and 5 m wide, recording specimen of *Diplodus sargus*, *Diplodus vulgaris*, *Coris julis*, *Thalassoma pavo* and *Sarpa salpa*, divided into 2 cm size classes. Sampling was performed on "pure" rocky areas, with other substrates - such as sand or seagrass - representing less than 5% in cover. Sampling was carried out in zones characterised by protection A, B and C as well as unprotected ones (named "EXT"), used as control sites. For each zone, 2 locations (Figure 3.3) were selected at a distance of 2.5 to 18 km and, for each location, 2 sites were randomly chosen, about 100 m apart from each other. Within each site, 4 replicates (*i.e.*, UVC transects) were performed at two depth intervals, namely 5-11 m and 12-19 m. This sampling scheme is summarised in Figure 3.2. Overall, for each acquisition campaign, 128 replicates were performed, 32 for each protection level.

Figure 3.1: A diver performing an underwater visual census. Pads are used to keep track of individuals encountered and their relative size class.
Photo credits: ISPRA – Istituto Superiore per la Protezione e Ricerca Ambientale
(https://www.youtube.com/watch?v=b7gYYg4n7SE)
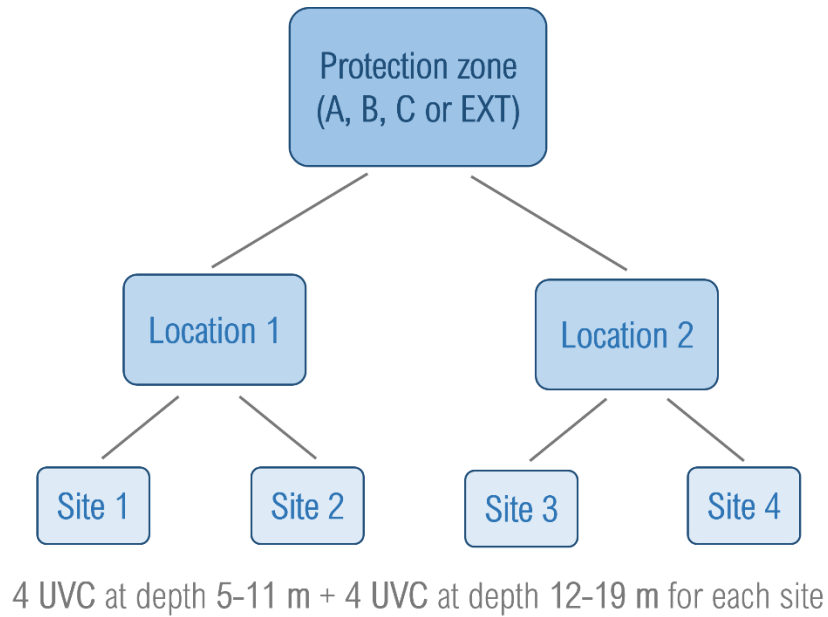
Figure 3.2: Underwater Visual Census (UVC) sampling scheme. In each campaign, a total of eight UVCs are performed in each site.
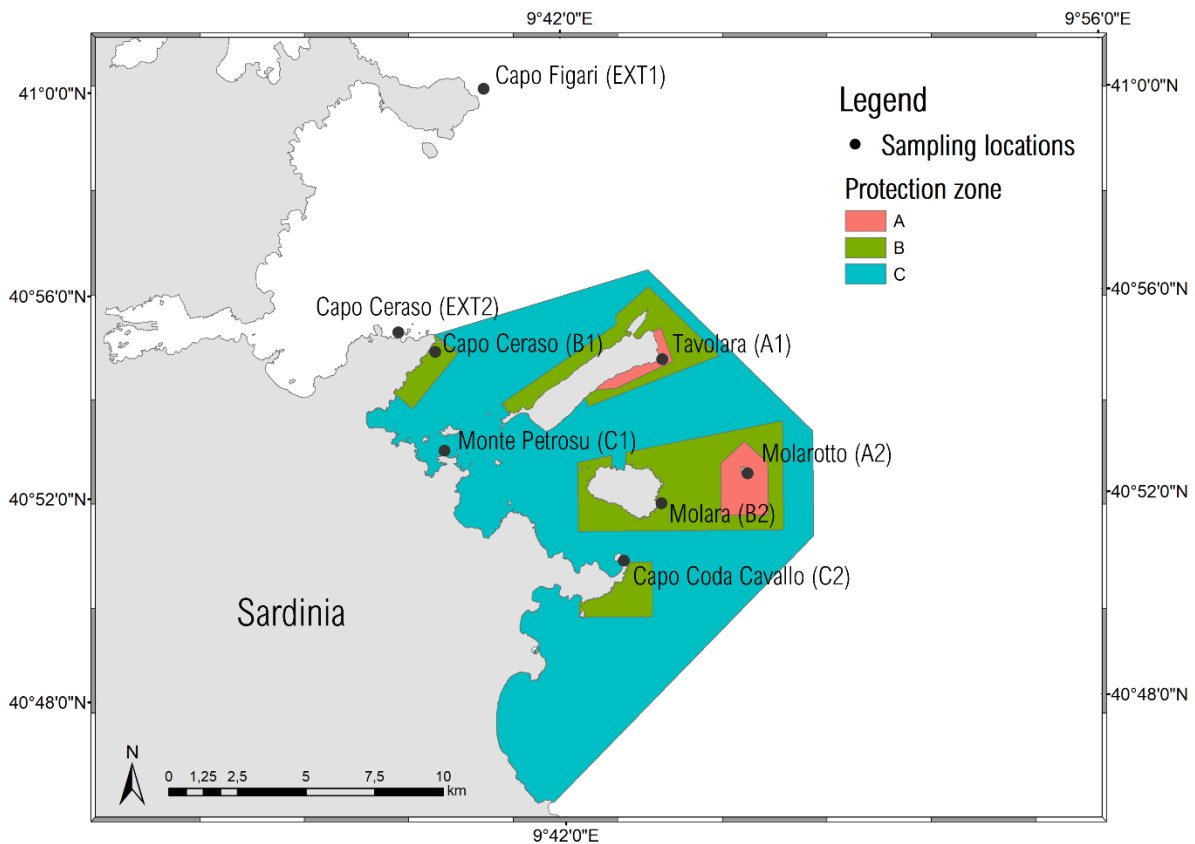
Figure 3.3: Sampling locations at Tavolara – Punta Coda Cavallo Marine Protected Area. For each protection zone, two locations were selected. Created using Esri ArcGIS software (http://www.esri.com/software/arcgis).

This very same procedure has been applied in all the 26 campaigns carried out between 2005 and 2021 (see Appendix, Table A.1), resulting into 3328 UVC observations for all species. Data are missing only for 2015, whereas for all other years one or two campaigns were carried out. Sampling locations remained unvaried through time, whereas some small changes, not impairing data consistency, have occurred at the level of sites due to operational needs.

UVC data are usually affected by high variability, as fish detection in each transect is dependent on a very wide array of environmental factors acting at the site-scale (*e.g.*, habitat composition, behavioural characteristics of fish). Furthermore, data are also affected by intrinsic UVC limitations (Edgar et al., 2004). There is an obvious dependence on the observer (*i.e.*, the diver), who might introduce systematic measurement errors by consistently under- or over- estimating fish lengths, for all size classes or only for a subset. Different divers might also have different detection abilities, or visibility conditions might change from one replicate to another.

At TMPA, effort was put in reducing the extent of sampling errors and enhancing data representativeness (P. Guidetti, personal communication) by:

i. Carrying out multiple replicates for the same sites (8 replicates per site, for a total of 128 replicates per campaign) and, when possible, more than one campaign per year.
ii. Selecting sites with similar habitat features.
iii. Limiting, as far as possible, changes in trained divers throughout the years.

Researchers at TMPA also tried to maintain homogeneity in substrate lithology among sampling sites but effort in this direction was limited by the exclusively granitic nature of the two partially protected areas (B and C), whereas zones A and EXT are represented by both granitic and calcareous sites. Among species included in this analysis, only *Thalassoma pavo* responds to substrate mineralogy and is more likely to be present at higher densities on calcareous zones (Guidetti et al., 2004). Unfortunately, this factor was out of researchers' control at TMPA.

3.1.2 FROM DENSITY TO BIOMASS DATA

From UVCs at TMPA, researchers obtained densities of observed fish of each species divided into size classes, expressed in number of individuals per transect or, alternatively, in number of individuals/125 m², as the transect dimensions are 25m × 5m. By means of relationships linking fish

length to their wet body weight, it was possible to obtain fish biomass data for each transect. Classical length-weight relationships are expressed by Eq. 1, where L (cm) is fish length and and W (g) is the associated wet weight.

$$W = aL^b \qquad \text{Eq. 1}$$

Parameters a and b are species-dependent and are obtained through linear regression on the logarithmic form of the equation (Eq. 2).

$$\log(W) = \log(a) + b \log(L) \qquad \text{Eq. 2}$$

As site-specific estimates of a and b were not available for TMPA, values have been taken from the literature and from FishBase (Froese & Pauly, 2023), selecting sets referring to Mediterranean samples whenever possible (Table 3.1, P. Guidetti, personal communication). Resulting biomass data for each species are therefore expressed in grams of fish/125 m².

Finally, for the sake of the analyses presented in the next sections of this chapter and in Chapter 4, three different datasets have been created, containing respectively:

i.   Density data (individuals/125 m²) divided into size classes, namely the "raw" dataset obtained from UVCs.
ii. Aggregated density data (individuals/125 m²), obtained from the "raw" dataset version by summing the densities of all size classes.
iii. Aggregated biomass data (grams/125 m²), obtained transforming density data of each size class in biomass through length-weight relationships and eventually summing biomasses relative to all size classes.

Table 3.1: Length-weight relationship (Eq. 1) parameters for the species involved in this analysis (P. Guidetti, personal communication).

	a	b
Diplodus sargus	0.0114	3.1317
Diplodus vulgaris	0.0149	3.0058
Coris julis	0.007	3.0462
Thalassoma pavo	0.007	3.0462
Sarpa salpa	0.0323	2.7004

3.2 STATISTICAL TREATMENT OF DATA

As discussed in the previous section, temporal and spatial changes in environmental conditions can result into high variability of UVC data. To reduce the effects of this noise source, data from sites belonging to the same location were averaged. Thus, in the ensuing versions of datasets, spatial specification of data does not go beyond the location level, still maintaining the specification of sampling depth.

The aim of the analyses presented in this chapter is to understand what are the drivers of the response to protection of five fish species at TMPA, as well as to unveil potential trends in their density or biomass through the years. To do so, we analysed density and biomass data[3] employing statistical multiple linear regression modelling. The rationale behind the use of such models typically falls into two broad categories. This technique can be used to find the parameters of a linear relationship between a dependent variable and multiple independent ones, thus obtaining a predictive tool that, once fed with "new" sets of independent variables, can give a prediction of the dependent one. Alternatively – but still laying on the same mathematical structure – multiple linear regressions can be used to explore whether a variation in the dependent variable (or "response") can be attributed to a variation of one or more independent ones, also called "explanatory" variables, or "covariates". In other words, linear regressions allow quantifying the strength of possible relationships between these two kinds of variables, by means of a hypothesis testing procedure. It is to be noted that relationships between variables individuated through regressions might be spurious, meaning that they are not necessarily of causal nature. However, if effort is put in creating appropriate experimental designs, it may be possible to rule out spuriousness and hypothesise the existence of some cause-effect relationships (Rosenthal, 2017). In the context of this work, we exploit multiple linear regression model in this latter declination, to understand to what extent protection zone, depth and year of sampling have an influence on observed densities and biomasses. The sampling scheme at TMPA was designed so to isolate the effects of protection from those of other environmental factors, such as habitat heterogeneity, to the maximum extent possible. However, obviously, not all the variability in the data can be explained by the independent variables included

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[3] Data used for this analysis are aggregated (*i.e.*, without the distinction into size classes) density and biomass, contained in datasets ii. and iii. as outlined in Section 3.1.2.

in the analysis due to unaccounted-for sources of variability and to the stochastic nature of environmental processes.

3.2.1 Multiple linear regression models

Using the software "R" (R Core Team, 2022), we fitted two linear regression models for each of the five species included in the analysis, one for density and one for biomass values. Models share the following shape:

$$y = \beta_0 + \beta_1 \cdot Pro + \beta_2 \cdot De + \beta_3 \cdot t + \gamma_1 \cdot Pro \cdot De + \gamma_2 \cdot Pro \cdot t + \gamma_3 \cdot De \cdot t + \varepsilon \qquad \text{Eq. 3}$$

where:

i. y = density (individuals/125 m²) or biomass (grams/125 m²) of the considered species.

ii. Pro = protection zone where sampling was carried out, a categorical variable with 4 levels ("A", "B", "C", "EXT"). In "EXT" zones protection is absent.

iii. De = depth of the sampling, a categorical variable with 2 levels ("5-11 m", "12-19 m").

iv. t = time of the sampling, expressed by the year when it occurred. It is a numerical variable belonging to the range 2005-2021.

v. ε = modelling error (individuals or grams/125 m²), $\varepsilon \sim N(0, \sigma^2)$ by linear regression hypothesis.

vi. $\beta_0, \beta_1, \beta_2, \beta_3, \gamma_1, \gamma_2, \gamma_3$ are the parameters of the regression and are estimated through the maximum likelihood method[4].

The cross-product terms introduced by γ coefficients in Eq. 3 are called "interaction terms" and have been included to assess whether the value assumed by a variable depends upon the value assumed by another one. For instance, the interaction between protection and depth allows understanding whether the effects of protection are felt differently at the two considered depths. The same structure of Eq. 3 was used to create two additional models, one for total density and one for total biomass observed in each transect.

A reduced form of each model was obtained using backward stepwise selection, with stopping rule chosen based on Akaike Information Criterion (AIC). AIC estimates the relative information loss of

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[4] Maximum likelihood method, under the hypothesis of normality and homoscedasticity of residuals, coincides with ordinary least squares.

a model with respect to other candidate models. Among models with the same explicative capability, the final choice falls on the one with the least number of parameters.

Finally, to assess the statistical significance of the regression parameters, we run an ANCOVA[5] (ANalysis of CO-VAriance) F-test on all regression models, testing hypothesis H_0 against the alternative H_1.

H_0: $\beta_1 = \beta_2 = \beta_3 = \gamma_1 = \gamma_2 = \gamma_3 = 0$

H_1:   at least one model coefficient is not equal to 0.

The significance threshold was set at *p-value* of 0.05, so, coefficients for which the calculated *p-value* exceeded the threshold were not considered significant. When ANCOVA revealed a significance in protection, the Tukey Honestly Significant Differences (Tukey HSD) *post-hoc* pairwise comparison test was run to understand which protection levels significantly differ from the others.

Finally, to make sure that the results of the models were not driven by seasonal variability among different campaigns, we repeated the same analyses considering only one campaign per year, carried out in spring or summer, and obtained the same results.

The above-described quantitative analyses were supported by a graphical counterpart, whose most informative elements are reported in Section 3.3.

3.2.2 VERIFICATION OF ANCOVA AND REGRESSION HYPOTHESES

Before running the ANCOVA test, we verified that the underlying assumptions were met by available data. In particular, we checked for data normality and homoscedasticity within each possible subpopulation, namely within the groups of observations characterised by the combination of all protection levels at all depth (8 groups, 4 protection levels × 2 depth levels). We used Shapiro-Wilk (Shapiro & Wilk, 1965) and Levene (Levene, 1960) tests to assess normality and homoscedasticity, respectively. To meet these assumptions, we applied some transformations on the independent variables (density and biomass data). Distributions of both variables were generally

---

[5] ANCOVA was used instead of ANOVA (ANalysis Of VAriance) as, other than the two categorical variables *Pro* and *De*, a continuous variable (T), that is co-varying with the response variable, is also present. The same function `anova()` is used in R software for both tests.

positively skewed, with higher variance associated to high values. To address these issues and obtain normal and homoscedastic data, we made use of logarithmic and Box-Cox transformations (Box & Cox, 1964), the latter shown by Eq. 4.

$$y' = \begin{cases} \frac{y^\lambda - 1}{\lambda}, & \lambda \neq 0 \\ ln(y), & \lambda = 0 \end{cases} \qquad \lambda \in \mathbb{R} \qquad\qquad \text{Eq. 4}$$

where y are the original observations and y' the transformed ones.[6]

For density and biomass data of all species, except for *Sarpa salpa*, downstream of the transformations outlined in Table 3.2, we obtained normality for almost all groups of observations whereas homoscedasticity was verified in all cases. However, ANCOVA test is generally considered robust to small departures from normality. Unfortunately, no transformation produced the desired outcomes for *Sarpa salpa*. We still used log-transformed data, as they were closer to normality and homoscedasticity than non-transformed ones, but we lowered the significance threshold for this species to a *p-value* of 0.01, to compensate for the increased likelihood of Type I error (sensu Underwood, 1996). Results for this species are anyway to be considered more cautiously. Difficulties in producing normal and homoscedastic data for *S. salpa* are probably ascribable to its schooling behaviour: if schools are not present while UVC is being carried out, it is very likely that no lone individuals are observed, resulting into a zero value in the UVC dataset record. Indeed, absence of specimen of *S. salpa* was recorder for 1275 replicates over the 3328 (38%) carried out from 2005 to 2021. Ultimately, the presence of many zero data points makes it more difficult to address normality and homoscedasticity issues through transformations.

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[6] To assess whether data transformation influenced the outcome of models, we run the non-parametric Scheirer Ray Hare test on original data and verified that they gave the same results as multiple regression models in terms of variable significance.

Table 3.2: Data transformations employed for density and biomass data. In some cases, $log(y + 1)$ transformation is used instead of $log(y)$ because the latter generates -Inf data points if zeroes are present in the dataset.

	Transformations of density data	Transformations of biomass data
Diplodus sargus	$log(y + 1)$	$log(y + 1)$
Diplodus vulgaris	Box-Cox, $\lambda = 0.600$	Box-Cox, $\lambda = 0.070$
Coris julis	$log(y)$	Box-Cox, $\lambda = 0.545$
Thalassoma pavo	Box-Cox, $\lambda = 0.250$	Box-Cox, $\lambda = 0.263$
Sarpa salpa	$log(y + 1)$	$log(y + 1)$
Total density or biomass	$log(y)$	$log(y)$

Finally, as we saw in Eq. 3, linear regressions assume the modelling error $\mathcal{E}$ to be normally distributed with homogeneous variance. We checked this by visual inspection of QQ-plots and studentised residuals *vs* fitted values plots.

In principle, ANCOVA and regression models also require observations to be temporally and spatially independent among each other. In the present case, spatial independence of observations was achieved thanks to a careful sampling design, while temporal independence is not met, as samplings follow the evolution of the same sites throughout the years. We addressed part of this problem with the inclusion of the temporal covariate T, which explains a certain amount of variability in density and biomass data. Despite the above-described methodology was held sufficiently robust to achieve the goals of this analysis and, more broadly, the purposes of this work, we still recognise the lack of temporal independence as a limitation of the analysis, leaving room for possible future improvements based on statistical techniques that are unsensitive to temporal dependence.

3.3 EFFECTS OF PROTECTION ON POPULATION DYNAMICS OF FIVE KEY FISH SPECIES

The aim of this section is to give a dynamic picture of the effectiveness of different protection regimes in force within TMPA boundaries, evaluated on four species of sea urchin predators (*Diplodus sargus*, *Diplodus vulgaris*, *Coris julis* and *Thalassoma pavo*) and on the herbivore *Sarpa salpa*, all participating to the trophic cascade presented in Section 1.3. To this end, results obtained from the ANCOVA

tests (Section 3.2) on both biomass and density (or "abundance") data, are reported together with supporting graphical analyses.

The rationale for keeping the two variables separated emerges clearly from Figure 3.4, which reports the shares of total biomass and density relative to each species observed during sampling years. Smaller fish like the two wrasses *C. julis* and *T. pavo*, although giving rather little contributions to total biomass, are instead more represented when data are expressed in terms of density, while the opposite is true for the two seabreams, particularly for *D. sargus*. Furthermore, the two variables typically differ both in terms of response to protection and of characteristics of the fish populations they depict.
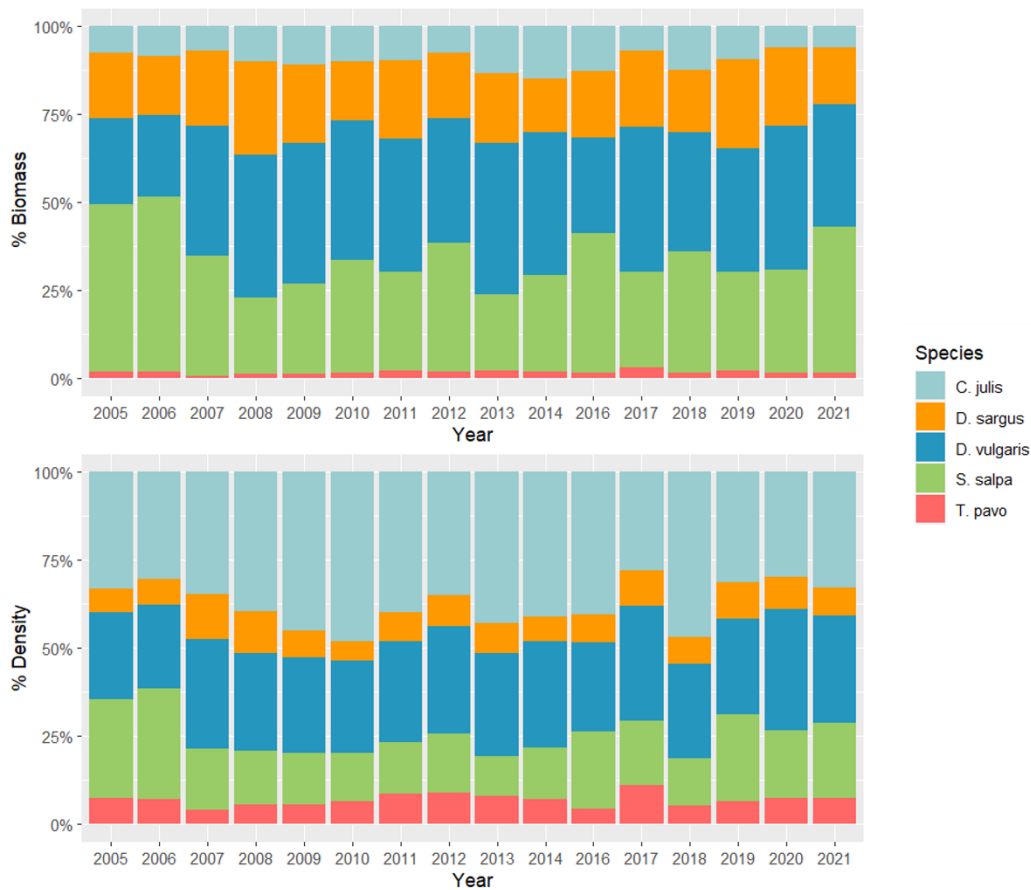
Figure 3.4: Relative contributions of each study species to total biomass (top-panel) and total density (bottom-panel) throughout the years. Shares remained rather constant during the study period.

A summary of the results obtained through ANCOVA tests are presented in Table 3.3 and Table 3.4, where statistically significant effects of the considered variables are shown. The most relevant aspect to highlight is that protection proved to be significant for each study species and for cumulative

variables, with data expressed both in terms of abundances and biomass (ANCOVA F-test, *p-value* << 0.05). *Post-hoc* pairwise comparison tests (Table A.2 and A.3, Appendix) revealed higher densities and biomasses in fully protected zones (A) with respect to partially protected (B, C) or unprotected ones (EXT), as visually perceivable from Figure 3.5 and Figure 3.6. Indeed, when considering the study period as a whole, mean biomass and density in fully protected locations were respectively 3.5 and 1.6 times higher than in unprotected ones.

As it emerges from this latter consideration and from a graphical comparison of the two study variables (Figure 3.5, Figure 3.6), however, a much clearer response to protection is observable in biomass rather than in density data.

Table 3.3: Summary of the results of the ANCOVA F-test on biomass data. Meanings of variables are reported in Section 3.2. S (green) = significant, *p-value* < 0.05, NS = non-significant, *p-value* ≥ 0.05, Upwards and downwards pointing arrows stands for positive and negative trends respectively. This information is drawn from the sign of the regression parameter associated with ***t***.

|	*Pro*	*De*	*t*	*Pro* × *t*	*Pro* × *De*	*De* × *t*
Diplodus sargus	S $p < 2*10^{-16}$	NS	NS	NS	NS	NS
Diplodus vulgaris	S $p < 2*10^{-16}$	S $p = 0.02$	NS	NS	NS	NS
Coris julis	S $p = 5.1*10^{-4}$	NS	S ↘ $p = 8.4*10^{-13}$	NS	NS	NS
Thalassoma pavo	S $p < 2*10^{-16}$	S $p = 5.3*10^{-14}$	S ↗ $p = 0.03$	NS	NS	NS
Sarpa salpa	S $p = 2.8*10^{-9}$	NS	NS	NS	NS	NS
Total biomass	S $p < 2*10^{-16}$	NS	S ↘ $p = 4.4*10^{-4}$	NS	NS	NS

Table 3.4: Summary of the results of the ANCOVA F-test on density data. Meanings of variables are reported in Section 3.2. S (green) = significant, *p-value* < 0.05, NS = non-significant, *p-value* ≥ 0.05, NS* (yellow) = weakly significant, 0.05 ≤ *p-value* ≤ 0.08. , Upwards and downwards pointing arrows stands for positive and negative trends respectively. This information is drawn from the sign of the regression parameter associated with *t*.

	Pro	*De*	*t*	*Pro* × *t*	*Pro* × *De*	*De* × *t*
Diplodus sargus	S $p = 1.4*10^{-8}$	S $p = 0.02$	NS	NS* $p = 0.06$	NS	NS
Diplodus vulgaris	S $p < 2*10^{-16}$	NS	NS	NS	NS	NS
Coris julis	S $p = 1.2*10^{-3}$	NS	S ↘ $p = 2.5*10^{-11}$	NS	NS	NS* $p = 0.08$
Thalassoma pavo	S $p < 2*10^{-16}$	S $p < 2*10^{-16}$	S ↗ $p = 0.02$	NS	NS	NS* $p = 0.08$
Sarpa salpa	S $p = 7.2*10^{-4}$	NS	NS	NS	NS	NS
Total density	S $p < 2*10^{-16}$	S $p = 0.01$	S ↘ $p = 7.6*10^{-6}$	NS	NS	NS
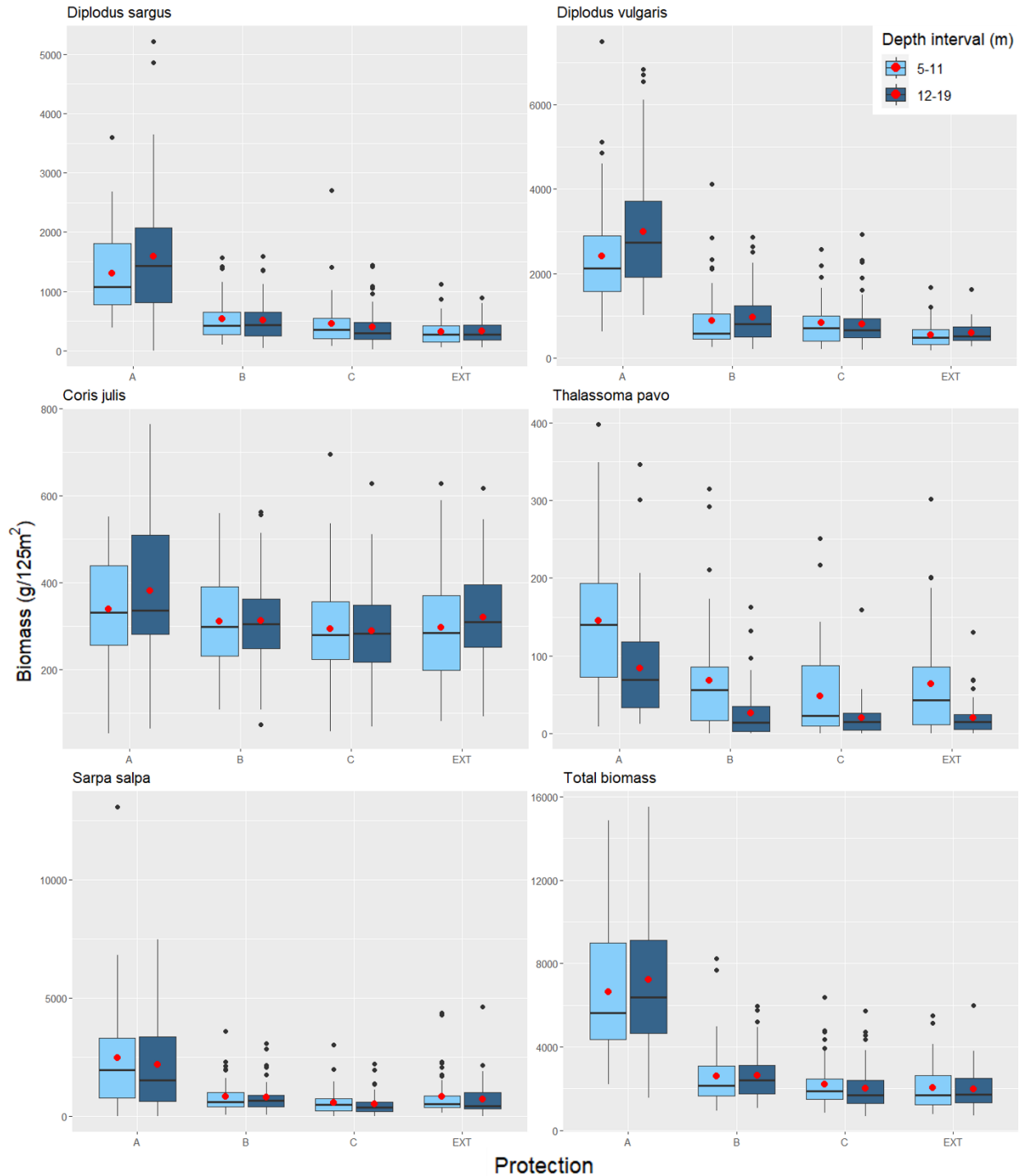
Figure 3.5: Interquartile ranges (IQR, boxes), median (horizontal bars) and mean (red dots) of biomass in protected and unprotected zones, in shallow (5-11 m) and deep (12-19 m) areas. The upper whisker is the maximum value within 1.5*IQR over the third quartile and the lower whisker is the minimum value within 1.5*IQR below the first quartile.
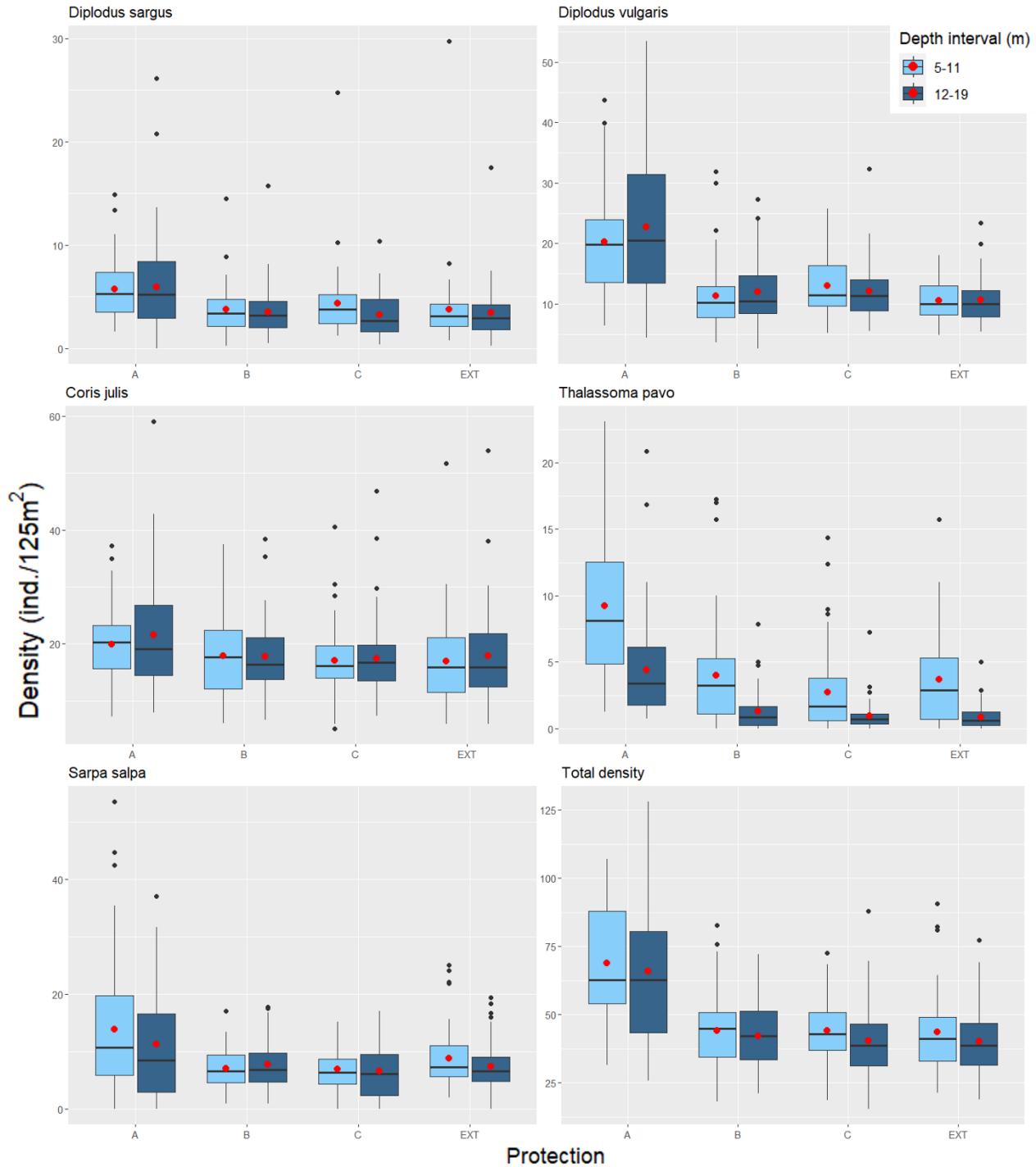
Figure 3.6: Interquartile ranges (IQR, boxes), median (horizontal bars) and mean (red dots) of density in protected and unprotected zones, in shallow (5-11 m) and deep (12-19 m) areas. The upper whisker is the maximum value within 1.5*IQR over the third quartile and the lower whisker is the minimum value within 1.5*IQR below the first quartile.

This is in line with previous results from the same MPA covering the period 2005-2007 (A. Di Franco et al., 2009), where effects on density were not detected at all, and other local (e.g., Abecasis et al., 2015) and Mediterranean-wide (e.g., Giakoumi et al., 2017) MPA assessments. The differential effect of protection on the two variables suggests that rather than fostering a large increase in fish density – which might be limited by the establishment of competition dynamics for shared resources – the relaxation of fishing pressure in fully protected zones mainly results in an increase in the average size of fish and, consequently, in biomass. This hypothesis is confirmed by the analyses on species distributions into size classes presented in Chapter 4. Indeed, as already recalled, fishing selectively targets large-sized fish due to their higher commercial value; as it happened at TMPA, once this stressor is removed, increases in size and biomass are typically attained.

Among the five studied species at TMPA, only the two sea breams *D. sargus* and *D. vulgaris* are directly targeted by commercial fishing. Not surprisingly, they are the two species benefiting the most from protection, with mean biomasses respectively 4.5 and 4.8 times higher inside fully protected zones than in open access fished areas. Another reason that might explain this high conservation success is inherent to *Diplodus* protandrism.[7] Since individuals switch sex from male to female at a given age, larger individuals living in fully protected zones (targeted by fishery outside), are likely to be big reproductive females that give a substantial contribution to population recovery in fully protected zones. The ratio between mean biomass under full protection over mean biomass in control sites (EXT) is instead lower for the other three species (1.2 for *C. julis*, 2.7 for *T. pavo* and 3.0 for *S. salpa*), but still relevant. This leads us to hypothesise that commercially unimportant species at TMPA are threatened by other forms of fishing (*e.g.*, recreational), or that they end up in fish landings as by-catch. The two wrasses (*C. julis* and *T. pavo*) are known to be recreational fisher targets (Froese & Pauly, 2023; Škeljo et al., 2012) . Concerning *S. salpa*, instead, the analyses presented in Chapter 4 and published evidence referring to Mediterranean sites (Buñuel et al., 2020), support the by-catch hypothesis. However, to be confirmed, these considerations should be underpinned by practical evidence emerging from field observations.

Overall, our results deliver a positive picture of TMPA effectiveness, very different from the one emerging from past samplings carried out before effective enforcement was in place (2003-2004, see

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[7] Prodandrism is more often reported in the literature for *Diplodus sargus* than for *Diplodus vulgaris* (see Section 1.3.3)

Section 2.2). All the five species had been included in samplings carried out in 2002-2003 at TMPA (Guidetti et al., 2008), from which no significant effects of protection emerged – neither in biomass nor in density – as fishing bans and access restrictions were not yet respected. From this comparison, it clearly emerges that the establishment of the MPA allowed the recovery of the considered species. Recovery seems to have occurred rather rapidly: as shown in Figure 3.7 and Figure 3.8, biomass in fully protected zones was already higher than that in partially protected and unregulated ones already in 2005, namely only two years after actual protection was established. As pointed out by A. Di Franco et al. (2009), there seems to be an apparent misalignment between the achievement of such high biomass values in only two years and the growth rates of the studied species. This can in fact be explained considering that fish tend to modify their behaviour after a reduction in anthropogenic disturbance is perceived. For instance, when fishing is no longer a threat, individuals typically rise from deeper reefs that they used as refuge towards shallower areas, re-populating shallow rocky reefs in a relatively short time (A. Di Franco et al., 2009).

Notwithstanding, fully protected zones kept hosting high levels of biomass and density over the years. Indeed, the interaction $Pro \times t$ is always non-significant (ANCOVA F-test, $p\text{-value} > 0.05$)[8]. From Figure 3.7 and Figure 3.8, it can be noticed that the lines representing the temporal evolution of the studied species in each protection zone are characterised by high noise. This is a typical characteristic of biological data as life-history traits (*e.g.*, birth, mortality and recruitment rates) are very much affected by random variations in environmental conditions. Moreover, sampling uncertainty certainly adds to these noise sources. Some trends can however be detected both graphically and quantitatively. ANCOVA highlighted significant linear trends in *C. julis* (negative) and *T. pavo* (positive) density and biomass across the years. A decreasing tendency in both variables for *C. julis* is also evident from Figure 3.7 and Figure 3.8, whilst positive trends of *T. pavo* are less visually clear. These results further confirm the observed Mediterranean-wide decline in populations of the cold-water wrasse *C. julis*, which is being displaced from large portions of the Mediterranean due to warming sea temperature, along with increases in populations of the thermophilic wrasse *T. pavo* (see Section 1.3.3). *T.pavo* preference for shallow and warmer waters clearly emerges from our analysis: sampling depth is significant both in terms of density and for biomass (ANCOVA F-test, *p-*

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[8] The interaction *Pro* × t is only weakly significant (*p-value* = 0.06) for *D. sargus* density. Its effects can be observed in Figure 3.8Figure 3.8 (first panel from the top): protection seem to have acted differently in the last study years, with densities in A zones approaching those in B, C and EXT zones.

value < 2*10^{-16} and p-value = 5.3*10^{-14} respectively). Significative negative trends also emerged for total biomass and density, regardless of protection regime (interaction *Pro* × *t* not significant). Declines are undetectable at the species level (except for *C. julis*) but turn out to be significant when all taxa are pooled. These declines might be due to local stressors (*e.g.*, potential increases in legal and illegal fishery) as well as to drivers acting on a wider spatial scale (*e.g.*, habitat degradation due to water pollution and climate change), making it very hard to identify specific causes. Sampling on other fish species in shallow rocky reefs at TMPA may contribute to assess whether declines in total density and biomass concern also wider group of species.

Further relevant results of the present analysis are relative to the role of partially protected zones (B and C), which unfortunately do not outperform control areas (EXT) as much as it may be expected. *Post-hoc* pairwise comparison tests revealed no differences at all between the two levels of partial protection and between partially protected and control zones for all species (A > B = C = EXT), when data were expressed in terms of density. This is in line with previous results at TMPA from A. Di Franco et al., (2009). Differently from that study, however, we found some statistically significant – but still small – differences when using biomass data. Zones B and C differ only in terms of *S. salpa* biomass and total biomass (B > C), while differences between partially protected zones and unprotected ones are significant only for the two *Diplodus* species. Previous analyses on a Mediterranean scale have reported overall limited effects of partial protection (Giakoumi et al., 2017; Sala et al., 2012) in recovering fish stocks, questioning their efficacy and ecological role (Giakoumi et al., 2017). These results might be explained by a possible concentration of fishing effort in areas immediately close to the boundaries of fully protected zones, to exploit potential spill-over of fish from the reserve. Despite fishing is regulated through permits in B and C zones, illegal fishing episodes have been documented at TMPA by Hogg et al. (2021) and they also emerge from grey literature found on the Internet. Despite direct evidence is needed – possibly through monitoring and interviews with MPA authority and coast guards – these episodes might partially explain our results.

Overall, the analysis presented in this chapter highlight the rather rapid and long-lasting effects of full protection at TMPA supporting the population recovery of sea urchin predators and the herbivore *S. salpa*. Full protection effects have been maintained, net of some fluctuations, during the whole duration of the study period for all species. Results also call for a more careful evaluation of aims and expected effects of buffer zones at TMPA, possibly including other important fish species in the analysis. Broadening the view to the dynamics of the whole ecosystem, the highlighted

protection effects on sea urchin predators can potentially cascade to lower levels of the trophic chain, namely sea urchins and forest-forming algae, as described in Chapters 1 and 2, inducing benefits at the ecosystem scale. Also the herbivore *S. salpa* was shown to benefit from protection and, despite it is not considered to cause relevant macroalgal decline alone, its relationship with macroalgal beds should be more carefully evaluated.

Very importantly, at TMPA, the indicative threshold of 15 *Diplodus* fish over 100 m^2 (Guidetti & Sala, 2007) needed to exert a top-down control of urchin populations has been reached and exceeded (22 individuals/100 m^2)[9], but only in fully protected areas. In these zones, there might be the right conditions for attaining a reduction of grazing pressure on macroalgae and for allowing natural or human-induced recovery of macroalgal forests.
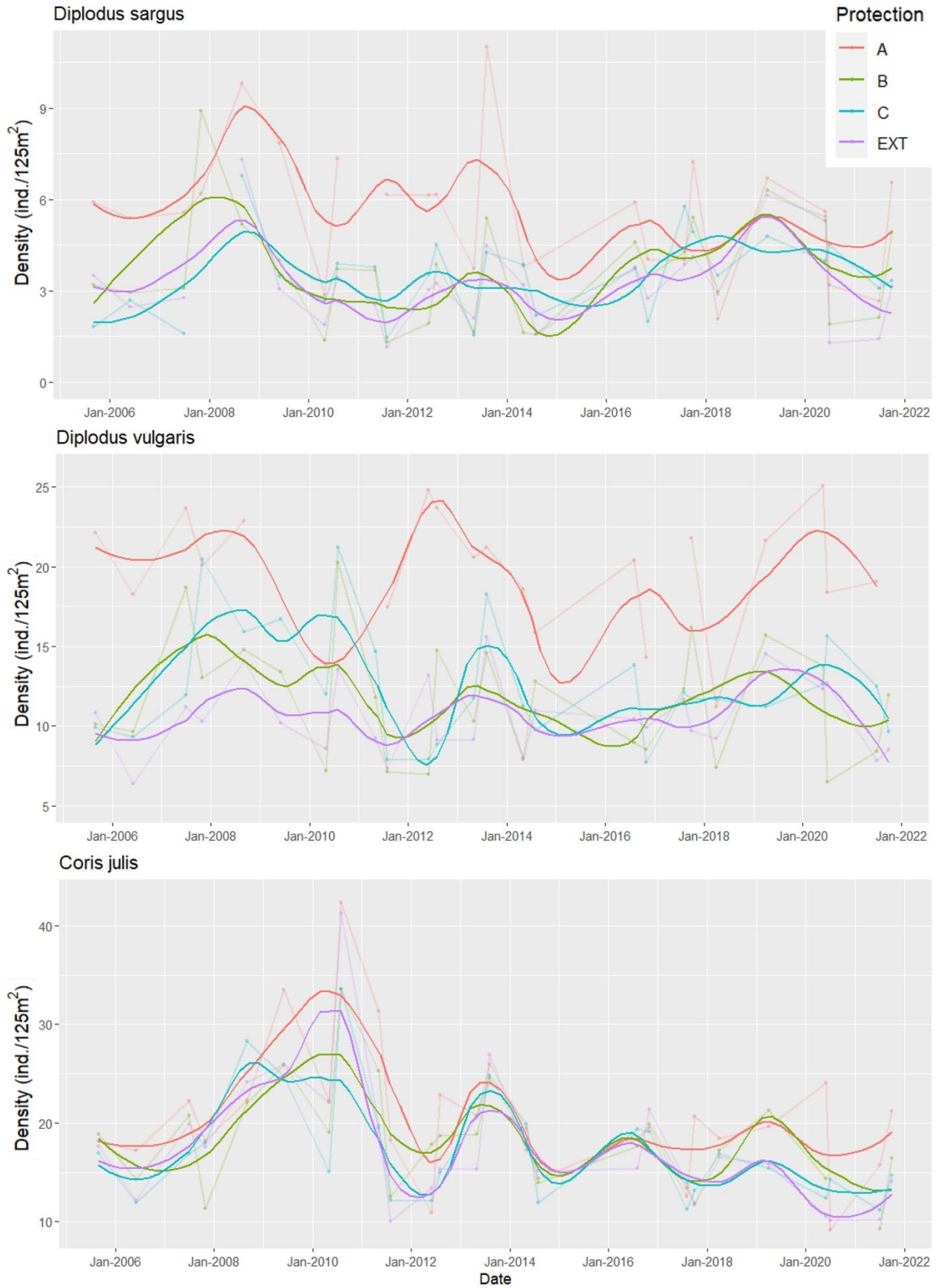
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[9] Mean densities on all study periods for the two *Diplodus* fish have been calculated and summed to obtain this value.
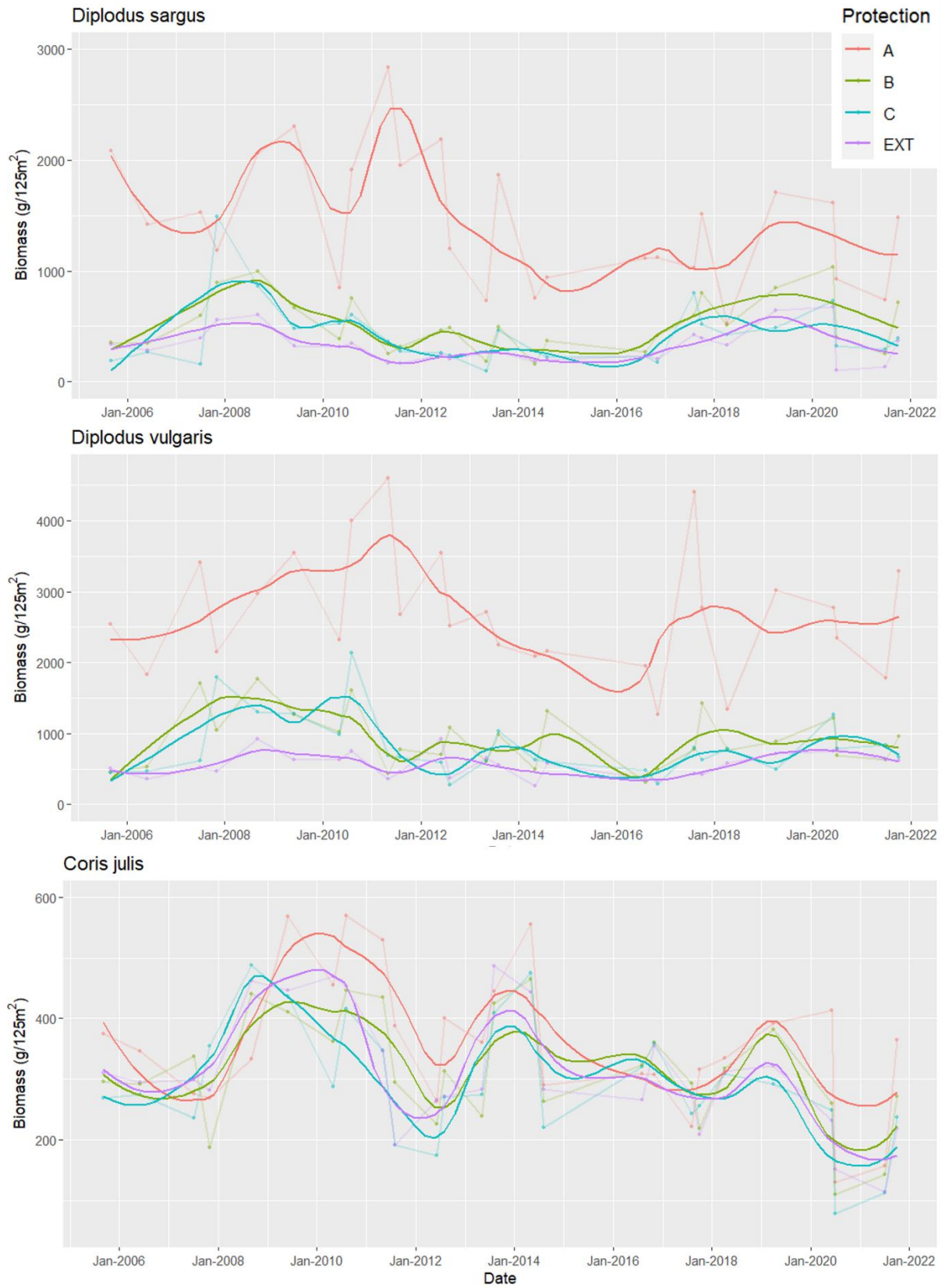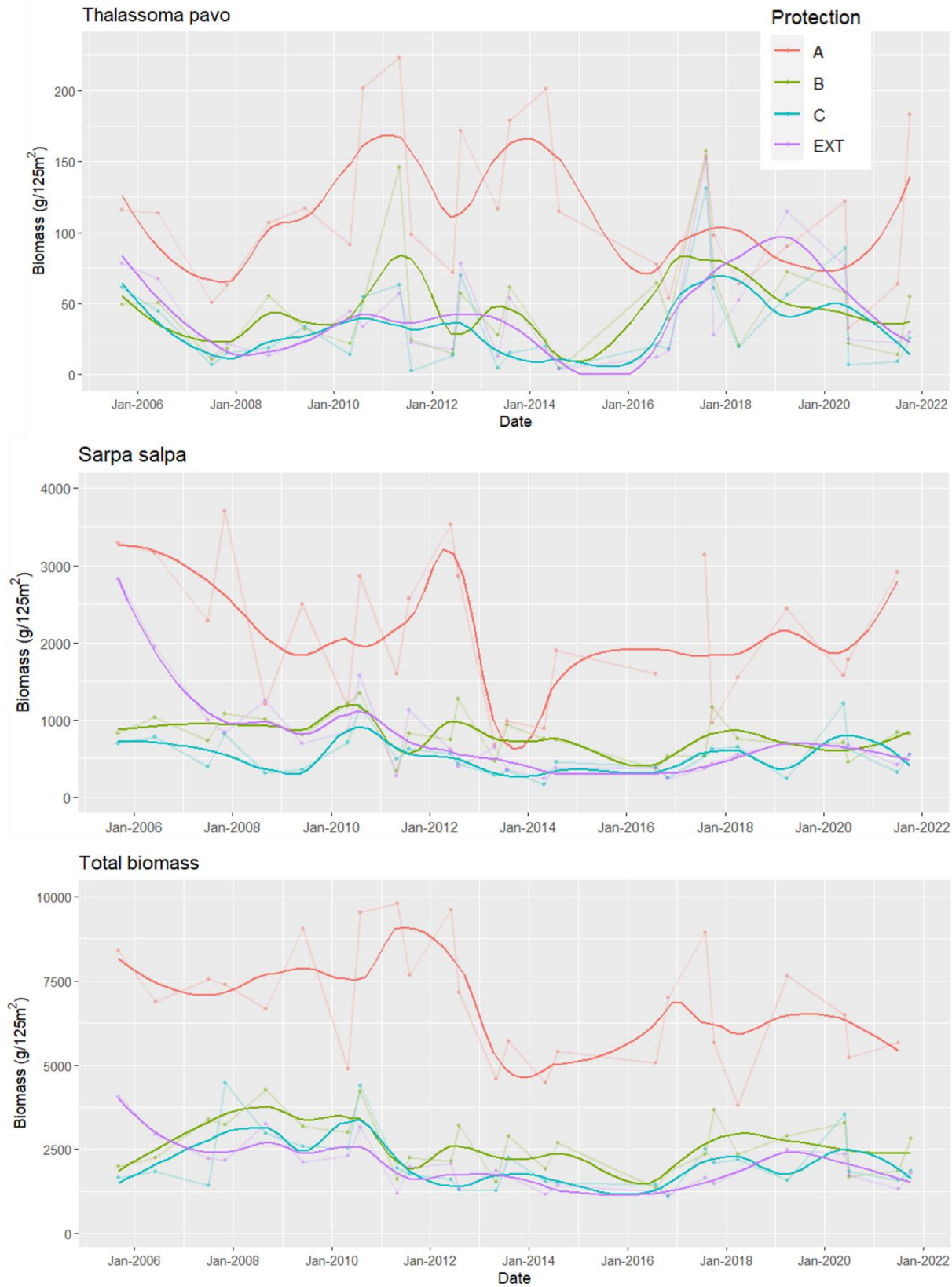
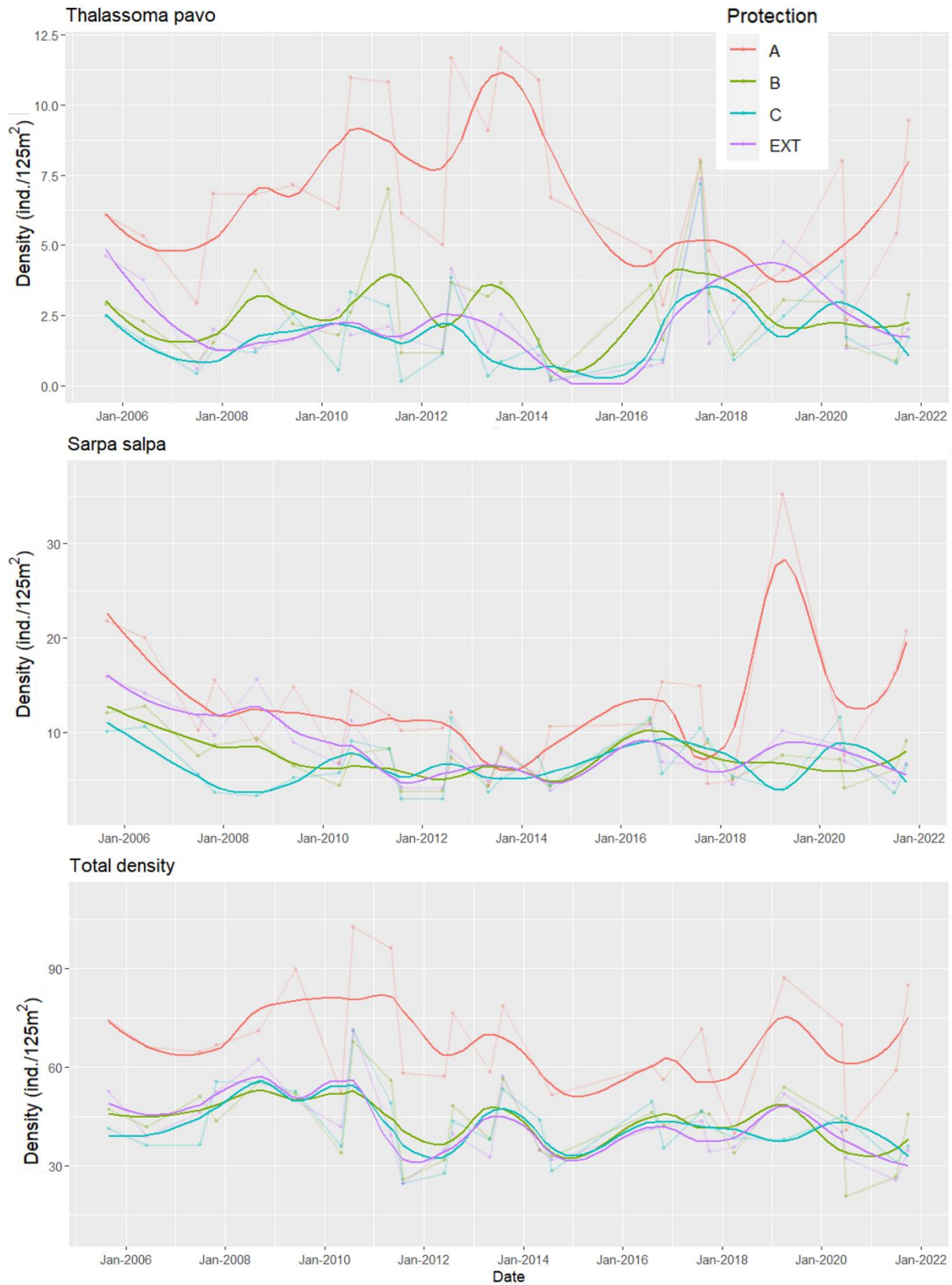**Figure 3.7:** Mean biomass in protected and unprotected zones from 2005 to 2021. Each dot represents a sampling campaign. Thicker lines are obtained applying LOESS smoother to experimental curves.

Figure 3.8: Mean density in protected and unprotected zones from 2005 to 2021. Each dot represents a sampling campaign. Thicker lines are obtained applying LOESS smoother to experimental curves.

# 4. ESTIMATING MORTALITY RATES UNDER DIFFERENT PROTECTION REGIMES

In Chapter 3, we presented an analysis of the effects of protection on biomass and density of five important fish species populating shallow rocky reefs at Tavolara – Punta Coda Cavallo Marine Protected Area (TMPA). In this chapter we expand the assessment to the effects of relaxed fishing pressure on fish body sizes attained by fish (Section 4.1) under different protection regimes. Furthermore, in Section 4.2 size-distribution data are exploited for obtaining an estimate of natural and fishing-induced mortality rates for the sea bream *Diplodus sargus*, one of the most active predators of sea urchins.

4.1 DISTRIBUTION IN SIZE CLASSES

Original data emerging from Underwater Visual Censuses (UVCs) at TMPA consist in fish densities (*i.e.*, fish counts per transect) of the five species under scrutiny (*Diplodus sargus*, *Diplodus vulgaris*, *Coris julis*, *Thalassoma pavo* and *Sarpa salpa*) disaggregated into 2 cm size classes (Section 3.1). Fish size is another key indicator of protection effectiveness as it is typically very responsive to fishing bans, with individuals allowed to grow to larger sizes within MPA boundaries (Pelletier et al., 2005).

Figure 4.1 shows, for each species, the mean densities per transect divided into size classes, in protected and unprotected zones. It is evident that even in the specific case of TMPA the fully protected areas host higher densities of large-sized individuals of species of high commercial value than the other areas. This is the case of the two sea breams *D. sargus* and *D. vulgaris*, for which the right-hand tail of the density distributions across size classes in zone A reaches higher values. Interestingly, also *S. salpa* responds to protection with increased sizes in the fully protected zone, supporting the hypothesis proposed in Chapter 3 that this species is a victim of by-catch in fished areas. For the two wrasses *C. julis* and *T. pavo*, the density distributions in size classes maintain the same shape in all zones, suggesting that the higher biomass values found in zone A for these species (Section 3.3) are mainly driven by increases in their densities rather than sizes.
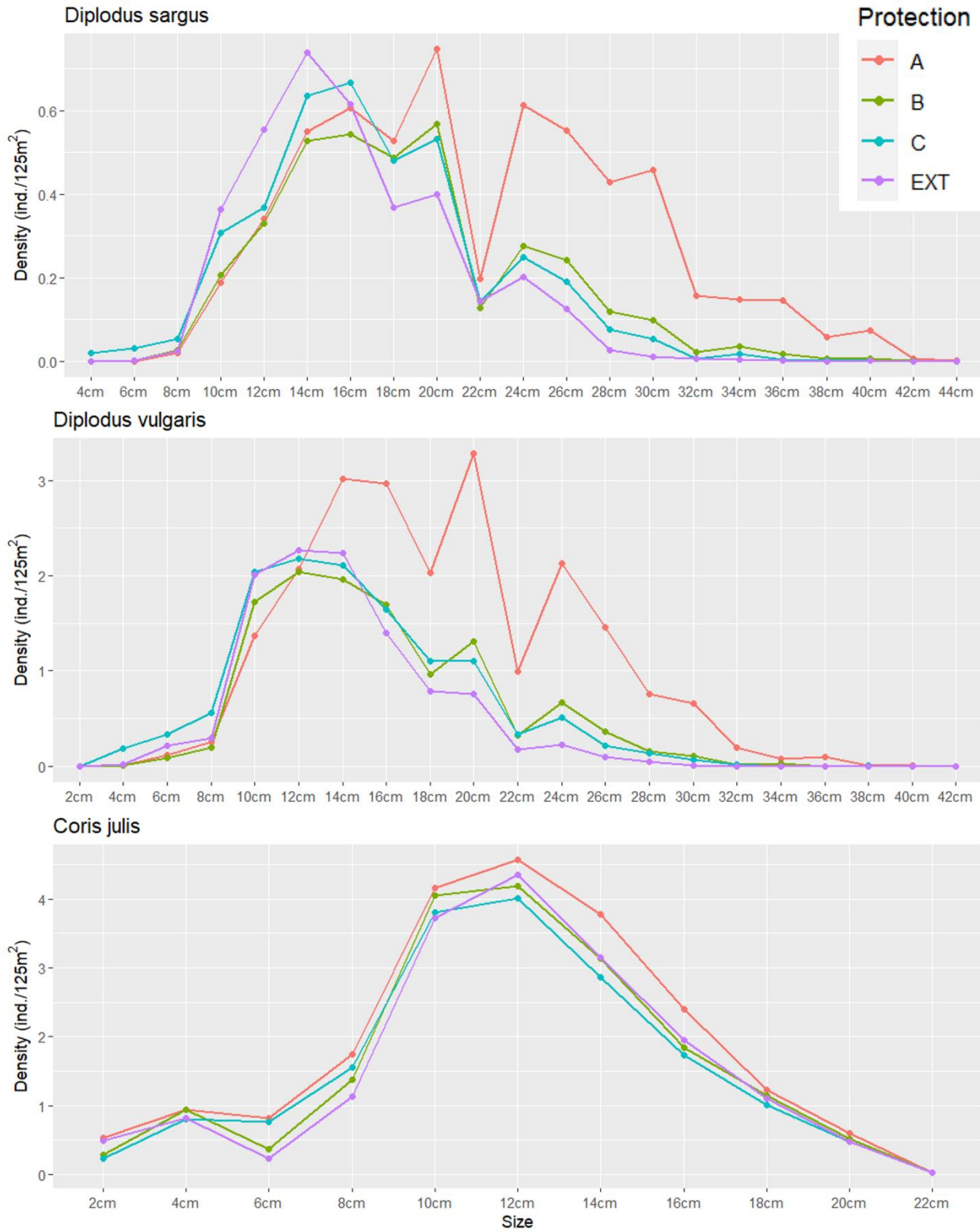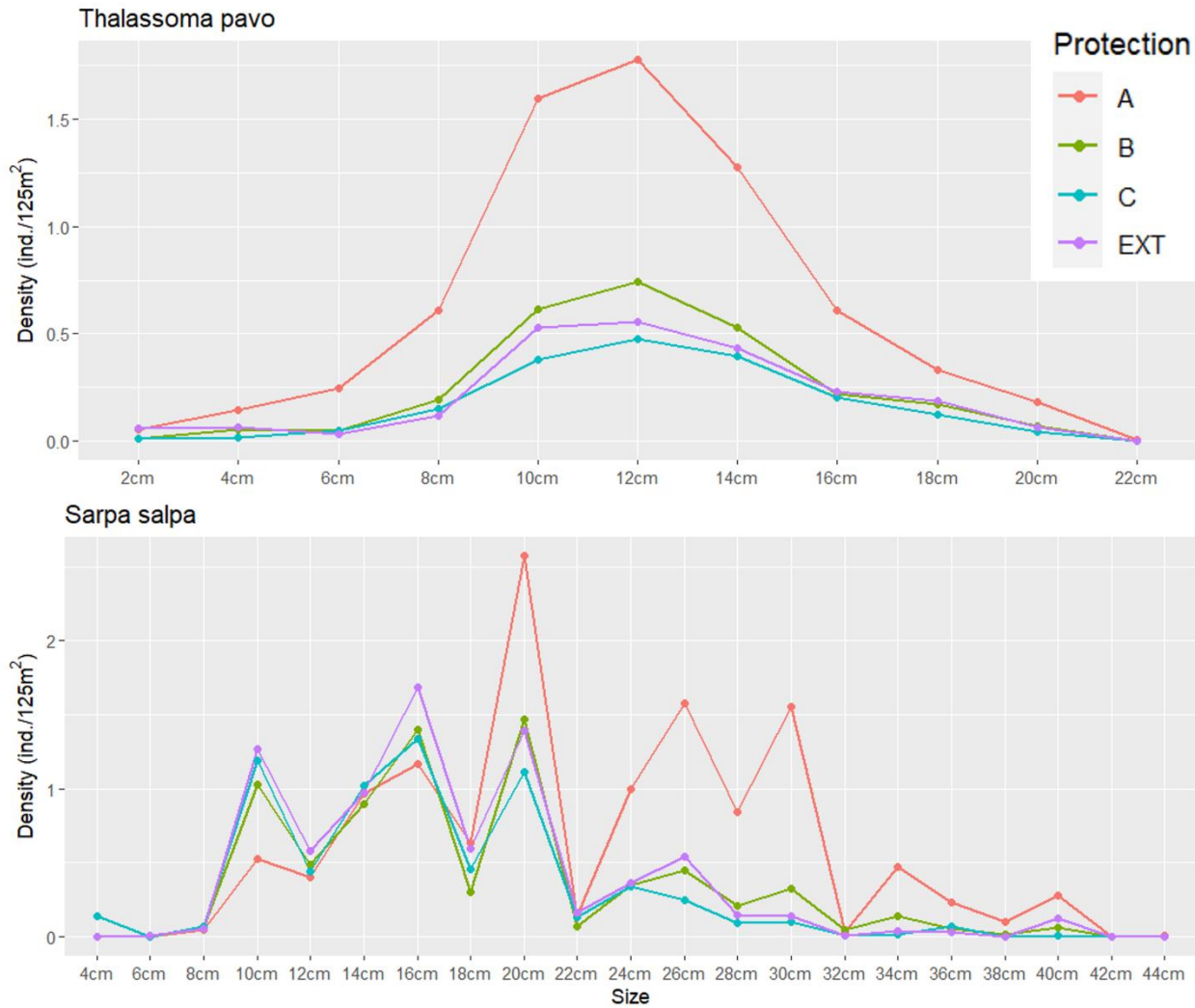
Figure 4.1: Mean densities per transect for each size class. Data refer to the whole study period (2005-2021).

It is worth mentioning that, in Figure 4.1, the presence of multiple adjacent peaks in the densities of *Diplodus* fish and *S. salpa* is most likely due to observer-dependent biases introduced in samplings. When assign sizes to specimen, they tend to approximate lengths to the nearest ten, resulting into higher frequencies of "round" size classes (*e.g.*, 20 cm) than adjacent ones (*e.g.*, 18, 22 cm). This does not happen for smaller fish, for which size class assignment is easier overall. However, as the effects of these biases are smoothed when focussing on multiple size classes rather than a single one, their presence is not considered to significantly reduce the information content of data.

4.2 ESTIMATION OF MORTALITY RATES

4.2.1 AGE-FREQUENCY METHOD

As we have seen, size data provide important insights on the effectiveness of MPAs. They also serve as a basis for obtaining relevant quantitative information on key demographic processes such as growth and mortality in marine populations (Bevacqua et al., 2010). Exploiting size data in this sense, we obtained numeric estimates of natural and fishing-induced mortality rates at TMPA for *D. sargus.*, *D. vulgaris*, *Coris julis* and *Sarpa salpa*. We used one of the most widely employed methods for fish mortality assessment in the ecological literature, namely the age-frequency method (FAO, 1998).[10] This method is based on following the evolution of multiple cohorts of individuals, where a cohort is a group of individuals with the same age.

It is reasonable to assume that, within a cohort of age x, the rate of change in the number of individuals $\left(\frac{dN_x}{dx}\right)$ due the infinitesimal age increment dx is proportional to the number of individuals of age x (Eq. 5). In other words, the more the survivors, the more will die.

$$\frac{dN_x}{dx} = -Z\,N(x)$$

Eq. 5

The proportionality coefficient, $-Z$, expressed in years^{-1} is called the "instantaneous total mortality rate" and represents the number of the individuals in the cohort who die in the unit time scaled to the size of the considered cohort. The word "total" refers to the fact that, in exploited populations such as those inhabiting fished areas at TMPA, Z includes the contributions of both natural mortality (M) and fishing-induced mortality (F). Thus,

$$Z = M + F$$

Eq. 6

To obtain estimates of total mortality for the population as a whole, and not just for the single cohort, the age-frequency method requires the following assumptions to be made:

i. Z is constant across each age class.
ii. Z is constant throughout the study period.

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[10] The age-frequency method is also referred to in the literature as the "catch curve method". However, we considered this latter denomination less appropriate for the present case study as underwater visual censuses, our data source, do not require "catching" fish but simply recording their presence.

iii.   In the considered populations, immigration and emigration phenomena are either absent or they balance out.

These assumptions are of course very hard to meet in actual populations. Mortality typically varies across age classes, with shared patterns at the species level[11], while it is seldom constant in time due to various mechanisms acting on both global and local scales (*e.g.*, competition dynamics, variability of environmental conditions).

Furthermore, a population inhabiting a non-confined area is obviously open to exchanges with external areas. The contributions of immigration and emigration are very difficult to assess numerically, so, if one does not offset the other, estimates of mortality rates typically include the hidden contribution of the net emigration rate.

Despite these limitations, estimates obtained with this method have proven to be informative (FAO, 1998) and are employed in many modelling applications.

Under these assumptions, Eq. 5 can be integrated resulting into

$$N_x = N_0 e^{-Zx} \qquad \text{Eq. 7}$$

where N_0 is the initial number of individuals in the considered cohort.

Log-transforming Eq. 7, we obtain

$$ln(N_x) = -Zx + ln(N_0) \qquad \text{Eq. 8}$$

From Eq. 8 it is evident that, if the number of individuals belonging to each cohort is known, one can fit a regression line of their log-transformation against age and estimate the total mortality Z.

4.2.2 MORTALITY RATES OF AT TAVOLARA – PUNTA CODA CAVALLO MARINE PROTECTED AREA

We obtained age-structured data at TMPA from the available size-structured ones, using the von Bertalanffy growth model (Eq. 9). This equation links length L (cm) of individuals to their relative age x (years).

$$L(x) = L_\infty(1 - e^{-k(x-x_0)}) \qquad \text{Eq. 9}$$

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[11] For instance, in fish populations it tends to be higher during early life stages.

L_∞ is the asymptotic length (cm), namely the length that fish in the population would reach if they grew indefinitely and k (year^{-1}) is a growth parameter called "Brody coefficient", expressing how quickly the asymptotic length is reached. The parameter x_0 represents instead the theoretical age of fish when their length is 0. The further this value is from 0, the less accurate is the model in representing growth at early stages of development (Gordoa & Molì, 1997). Estimates of fish age and, consequently, of these parameters are commonly derived from otoliths readings. Otoliths are small ear bones of fish made of calcium carbonate. From their cross-sections it is possible to identify pairs of opaque and translucent rings, each of which marks one year of age. Estimates of von Bertalanffy equation parameters concerning the species under scrutiny were not available for the specific case of TMPA. Therefore, we selected from the available literature the sets of parameters reported in Table 4.1, which refer to the Mediterranean basin. Unfortunately, since no parameter estimates were found for the wrasse *Thalassoma pavo*, we have not been able to estimate mortality rates for this species.

Table 4.1: von Bertalanffy growth equation parameters for each species and relative source.

	Diplodus sargus	*Diplodus vulgaris*	*Coris julis*	*Sarpa salpa*
Source	Belharet et al. (2020)	Man-Wai (1985)	Škeljo et al., (2012)	Criscoli et al. (2006)
L_∞ **(cm)**	41.67	37.8	25.24	37.3
k (y^{-1})	0.17	0.18	0.16	0.27
x_0 **(y)**	-0.99	0.83	-1.17	-0.53

Figure 4.2 shows von Bertalanffy growth curve obtained for each species using parameters in Table 4.1. Its inversion allowed us to estimate age values corresponding to each size classes.[12] Tables A.4-7 in Appendix report this correspondence, as well as the subdivision into age classes. Thus, we obtained age-structured data, from which it was possible to follow the development of the different cohorts. At this regard, since age is discretised with one year time step, we considered only one campaign per year (i.e., those coloured in blue in Table A.1 in the Appendix) when more than one was available.

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[12] At TMPA, few individuals of *D. sargus*, *D. vulgaris* and *S. salpa* exceeding the asymptotic length (L∞) were found during the study period. However, these data points could not be considered, as inverted Von Bertalanffy growth equation loses mathematical meaning for lengths greater than L∞.
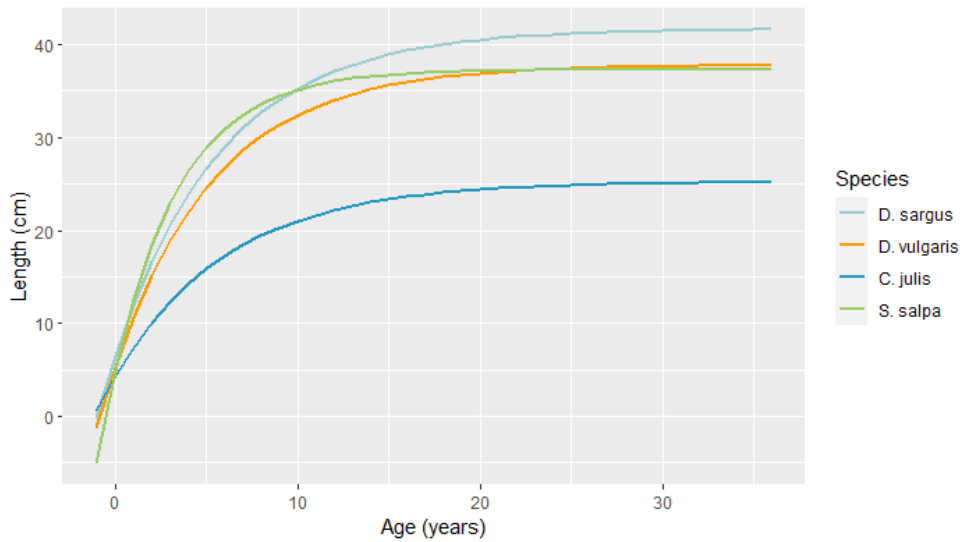
Figure 4.2: von Bertalanffy growth curve obtained for each species. The corresponding parameters are reported in Table 4.1.

Finally, using Eq. 8, we fitted one linear regression of the logarithm of density against age for each species and for each protection zone and depth level. As an example, Figure 4.3 shows the regression lines obtained for *D. vulgaris* at 5-11 m depth.
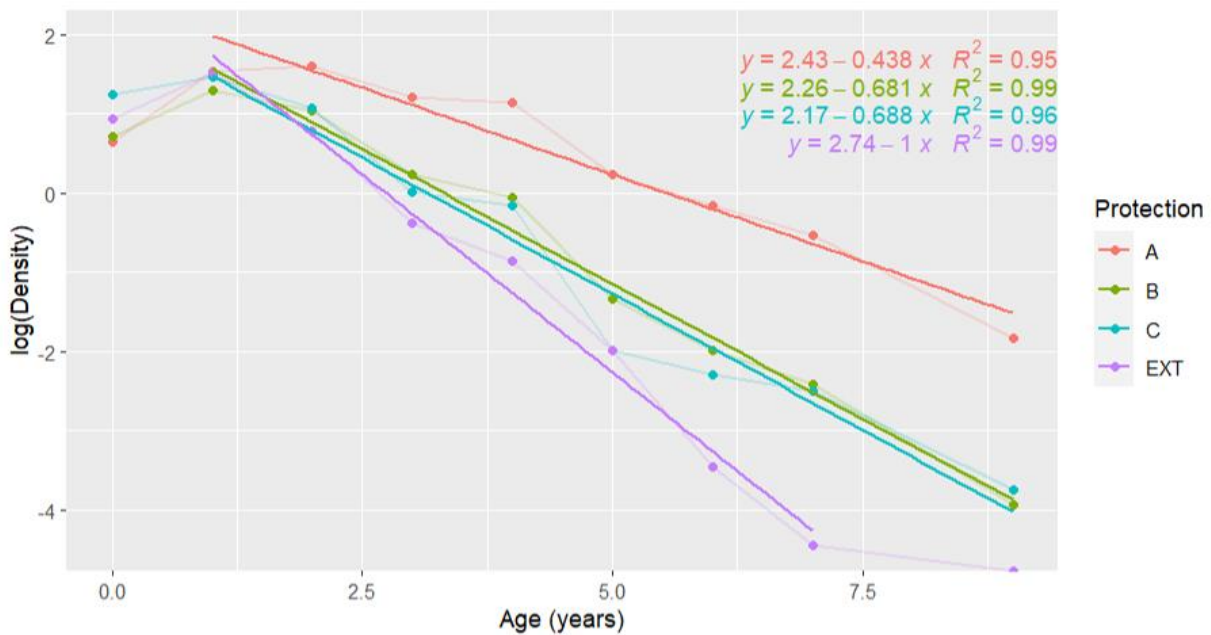

Figure 4.3: Regressions of $\log(N_x)$ against age (x) for protected and unprotected zones at 5-11 m depth. Regression equations and their relative coefficients of determination are reported on the graph. The slopes of the lines represent mortality rates (y^{-1}).

As recommended by the methodological guidelines we followed (FAO, 1998, 2005) regression lines do not include the first age class for two main reasons. First, small (*i.e.*, young) individuals might be more difficult for the diver to detect and be therefore under-represented in the data. Second,

juveniles of the considered species typically inhabit different habitats before joining the adult population (Giacalone et al., 2022; Harmelin-Vivien et al., 1995; Macpherson et al., 2000) and therefore do not enter visual census counts. We also excluded from the regressions the last age classes, which count only few individuals and are therefore affected by higher uncertainty (FAO, 1998). The estimates of mortality rates are reported in Table 4.2 along with their standard error, 95% confidence interval and coefficient of determination (R^2) and graphically shown in Figure 4.4. From these values, we can separate the two contributions of natural (M) and fishing (F) mortality by considering fully protected areas as representative of natural (*i.e.*, unfished) conditions – with a certain degree of approximation – and subtracting mortality obtained for these zones to total mortality Z in unprotected areas (EXT) to find fishing mortality.

Table 4.2: Estimates of total mortality rate (Z), standard error (SE), confidence interval (CI) and coefficient of determination of the regression line (R^2) for each species at depths 5-11 m and 12-19 m.

		5-11 m				12-19 m			
		$Z_{5\text{-}11\,m}$ (y^{-1})	SE (y^{-1})	CI (y^{-1})	R^2	$Z_{12\text{-}19\,m}$ (y^{-1})	SE (y^{-1})	CI (y^{-1})	R^2
Diplodus sargus	A	0.271	0.099	0.233	0.52	0.222	0.076	0.179	0.55
	B	0.556	0.087	0.206	0.85	0.525	0.087	0.188	0.86
	C	0.796	0.135	0.331	0.85	0.647	0.131	0.323	0.8
	EXT	0.891	0.111	0.271	0.92	0.700	0.085	0.199	0.91
Diplodus vugaris	A	0.438	0.043	0.104	0.95	0.404	0.043	0.106	0.94
	B	0.681	0.034	0.084	0.99	0.677	0.039	0.097	0.98
	C	0.688	0.058	0.141	0.96	0.678	0.036	0.088	0.98
	EXT	1.000	0.052	0.133	0.99	0.904	0.091	0.234	0.95
Coris julis	A	0.305	0.028	0.079	0.97	0.285	0.026	0.075	0.97
	B	0.338	0.026	0.073	0.98	0.315	0.016	0.045	0.99
	C	0.333	0.021	0.059	0.98	0.315	0.017	0.047	0.99
	EXT	0.333	0.042	0.118	0.94	0.284	0.033	0.091	0.95
Sarpa salpa	A	0.419	0.070	0.281	0.90	0.172	0.049	0.135	0.76
	B	0.359	0.057	0.161	0.91	0.364	0.120	0.389	0.75
	C	0.364	0.149	0.476	0.67	0.538	0.107	0.322	0.86
	EXT	0.447	0.098	0.273	0.84	0.445	0.145	0.402	0.70
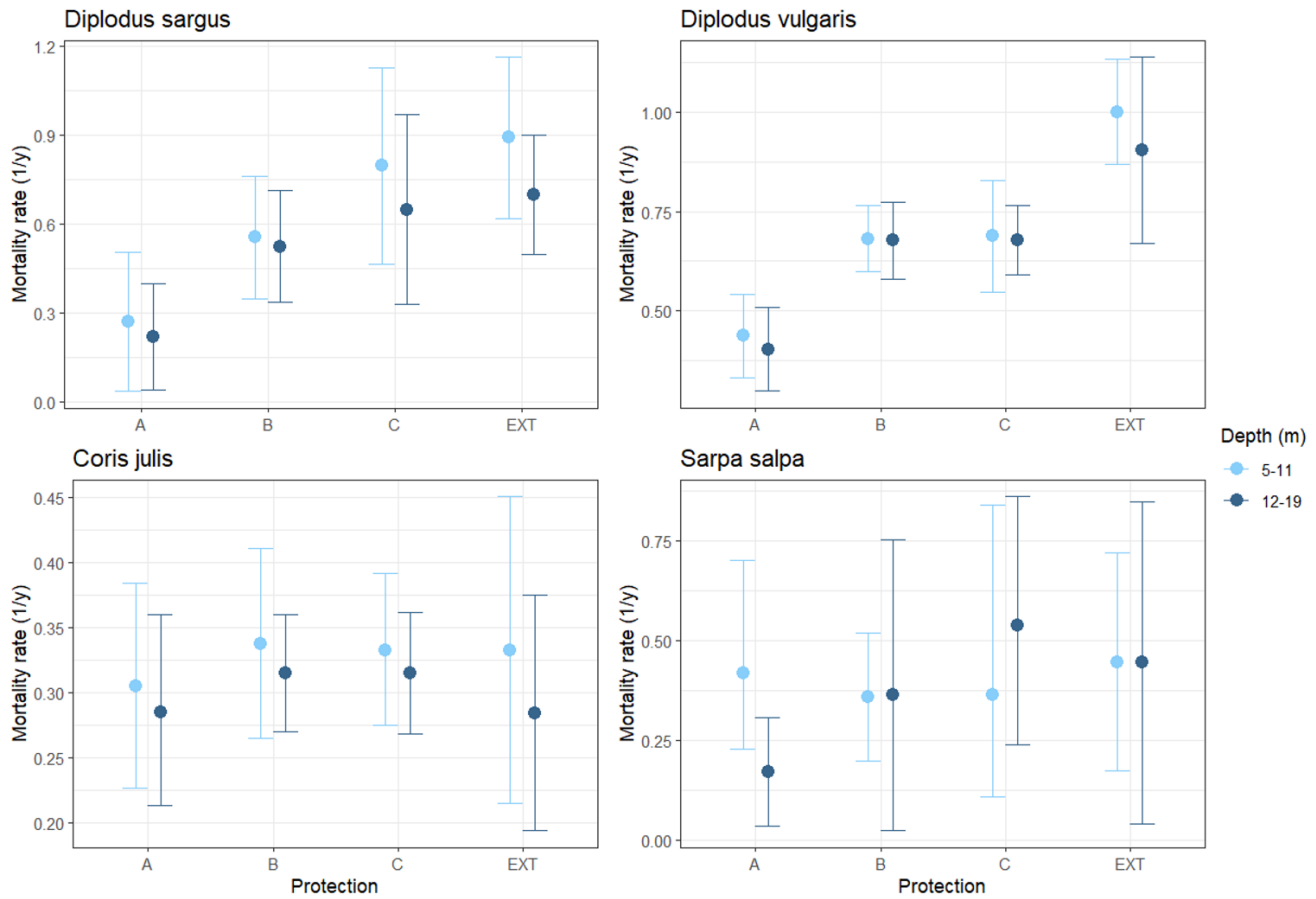
Figure 4.4: Estimates of total mortality rate (circles) and associated 95% confidence interval (lines) under each protection regime.

From the estimates we obtained, the effects of protection are very evident on commercially important species, namely the two seabreams *D. sargus* and *D. vulgaris*. At both considered depth levels, increasing stringency in fishing bans results into decreasing mortality rates. In shallow (5-11 m) unprotected zones (EXT), fishing induced mortality is 0.62 y^{-1} and 0.56 y^{-1} for *D. sargus* and *D. vulgaris* respectively, hence, more than twice the natural mortality. Calculating the value of e^{-z} we get the interannual survival probability. Hence, at this sampling depth, *D. sargus* individuals have $e^{-0.27}$ = 0.76 annual survival probability in fully protected zones, while in unprotected ones (EXT) this probability drops down to 0.41. It is evident that in fully protected areas, populations of the two sea breams strongly benefit from protection. Less sharp are instead the responses of the other two species, not directly targeted by commercial fishing. The estimated mortality rates for *C. julis* do not differ much among protection levels and the same holds for *S. salpa* in shallow waters (5-11 m). On the contrary, *S. salpa* seems to benefit from reduced mortality in fully protected areas in deeper waters (12-19 m). However, confidence intervals for *S. salpa* are rather large, indicating higher uncertainty related to estimates for this species. For *D. sargus*, *D. vulgaris* and *C. julis*, estimated

mortalities in unprotected zones tend to be higher in shallower waters. We can hypothesise as a possible explanation the fact that the effects of fishing typically have heavier repercussions in the first meters than in deeper areas. However, this difference is observable to a smaller extent also in A zones, where fishing is in principle prohibited, thus leading to question this hypothesis.

When evaluating these results, we must take into account the methodological limitations affecting them. We conducted mortality analyses chiefly with the aim of assessing the potential of fishing in inducing fish stock depletions, by comparing protected zones with controls (EXT zones). The estimates we obtain for each zone are very likely to be affected to the same extent by the violations of the underlying assumptions, somehow allowing for a fair comparison among zones. We therefore suggest taking the estimated values *per se* as approximations of the real parameters, while considerations emerging from comparisons among zones are, in our view, more robust.

CONCLUSIONS AND FURTHER DEVELOPMENTS

In Chapter 1 of this work, we extensively discussed the trophic cascade mechanism linking overfishing of sea urchin predators and erect macroalgal forests decline, mediated by the overgrazing activity of sea urchins. The broad question underlying the present analysis is whether Marine Protected Areas (MPAs) can be effective management tools in repairing the negative consequences of overfishing felt at the ecosystem-scale, ultimately allowing macroalgal forests conservation and/or restoration. Evidence in this direction referred to the Mediterranean basin, despite encouraging, is still limited. Given the importance of the compartment of sea urchin predators – chiefly composed of the species *Diplodus sargus*, *Diplodus vulgaris*, *Coris julis* and *Thalassoma pavo* – in shaping ecosystem dynamics, we considered essential to investigate their response to different protection regimes, as a first step to approach this very vast research field. We did so by using the Mediterranean MPA of Tavolara – Punta Coda Cavallo (TMPA) as experimental ground (Chapter 2), for which outstandingly long time series (17 years, from 2005 to 2021) are available. TMPA is very suitable to our aims as it allows exploring the effects of both integral and partial protection regimes. We also investigated the response to protection of the herbivore fish *Sarpa salpa*, which is thought to contribute to grazing of forest-forming algal species without however inducing strong algal declines alone.

From our analyses of density and biomass of fish performed through ANCOVA tests (Chapter 3), it emerges that full protection at TMPA had rather rapid effects which have been maintained, net of some fluctuations, for all analysed species during the whole duration of the study period (2005-2021). Notably, at TMPA, the indicative threshold of 15 *Diplodus* individuals over 100 m² (Guidetti & Sala, 2007) needed to exert a top-down control of urchin populations have been exceeded, but only in fully protected areas. Although protection effects are observable across all the study years, the analysis revealed decreasing trends of total biomass and density, which require further investigation accounting also for other important species inhabiting shallow rocky reefs. Negative trends were also observed for the cold-water wrasse *Coris julis*. This result is in line with several studies across the Mediterranean which report declining *C. julis* populations due to the climate change-induced rise in sea water temperature. A weak increase was instead found in density and biomass of the thermophilic wrasse *Thalassoma pavo*.

Our findings from density and biomass data also call for a more careful evaluation of the role of buffer (*i.e.*, partially protected) zones at TMPA. They did not outperform unprotected zones when data were expressed in terms of density, whilst for some species, small but statistically significant differences were detected in terms of biomass.

The analyses of data disaggregated into size classes highlight that in fully protected areas, commercially important fish (*i.e.*, *D. sargus* and *D. vulgaris*) are allowed to grow to larger sizes, which are those that are chiefly targeted by fishing. This is reflected also by the estimates of mortality rates we obtained (Chapter 4), which decrease with increasing stringency of fishing bans. For the other species, response to protection in terms of size and mortality rates is less evident.

Overall, our analysis depicts positive effects of full protection on sea urchin predators at TMPA. Under strict regulations, predators reached sufficient densities, biomass and sizes to effectively control the dimensions of sea urchin populations. Therefore, under these management conditions, there might be the chances of attaining a reduction of grazing pressure on macroalgae and for allowing natural or human-induced recovery of macroalgal forests. Evidence pointing in this direction is available in recently published literature (E. Di Franco et al., 2021; Giakoumi et al., 2017), even though further experimental work is required to test the effects of full protection directly on macroalgal stands. In this sense, it would be interesting to expand the considerations of the present work in light of samplings on sea urchins and erect macroalgae in the same reserve, which either do not exist or were unretrievable. With these data, tri-trophic models may also be built to explore dynamics underlying the transitions between macroalgal forests and bare rocky beds. Combining result from the present analysis with additional information concerning the two trophic levels of herbivores and primary producers, it would be possible to assess whether healthy predator populations in fully protected zones are in actual facts related to prosperous macroalgal communities. These results would allow a better comprehension of the considered trophic cascade mechanism whose relevance goes far beyond the borders of the analysed reserve. Indeed, as already recalled throughout the work, such inter-specific dynamics may be at the basis of algal declines recorded not only in Mediterranean sites but also worldwide.

To exploit the full potential of the available data for TMPA, possible future improvements of the current analytical framework include: (i) supporting the linear trend detection that we performed using multiple regression models with other statistical techniques specific to time series analyses, such as autoregressive – moving-average models (ARMA), so to gain more precise insights on the

temporal evolution of the studied populations. (ii) Employing multivariate statistical techniques, which allow including and quantifying relationships among studied species in the assessments, in an overarching way. (iii) Exploring the dynamics of the study species building mono- or multi-specific demographic models. (iv) Using zero-inflated models for analysing data of *S. salpa*. As already discussed, observations from this species contain many zero data points due to the schooling behaviour of this fish. Zero-inflated models allow distinguishing "real" zeroes (*i.e.*, the fish is absent because of habitat unsuitability) and "excess" zeroes (*i.e.*, the fish is absent because its school is not in the sampling location when the visual census takes place). (v) Experimentally obtaining site-specific estimates for von Bertalanffy growth equation (Chapter 4), so to establish a more precise correspondence between size of fish and their relative age.

On a final note, we recognise that this work has only been possible thanks to continuative and consistent data collection, which of course has required much organisational and economic effort. In an era of global changes such as the one we are witnessing, it is of utmost importance to allocate ever more resources to ecosystems monitoring, as it allows identifying threats and answering important questions about the effectiveness of management strategies that are put in place to maintain or restore ecosystem health.

APPENDIX

Table A.1: Number and dates of sampling campaigns per year. The campaigns that have been used for obtaining the estimates of mortality rates are coloured in blue.

Year	Number of campaigns	Date
2005	1	September-October 2005
2006	1	June 2006
2007	2	November-December 2007, July-August 2007
2008	1	August-October 2008
2009	1	June-July 2009
2010	2	May 2010, August 2010
2011	2	May 2011, August 2011
2012	2	June 2012, August 2012
2013	2	May 2013, August 2013
2014	2	May 2014, August 2014
2015	-	-
2016	2	November 2016, August 2016
2017	2	October 2017, August 2017
2018	1	April-May 2018
2019	1	April 2019
2020	2	June 2020, July-August 2020
2021	2	July-August 2021, October 2021
	TOT = 26 campaigns	

Table A.2: *p-values* of Tukey HSD post-hoc test on biomass models. Significance threshold set at *p-value* = 0.05.

	D. sargus	*D. vulgaris*	*C. julis*	*T. pavo*	*S.salpa*	Tot biomass
A - B	$< 2*10^{-16}$	$< 2*10^{-16}$	0.038	$< 2*10^{-16}$	0.003	$< 2*10^{-16}$
A - C	$< 2*10^{-16}$	$< 2*10^{-16}$	$3.1*10^{-4}$	$< 2*10^{-16}$	$< 2*10^{-16}$	$< 2*10^{-16}$
A - EXT	$< 2*10^{-16}$	$< 2*10^{-16}$	0.015	$< 2*10^{-16}$	$< 2*10^{-16}$	$< 2*10^{-16}$
B - C	0.097	0.648	0.502	0.314	0.012	0.004
B - EXT	$3.5*10^{-4}$	$4.7*10^{-6}$	0.99	0.911	0.806	$1.5*10^{-4}$
C - EXT	0.302	$0.8*10^{-4}$	0.695	0.715	0.131	0.848

Table A.3: *p-values* of Tukey HSD post-hoc test on density models. Significance threshold set at *p-value* = 0.05.

	D. sargus	*D. vulgaris*	*C. julis*	*T. pavo*	*S.salpa*	Tot density
A - B	$1.8*10^{-6}$	$< 2*10^{-16}$	0.032	$< 2*10^{-16}$	0.033	$< 2*10^{-16}$
A - C	$2.0*10^{-5}$	$< 2*10^{-16}$	0.005	$< 2*10^{-16}$	$3.4*10^{-4}$	$< 2*10^{-16}$
A - EXT	$2.0*10^{-7}$	$< 2*10^{-16}$	0.002	$< 2*10^{-16}$	0.203	$< 2*10^{-16}$
B - C	0.959	0.533	0.934	0.221	0.548	0.989
B - EXT	0.97	0.678	0.848	0.567	0.867	0.935
C - EXT	0.778	0.067	0.996	0.924	0.156	0.992

Table A.4: Correspondence between UVC size classes and ages for *D. sargus*, calculated with inverted Von Bertalanffy growth equation.

UVC class (cm)	Age (y)	Age class
4	-0.40	
6	-0.08	<1
8	0.26	
10	0.62	
12	1.01	
14	1.42	1
16	1.86	
18	2.34	2
20	2.86	
22	3.43	3
24	4.06	4
26	4.76	
28	5.57	5
30	6.50	6
32	7.60	7
34	8.97	8
36	10.74	10
38	13.30	13
40	17.93	17

Table A.5: Correspondence between UVC size classes and ages for *D. vulgaris*, calculated with inverted Von Bertalanffy growth equation.

UVC class (cm)	Age (y)	Age class
2	-0.53	
4	-0.21	
6	0.13	<1
8	0.49	
10	0.88	
12	1.29	1
14	1.74	
16	2.23	2
18	2.76	
20	3.35	3
22	4.02	4
24	4.77	
26	5.64	5
28	6.67	6
30	7.94	7
32	9.58	9
34	11.93	11
36	16.08	16

Table A.6: Correspondence between UVC size classes and ages for *C. julis*, calculated with inverted Von Bertalanffy growth equation.

UVC class (cm)	Age (year)	Age class
2	-0.65	
4	-0.09	<1
6	0.53	
8	1.21	1
10	1.98	
12	2.86	2
14	3.89	3
16	5.11	5
18	6.64	6
20	8.66	8
22	11.66	11

Table A.7: Correspondence between UVC size classes and ages for *S. salpa*, calculated with inverted Von Bertalanffy growth equation.

UVC class (cm)	Age (year)	Age class
4	-0.11	
6	0.12	<1
10	0.63	
14	1.21	1
16	1.55	
20	2.32	2
24	3.29	3
26	3.90	
30	5.52	5
34	8.48	8
36	11.99	12

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