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A quantitative and functional assessment of fish assemblages of the Port-Cros Archipelago (Port-Cros National Park, north-western Mediterranean Sea)

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Abstract. The Port-Cros National Park (PCNP) was established in 1963. It encompassed the Island of Port-Cros and the neighbouring island and islets (the Port-Cros Archipelago). Progressively, the PCNP has been entrusted with the management of an increasing number of territories outside the initial territory of 1963. Between 2012 and 2016, the PCNP was engaged in a major redefinition and extension of its territory; the new Port-Cros National Park (N-PCNP), established in 2016, includes the Port-Cros and Porquerolles Archipelagos as core areas (both terrestrial and marine), a vast Adjacent Marine Area (AMA) including the Gulf of Hyères and extending seawards to the edge of the continental shelf, and a discontinuous continental area (Adhesion Area, AA) including five municipalities. The management of the marine area of the Port-Cros Archipelago MPA (Marine Protected Area) can clearly be referred to the MUM type (Multi-Use Management) characterized by a complex zoning of the marine part of the MPA, based upon the uses, the goals of conservation of the habitats and the ecosystems and priorities clearly displayed (artisanal fishing rather than recreational fishing). MUM management strongly contrasts with NTZ (No-Take Zone) management, where any form of human activity is prohibited. In addition to the ban on spear fishing, angling and trawling, the Port-Cros Archipelago MPA has its own artisanal fishing regulations, enshrined in a fishing charter; those regarding maximum vessel length, soak time, mesh size, net length, number of hooks and traps, are more restrictive than outside the MPA; these regulations are strictly enforced, in contrast with a number of Mediterranean MPAs which are actually 'paper parks'. It is worth noting that, as far as the conservation of the natural heritage is concerned, MUM management, as practiced in the Port-Cros Archipelago MPA, is at least as efficient as NTZ management. In addition, it is compatible with sustainable fisheries in particular, sustainable development in general, and fits well with the concept of the socio-ecosystem.

We have seized the opportunity of having at our disposal one of the oldest Mediterranean MPAs, with exemplary protection and an exceptional level of scientific knowledge, to assess the species diversity (point diversity and alpha diversity), the biomass and the trophic structure of fish (teleosts) assemblages in 5 habitats, - shallow rocky reefs (RS, 0-3 m depth), deep rocky reefs (RD, 5-15 m), relatively shallow *Posidonia oceanica* seagrass meadows (PS, 10-

15 m), deep *P. oceanica* meadows adjacent to circalittoral habitats soft bottoms (PD, 30-35 m) and coralligenous habitats (C, 25-40 m) -, by sector and type of management. Within the framework of MUM management, three types of management were considered: (i) sites reserved for scuba diving, where artisanal and recreational fishing are totally prohibited (NT, no-take areas); (ii) sites where longlines and trawling (artisanal fishing), spear fishing and angling (recreational fishing) are prohibited (RF, restricted fishing areas); and (iii) sites reserved for artisanal fishers, where spear fishing, angling and trawling are prohibited (AF, artisanal fishing areas). The fish assemblage was assessed at 40 sites, in September and October 2014; at each site, 10 random transects 25 m (50 m at PS) long and 5 m wide were surveyed by scuba diving (RD, PS, PD, C) or snorkelling (RS). The teleost fish species were classified, according to their diet, into 6 trophic groups: planktivorous, piscivorous, macrocarnivorous, omnivorous, mesocarnivorous and herbivorous.

The alpha diversity (number of species per site), mean point diversity (number of species per transect), mean abundance (number of individuals per 100 m²) and mean biomass (kg per 100 m²) were respectively (i) 17-23, 9, 63 and 4 in RS (shallow rocky reefs), (ii) 23-30, 12, 158 and 7 in RD (deep rocky reefs), (iii) 18-28, 9, 60 and 1 in PS (shallow *Posidonia oceanica* meadow), (iv) 5-10, 3, 137 and 2 in PD (deep *P. oceanica* meadows) and (v) 10-29, 8, 596 and 18 in C (coralligenous). The trophic structure presented sharp differences between habitats: the dominant groups were mesocarnivorous and omnivorous (RS), piscivorous and mesocarnivorous (RD), herbivorous and planktivorous (PS), planktivorous and mesocarnivorous (PD) and piscivorous and planktivorous (C; with strong contrasts between sites and types of management). The type of management (NT, RF and AF) generally does not matter, with the exception of the coralligenous habitat. This result may seem surprising but it is quite logical: the three types of management that we have considered in Port-Cros Archipelago are just facets of the same type of management, MUM management; they constitute a spatial mosaic, with areas between which most of the fish considered here are constantly moving; it is therefore logical that the differences between these facets of the MUM management are rarely significant.

Overall, the exceptional preservation of the natural heritage around the archipelago of Port-Cros (PCNP), the richness in fish, especially in top predators, and the compatibility with a sustainable artisanal fishery, are the result of an original type of management (MUM management), a severe restriction of the artisanal fishing effort, the prohibition of recreational fishing, effective surveillance and 55 years of rigorous management of human activities. But the balance that has been achieved could be jeopardized tomorrow. The current generation of intelligent fishers is, because of its age, being replaced. Will the new fishers have the wisdom of their elders? But the law is on the side of the PCNP; it arms the Park with powerful weapons, and it is up to the PCNP to ensure that the general interest prevails, that of all current and future users, that of the natural and cultural heritage, against possible depredations of people seeking quick but non-sustainable profits.

Keywords: artisanal fishery, biomass, coralligenous, fishes, management, Marine Protected Area, *Posidonia oceanica*, rocky reefs, species diversity, trophic groups.

Résumé. Le peuplement de poissons de l'archipel de Port-Cros (Parc national de Port-Cros, Méditerranée nord-occidentale) : évaluation quantitative et fonctionnelle.

Le Parc national de Port-Cros (PNPC) a été créé en 1963. Il était constitué par l'île de Port-Cros et par les îles et îlots voisins (archipel de Port-Cros). Par la suite, le PNPC a été chargé de la gestion d'un nombre croissant de territoires, extérieurs à son périmètre initial de 1963. Entre 2012 et 2016, le PNPC s'est engagé dans une profonde redéfinition et extension de son territoire initial ; le nouveau Parc national de Port-Cros (N-PNPC), créé en 2016, est constitué (i) de deux zones cœurs, à la fois terrestres et marines (les archipels de Port-Cros et de Porquerolles), (ii) d'une vaste Aire Maritime Adjacente (AMA), incluant le golfe de Hyères et s'étendant jusqu'au bord du plateau continental, et (iii) d'une zone continentale discontinue (Aire d'Adhésion, AA) constituée par cinq communes ayant librement adhéré au N-PNPC.

La gestion de l'Aire Marine Protégée (AMP) de l'archipel de Port-Cros se réfère clairement au type dit 'MUM' (*Multi-Use Management*) et se caractérise par un zonage complexe de la zone marine de l'AMP, basé sur les usages, les objectifs de conservation des habitats et des écosystèmes et des priorités clairement assumées (la pêche artisanale plutôt que la pêche de loisir). La gestion de type MUM contraste donc fortement avec la gestion de type NTZ (*No-Take Zone*), où tout prélèvement est interdit. Dans le cadre de la gestion MUM, dans l'AMP de l'archipel de Port-Cros, outre l'interdiction de la chasse sous-marine, de la pêche à la ligne et des arts trainants, la pêche artisanale est encadrée par une charte plus contraignante que la réglementation nationale et celle de la prud'homie des pêcheurs : taille maximale des bateaux, durée des calées, maille des filets, longueur des filets, nombre d'hameçons des palangres, nombre des paniers à poissons, etc. Cette réglementation est strictement appliquée, contrairement à ce qui se passe dans un certain nombre d'AMPs méditerranéennes, qui sont en fait des '*paper parks*' (parcs de papier). Il est important de souligner que, en ce qui concerne la conservation du patrimoine naturel, la gestion MUM, telle qu'elle est pratiquée dans l'AMP de l'archipel de Port-Cros, est au moins aussi efficace que la gestion NTZ. De plus, elle est compatible avec, en particulier, le maintien d'une pêche artisanale durable, et de façon plus générale avec le développement durable, l'un des objectifs du N-PNPC. Enfin, la gestion MUM s'intègre bien dans la notion de socio-écosystème.

Nous avons saisi l'opportunité de disposer de l'une des plus anciennes AMPs de Méditerranée, bénéficiant d'une protection exemplaire et d'une base exceptionnelle de données scientifiques, pour évaluer la diversité spécifique (*point diversity* et diversité alpha), la densité (nombre d'individus), la biomasse (masse humide) et la structure trophique des peuplements de poissons (téleostéens). Cinq habitats ont été étudiés : la roche infralittorale superficielle (RS, 0-3 m de profondeur), la roche infralittorale profonde (RD, 5-15 m), les prairies relativement superficielles à *Posidonia oceanica* (PS, 10-15 m), les prairies profondes à *P. oceanica*, contigües des substrats meubles de l'étage circalittoral (PD, 30-35 m) et le coralligène (C, 25-40 m). Les 40 stations étudiées, en septembre et octobre 2014, sont réparties tout autour de l'archipel de Port-Cros et dans des secteurs représentatifs des trois types de gestion de la pêche, dans le cadre de la gestion MUM : (i) stations réservées à la plongée en scaphandre, où la pêche artisanale et de loisir (chasse et pêche à la ligne) sont totalement prohibées (NT, zones de non prélèvement) ; (ii) stations où les palangres et les arts trainants (pêche artisanale), ainsi que la chasse et la pêche à la ligne (pêche de loisir) sont prohibées (RF, zones avec restriction de la pêche); et (iii) stations réservées à la pêche artisanale, dans le respect des règlements de la charte de la pêche, où les arts trainants et la pêche de loisir sont prohibés (AF, zones de pêche artisanale). Dans chaque station, le peuplement de poissons a été étudié en plongée sous-marine (RD, PS, PD, C) ou en PMT (palmes, masque, tuba) (RS), le long de 10 transects placés au hasard, longs de 25 m et larges de 5 m, sauf dans les prairies relativement superficielles à *P. oceanica*, où les transects sont longs de 50 m. Les espèces de poissons ont été réparties, en fonction de leur régime alimentaire, en six groupes trophiques : planctonophages, piscivores, macrocarnivores, omnivores, mésocarnivores et herbivores.

Les paramètres étudiés ont présenté des valeurs très contrastées entre habitats, et une forte variabilité au sein d'un habitat donné (entre transects et entre stations). La diversité alpha (nombre d'espèces par station), la *point diversity* moyenne (nombre d'espèces – esp. – par transect), la densité moyenne (nombre d'individus – ind. – par 100 m²) et la biomasse moyenne (masse humide, en kg par 100 m²) observés ont été respectivement de (i) 17-23 esp./station, 9 esp./transect, 63 ind./100 m² et 4 kg/100 m² dans RS (roche infralittorale superficielle), (ii) 23-30 esp./station, 12 esp./transect, 158 ind./100 m² et 7 kg/100 m² dans RD (roche infralittorale profonde), (iii) 18-28 esp./station, 9 esp./transect, 60 ind./100 m² et 1 kg/100 m² dans PS (prairie superficielle à *P. oceanica*), (iv) 5-10 esp./station, 3 esp./transect, 137 ind./100 m² et 2 dans PD (prairie profonde à *P. oceanica*) et (v) 10-29 esp./station, 8 esp./transect, 596 ind./100 m² et 18 kg/100 m² dans C (coralligène). La structure trophique a présenté de fortes différences entre habitats : les groupes dominants ont été les mésocarnivores et les omnivores (RS), les piscivores et les mésocarnivores (RD), les herbivores et les planctonophages (PS), les planctonophages et les mésocarnivores (PD) et les

piscivores et les planctonophages (C ; avec de fortes différences entre stations et en fonction du type de gestion). Le type de gestion (NT, RF and AF) n'a généralement pas d'influence, à l'exception du coralligène. Ce résultat peut paraître étonnant, mais est en fait logique : les trois types de gestion que nous avons considérés dans l'AMP de l'archipel de Port-Cros ne sont que des facettes d'un seul type de gestion, la gestion MUM ; ils se répartissent dans l'espace en une mosaïque, et la plupart des poissons considérés ici peuvent se déplacer en permanence entre les éléments de cette mosaïque ; il est donc logique que les différences entre ces trois facettes de la gestion MUM soient rarement significatives.

Au total, l'exceptionnelle préservation du patrimoine naturel autour de l'archipel de Port-Cros (PCNP), la richesse en poissons, en particulier en *top-predators*, et la compatibilité avec une pêche artisanale durable, sont le résultat d'un type de gestion original (la gestion MUM), d'une sévère restriction de l'effort de la pêche artisanale, de l'interdiction de la pêche de loisir, d'une surveillance efficace et de 55 années de gestion rigoureuse des activités humaines. Mais l'équilibre qui a été réalisé peut être remis en question dans le futur. La génération de pêcheurs intelligents qui a contribué à cet équilibre est en voie de disparition, en raison de son âge. Les nouveaux pêcheurs auront-ils la sagesse de leurs aînés ? Ou voudront-ils s'attaquer au capital, à cette sorte de coffre-fort que représente une AMP ? De toutes façons, la Loi est du côté du PNPC, et lui donne les moyens de faire respecter l'intérêt général, celui des usagers actuels et futurs, celui du patrimoine naturel et culturel, contre d'éventuels usagers pressés de réaliser un profit non-durable.

Mots-clés : Aire Marine Protégée, biomasse, coralligène, diversité spécifique, gestion, groupes trophiques, pêche artisanale, peuplements infralittoraux sur roche, poissons, *Posidonia oceanica*.

Introduction

Teleost fishes play a role of paramount importance in the functioning of Mediterranean coastal ecosystems (e.g. Guidetti and Dulčić, 2007; Vergés *et al.*, 2009; Sala *et al.*, 2012; Banaru *et al.*, 2013; Prato *et al.*, 2013; Personnic *et al.*, 2014; Ruitton *et al.*, 2014; Ourgaud *et al.*, 2015; Thibaut *et al.*, 2017). Within coastal ecosystems, they can belong to a variety of functional compartments: herbivores, invertivores (consuming small benthic invertebrates), plankton-feeders, predators of benthic macro-invertebrates, predators of fish, etc. Fish constitute the main target of artisanal (small-scale) fisheries (e.g. Tzanatos *et al.*, 2006; Guyader *et al.*, 2013; Leleu *et al.*, 2014). Crustaceans (e.g. the spiny lobster *Palinurus elephas*) and sea urchins (mainly *Paracentrotus lividus*) are also targeted by Mediterranean small-scale fisheries (Le Diréach *et al.*, 1987. Goñi and Latrouite, 2005; Pais *et al.*, 2007). Everywhere in the Mediterranean, with the exception of a few well-enforced Marine Protected Areas (MPAs), fish stocks are more or less severely overexploited by small-scale fisheries (e.g. Sala *et al.*, 2012; Colloca *et al.*, 2017). The steady decline of fish stocks has been widely perceived by small-scale fishers for several centuries (Faget, 2009, 2011). The impact of legal artisanal fishing can be aggravated by several practices and factors: (i) recreational fishing (angling and spear fishing), with catches in coastal areas which can be of the same order of magnitude, or can even exceed, those of the artisanal fishery (Combelles, 1991; Bernard *et al.*, 1998; Daniel *et al.*,

1998; Chavoin and Boudouresque, 2004; Lloret *et al.*, 2008; Font *et al.*, 2012; Leleu, 2012; Font and Lloret, 2014); (ii) poaching, with the illegal capture of fish by scuba diving, spear fishing by night and the use of explosives (dynamite) (Harmelin *et al.*, 1996; Faget, 2015; Garrido Escobar, 2015); in some Mediterranean countries, artisanal fishers may be both fishermen and poachers; (iii) underestimation of total catch due to illegal, unreported and unregulated (IUU) landings: they constitute 54 % of the total reconstructed catch in Italy (Piroddi *et al.*, 2015; Falautano *et al.*, 2018); (iv) some fishing gear, such as trawls (including the so-called ‘ganguis’ of French fishers), which degrade *Posidonia oceanica* seagrass meadows and undermine their nursery role (e.g. Sanchez-Jerez, 1994; Pasqualini, 1997; IDEE *et al.*, 2002; Ganteaume *et al.*, 2005a; Bonacorsi *et al.*, 2011; Kiparissis *et al.*, 2011; Ben Hmida *et al.*, 2014; Giakoumi *et al.*, 2015; Faget, 2017); (v) non-compliance by some fishers with the regulations in force in the area or the country concerned (minimum mesh size, maximum soak times, prohibition of trawling gear, etc.) (Boudouresque *et al.*, 2005; Cadiou *et al.*, 2009); (vi) ghost fishing, i.e. lost fishing gear which continue to fish (Ayaz *et al.*, 2010; Houard *et al.*, 2012; Monet, 2015; Ozyurt *et al.*, 2016).

Within MPAs (Marine Protected Areas), regulations are established, e.g. the banning of angling, spear fishing, trawling, mooring, artisanal fishing, or just some of them. As far as artisanal fishing is concerned, regulations can deal with the minimum mesh size of fishing nets, the maximum soak time, the maximum length of fishing nets, the maximum length of fishing vessels, etc. (e.g. Ramos, 1990; Boudouresque *et al.*, 2004, 2005; Cadiou *et al.*, 2009; Robert, 2013a; Batista *et al.*, 2015). In addition, MPAs are usually the only sites where existing legislation, i.e. regulations that concern the whole of coastal areas (not only MPAs) (e.g. mesh size and prohibition of trawling close to the shore), is actually enforced (Boudouresque *et al.*, 2005).

Two major categories of MPAs can be distinguished. (i) MPAs where any form of human activity is prohibited, mainly recreational fishing and artisanal fishing. They are referred to as No-Take Zones (NTZ). (ii) MPAs where the area is zoned, each area being reserved for an activity and excluding activities that would generate conflicts of use, while organizing these activities so that they are compatible with habitat and species conservation. For example, diving is incompatible with fishing and navigation. Where artisanal fishing is allowed, it is subject to constraints (e.g. larger mesh size, shorter net length, reduced soak time, etc.) compared to general legislation that applies outside the MPA. Recreational fishing is often prohibited or subject to strict restrictions, in order to reserve catches for artisanal fishers. This category of MPAs is referred to as Multi-Use Management (MUM). The management of the Port-Cros Archipelago (Port-Cros National Park) is of the MUM type. In

fact, many Mediterranean MPA are a combination of both categories, NTZ and MUM. In any case, considering the preservation of species and ecosystems, NTZ and MUM management appear to be as effective as each other (Boudouresque *et al.*, 2004; Cadiou *et al.*, 2009; Personnic *et al.*, 2014; Thibaut *et al.*, 2017).

The establishment of an MPA results in a trend towards the recovery of 'natural' populations and ecosystems, in particular of the 'top predators' compartment. This trend is called the 'reserve effect' (e.g. Halpern and Warner, 2002; Boudouresque *et al.*, 2005; Guidetti, 2006; Guidetti and Sala, 2007; Harmelin-Vivien *et al.*, 2008; Stobart *et al.*, 2009; Gianni *et al.*, 2013; but see Bayle-Sempere and Ramos-Esplá, 1993). In the case of teleosts, this return can be rapid, about 5 years, at least for most species (Halpern and Warner, 2002; Seytre and Francour, 2008, 2009; Coll *et al.*, 2013). In the case of long-lived species, such as the grouper *Epinephelus marginatus* and the brown meagre *Sciaena umbra*, at Port-Cros, ~50 years after the creation of the National Park, numbers continue to increase, perhaps reflecting a still uncompleted return to the 'natural' state (Harmelin and Marinopoulos, 2000; Harmelin *et al.*, 2010; Ruitton and Harmelin, 2010; Harmelin, 2013). Size and age of the MPA matter (Claudet *et al.*, 2008). In addition, there is evidence of spillover (exportation of biomass) of fish from the MPAs to the adjacent areas, with a positive effect on the exploitable fish community and artisanal fishery (Boudouresque *et al.*, 2005; Harmelin-Vivien *et al.*, 2008; Stobart *et al.*, 2009).

The Port-Cros National Park (PCNP) is located in Provence (France, north-western Mediterranean Sea) (Barcelo and Boudouresque, 2012). The Port-Cros Archipelago constitutes a core area of the PCNP and has been protected since 1963 (Augier and Boudouresque, 1973; Boudouresque, 1976). The management of the marine part of the Port-Cros Archipelago MPA is of the MUM type (see next section). In contrast with many Mediterranean and non-Mediterranean MPAs, which are poorly or not-at-all enforced, the so-called 'paper parks' (see e.g. Guidetti *et al.*, 2008; Sala *et al.*, 2012; Giakoumi *et al.*, 2018), the enforcement of the Port-Cros Archipelago MPA is strict, efficient and long-lasting.

Here, we have seized the opportunity of having at our disposal one of the oldest Mediterranean MPAs, with exemplary protection and an exceptional corpus of scientific knowledge (species, habitats, ecosystems, habitat mapping, artisanal fishing - fishing pressure, total catch, Catch Per Unit of Effort, CPUE) (Farsac *et al.*, 2013; Boudouresque *et al.*, 2013b), to assess the biomass and trophic structure of fish (teleosts) assemblages in 5 habitats (shallow rocky reefs, deep rocky reefs, relatively shallow *Posidonia oceanica* seagrass meadows, deep

P. oceanica meadows adjacent to circalittoral habitats soft bottoms and coralligenous habitats), by sector and type of management.

Context: the Port-Cros Archipelago (Port-Cros National Park)

The Port-Cros National Park (PCNP) was established in December 1963. It encompassed the Island of Port-Cros and the neighbouring island and islets (Bagaud Island, La Gabinière Islet and Le Rascas Islet), i.e. the Port-Cros Archipelago, situated about 8 km off the continental coast of eastern Provence (Fig. 1). Together with the land areas of the islands and islets, the PCNP included a band of sea 600 m wide, 1 300 ha in surface area, surrounding the archipelago (Boudouresque *et al.*, 2013a). Progressively, the PCNP has been entrusted with the management of an increasing number of territories outside the initial territory of 1963. Since 1985, the PCNP manages the land (~950 ha), bought by the French state in 1974, situated on the neighbouring island of Porquerolles. Since 1984, the park manages the lands of the *Conservatoire de l'Espace Littoral et des Rivages Lacustres* (CERL) (Conservatoire of coastal areas and lake shores) situated at Cap Lardier, and since 1997 those situated on the island of Porquerolles (Grand Langoustier) and the Giens Peninsula (Escampobarieu). Since 1999, the PCNP has run Natura 2000 for the islands of Port-Cros and Porquerolles and is the operator of Natura 2000 for the island of Le Levant and the salt marshes at Hyères. Since 2000, the PCNP has been responsible for running the French part of the PELAGOS Sanctuary for marine mammals. Since 2004, the PNPC is the technical and scientific assistant for the *Communauté d'Agglomération Toulon Provence Méditerranée* (TPM) for the management of the CERL territories of Les Pesquiers and Les Vieux-Salins (Boudouresque *et al.*, 2013a; Barcelo *et al.*, 2013a; Sanctuaire PELAGOS, 2018). Between 2012 and 2016, the PCNP was engaged in a major redefinition and extension of its territory; the new Port-Cros National Park (N-PCNP), established in 2016, includes the Port-Cros and Porquerolles Archipelagos as core areas (both terrestrial and marine), a vast Adjacent Marine Area (AMA – *Aire Maritime Adjacente*) including the Gulf of Hyères and extending seawards to the edge of the continental shelf, and a discontinuous continental area, the Adhesion Area (AA – *Aire d'Adhésion*) including five *communes* (municipalities; the *commune* is the smallest territorial division in France) (Fig. 1; Barcelo and Boudouresque, 2011, 2012). The *communes* of the AA have voluntarily joined the National Park, through the signing of a charter which defines the objectives of the National Park regarding the conservation of natural and cultural heritage and sustainable development (Thompson *et al.*, 2011; Sellier, 2015; Hogg *et al.*, 2018).

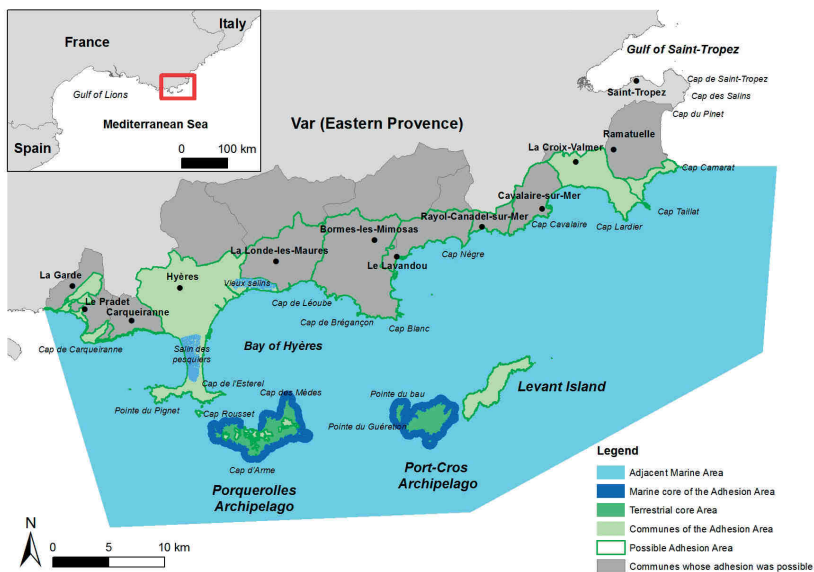


Figure 1. Map of the new Port-Cros National Park (N-PCNP), established in 2016. The initial PNPC, established in 1963, was restricted to the Archipelago of Port-Cros.

The management of the marine area of the Port-Cros Archipelago, which belongs to the core area of the N-PCNP, began when the Park was established in 1963, that is, 55 years ago. At that time only spearfishing and trawling were prohibited; these were very important measures, considering the extent of catches by spearfishing (Perraud, 1976; Ramos-Esplá, 1985; Chavoin and Boudouresque, 2004; Font and Lloret, 2014), and the severity of the damage caused by trawling, especially to *Posidonia oceanica* seagrass meadows (Ramos-Esplá, 1984; Paillard *et al.*, 1993; Pasqualini, 1997; Cadiou *et al.*, 2009; Boudouresque *et al.*, 2012; Pergent *et al.*, 2013; Giakoumi *et al.*, 2015). Until 1999, artisanal fishing in the Port-Cros Archipelago MPA was governed by French national regulations and by local regulations, established by the *prud'homie des pêcheurs* (fishers' guild) of Le Lavandou, to which the MPA belongs (Table I; Cadiou *et al.*, 2009). Since 1999, the Port-Cros Archipelago MPA (PCNP) has had its own artisanal fishing regulations enshrined in a fishing charter. The charter represents an agreement between fishers and MPA managers and is based largely on the *prud'homie* rules; however, the charter regulations are far stricter than the national and local (*prud'homie*) rules (Table I). To be authorized to fish inside the MPA, each fisher has to sign the charter each year and abide by its rules. In addition, fishers have to communicate details of their catches to the MPA managers *via* a fishing logbook (Cadiou *et al.*, 2009; Robert, 2013a, 2013b). The charter is updated annually, based on scientific monitoring and in consultation

with the fishers. It is worth noting that amendments to the charter have so far been minor, and that prohibited fishing areas (areas dedicated to bathing, to an underwater nature trail and to scuba diving) represent ~5 % of the surface area of the MPA. It is also important to note that existing regulations are strictly enforced inside the MPA, but usually not, or poorly, outside (Boudouresque *et al.*, 2005; Cadiou *et al.*, 2009).

Between 1990 and 2014, in incremental steps, recreational fishing has been almost completely banned, except trolling in certain areas (Fig. 2; Cadiou *et al.*, 2009). Three main considerations justify the almost-total banning of recreational fishing: (i) scientists have become aware of the huge catches taken by recreational fishing (Moreteau, 1981; Combelles, 1991; Bennett and Attwood, 1993; Coll *et al.*, 2004; Boudouresque *et al.*, 2005; Morales-Nin *et al.*, 2005; Lloret *et al.*, 2008; Leleu, 2012; Lloret and Font, 2013; Font and Lloret, 2014); (ii) recreational fishing was felt to be incompatible with the image of a national park; its presence in an MPA was perceived as shocking by visitors, including the recreational fishermen themselves, so that its prohibition appeared to be socially acceptable (Cadiou *et al.*, 2009); (iii) regulation of recreational fishing was seen as a management tool, increasing the fish stock available to artisanal fishers, and therefore helping make an increase in the restriction of artisanal fishing acceptable (Boudouresque *et al.*, 2004, 2005; Cadiou *et al.*, 2009).

Table I. Artisanal fishing regulations outside (*prud'homie des pêcheurs* of Le Lavandou local rules of January 1990) and inside the MPA (Port-Cros Archipelago, PCNP, fishing charter of 2014). From Cadiou *et al.* (2009) and Parc National de Port-Cros (2014). Some minor constraints are not mentioned here.

Vessel and gear specification			<i>Prud'homie des pêcheurs</i>	MPA: Port-Cros Archipelago (PCNP)
Vessel size			Free vessel size	Vessel size < 12 m
Nets	Maximum soak times	Small mesh size (23 mm) ^a	24 h	Depth < 30 m: between 16:00 and 9:00 Depth > 30 m: 48 h
		Small to medium mesh size (24-41 mm)	24 h	Depth < 30 m: 24 h Depth > 30 m: 48 h
		Medium (42 mm) and large (> 42 mm) mesh size	48 h	Depth < 30 m: 24 h Depth > 30 m: 48 h
	Minimum mesh size	Depth < 30 m	23 mm	Daytime: 23 mm Night-time: 36 mm
		Depth > 30 m	23 mm	42 mm

Vessel and gear specification			<i>Prud'homie des pêcheurs</i>	MPA: Port-Cros Archipelago (PCNP)
	Maximum number of lengths of net ^b	Depth < 30 m	30 lengths of net (+ 7 for each fisher on board over 2) ^c	15 lengths of net (split up into three fishing sets composed of five lengths of net)
		Depth > 30 m	30 lengths of net (+ 7 for each fisher on board over 2) ^c	20 lengths of net (split up into four fishing sets composed of five lengths of net)
	Length of fishing sets	Maximum distance between the two surface buoys	700 m	Around 500 m (five lengths of net)
Hooks		Number	1 000 per boat	500 per boat ^d
		Period allowed	Period decided each year	Prohibited 1st July-31 August
		Sectors	Sectors banned decided each year	Prohibited to the south of the MPA, near diving sites and within a 50-m wide belt off the shoreline (Fig. 2)
		Soak time	No constraints	Between one hour before sunset and one hour after sunrise
Traps		Number	50 per boat (+ 25 for each fisher on board over 2)	Six per boat
Trawling gear		Small drag	15 December – 15 April	Banned
		Others	Banned	Banned
Sea urchins			Periods and amounts decided each year	Banned

Fishing periods, where not indicated, are the same inside and outside the MPA (i.e. the *prud'homie* regulations). Only fishing activities that are performed or could be performed within the MPA if no proper regulation existed are mentioned. The national regulations, less restrictive than those of the *prud'homie*, are not mentioned.

^a The mesh size, which was indicated in customary units used by fishers, has been converted here into SI units.

^b The length of a piece of net (length of net) is ~100 m.

^c Fishers can use 30 lengths of net (small to medium mesh size), plus up to 30 lengths of net (large mesh size), so that the maximum number of lengths of net is 60.

^d No more than two longliners fishing simultaneously within the MPA.

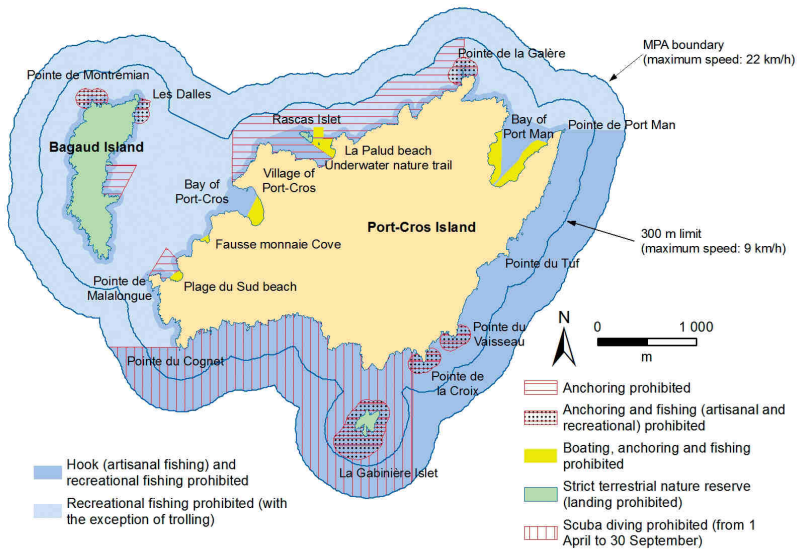


Figure 2. Artisanal and recreational fishing regulations (in force in 2014) within different areas of the Port-Cros Archipelago MPA (PCNP).

Overall, the management of the Port-Cros Archipelago MPA can clearly be referred to the MUM type. It is characterized by a complex zoning of the marine part of the MPA, based upon the uses, the goals of conservation of the habitats and the ecosystems (and the species which live there) and priorities clearly displayed (artisanal fishing rather than recreational fishing) (Fig. 2 and 3, Table II). Is this zoning complexity a little excessive? This question falls beyond the scope of the present paper. However, the PCNP's success, recognized worldwide, in both sustainable artisanal fishing and natural heritage conservation, suggests that such complexity is quite manageable and that it is working. Many authors have suggested designs for ideal MPAs that perhaps will never exist, have described interesting and theoretically perfect modes of management, while the 'perfect' MPAs they cited were sometimes mere paper parks; these studies are of course of great interest, and their utility is not in question (e.g. Belbin, 1995; Sala *et al.*, 2002; Halpern *et al.*, 2006; Deros *et al.*, 2007; Scianna *et al.*, 2015; Bianchi *et al.*, 2018; Scianna *et al.*, 2018). However, it is interesting to note that the management of Port-Cros MPA did not follow a pre-established plan, either when it was established or later on. The management process was developed step by step, throughout the 55 years of existence of the National Park, according to clear long-term objectives (the protection of natural and cultural heritage, sustainable tourism and artisanal fishing, maintaining the presence of the inhabitants in the core area of the Park). But in fact,

the managers have seized the opportunity of scientific results, changing attitudes and what is ‘socially acceptable’, to move forward and evolve constantly, towards the current management model.

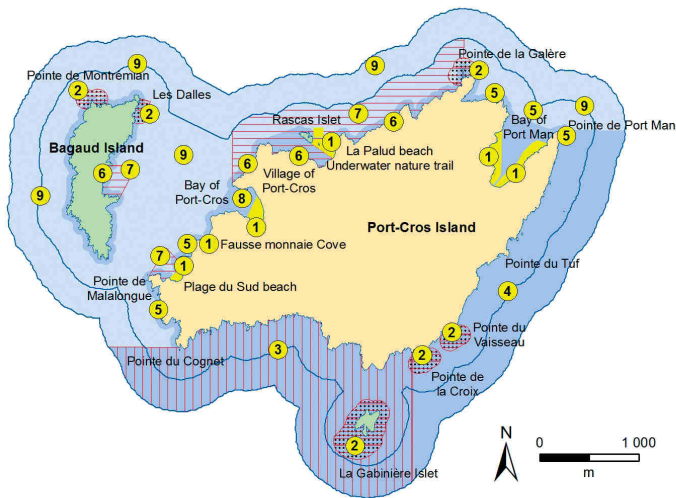


Figure 3. Regulation of uses (fishing, boating, anchoring, mooring, scuba diving) within the marine area of the Port-Cros Archipelago core area of the Port-Cros National Park (PCNP) (in force in 2014). Zones 1 through 9: see Table II.

Table II. Regulation of uses within the marine area of the Port-Cros Archipelago core area of the Port-Cros National Park (PCNP) (in force in 2014). Zones 1 through 9 (see Fig. 3). + = Yes. - = No or non-applicable.

Regulation	Zones								
	1	2	3	4	5	6	7	8	9
Boating (motor boats) prohibited	+	-	-	-	-	-	-	-	-
Anchoring prohibited (all vessels)	+	+	-	-	-	+	+	+	-
Anchoring prohibited (vessels size > 30 m)	+	+	+	+	+	+	+	+	+
Mooring (on buoys) mandatory	-	-	-	-	-	-	-	+	-
Mooring on buoys: scuba diving boats have priority	-	+	-	-	-	-	-	-	-
Artisanal fishing prohibited	+	+	-	-	-	-	-	+	-
Artisanal fishing allowed, in accordance with the rules of the fishing charter ^(a)	-	-	+	+	+	+	+	+	+

	Zones								
Regulation	1	2	3	4	5	6	7	8	9
Recreational angling prohibited	+	+	+	+	+	+	+	+	+
Spear fishing prohibited	+	+	+	+	+	+	+	+	+
Trolling prohibited	+	+	+	+	+	+	-	+	-
Scuba diving prohibited (from April, 1 st to September, 30)	-	-	+	-	-	-	-	+	-

^(a) The fishing charter is governed by a decree of the *Préfet* (representative of the French State) of Eastern Provence (French administrative division, the Var).

Zone 1: Plage du Sud beach, head of the Port-Cros Bay, Fausse-Monnaie Cove, underwater nature trail of La Palud Bay, east and west sides of Port-Man Bay.

Zone 2: Pointe Montrémian, Les Dalles, Pointe de La galère, Pointe du Vaisseau, Pointe de la Croix, La Gabinière Islet.

Zone 3: From Pointe du Cognet to Pointe de la Croix.

Zone 4: From Pointe de la Croix to Pointe de Port-Man.

Zone 5: From Pointe de Port-Man to Pointe de la Galère (up to 50 m offshore), central area of Port-Man Bay, From Port-Cros Bay to Pointe du Cognet (up to 50 m offshore), Bagaud Island (up to 50 m offshore).

Zone 6: From Pointe de la Galère to Port-Cros Bay (up to 50 m offshore), La Palud Bay, pier area of East Bagaud (up to 50 m offshore).

Zone 7: From Pointe de la Galère to Port-Cros Bay (from 50 m to 300 m off the shore), Plage du Sud, pier area of East Bagaud (from 50 m to 300 m off the shore).

Zone 8: Mouth of Port-Cros Bay.

Zone 9: Light blue on the map.

The Archipelago of Port-Cros is one of the regions of the world ocean on which have been focused the greatest number of studies (>1 500) for such a small surface area (~13 km²) (Farsac *et al.*, 2013; Boudouresque *et al.*, 2013b): e.g. physical oceanography (Taupier-Letage *et al.*, 2013), macroalgae (Augier and Boudouresque, 1971; Boudouresque *et al.*, 1972; Belsher *et al.*, 1976; Coppejans and Boudouresque, 1976), seagrasses (Molinier and Picard, 1952; Augier *et al.*, 1970a, 1970b; Boudouresque *et al.*, 1975; Pergent *et al.*, 1983; Libes and Boudouresque, 1987; Bonhomme *et al.*, 2010), sponges (Perez and Capo, 2001), bryozoans (Harmelin, 1978, 2017a, 2017b), fish (Harmelin-Vivien, 1982; Harmelin and Marinopoulos, 1993; Harmelin *et al.*, 2010; Ruitton and Harmelin, 2010; Harmelin, 2013; Astruch *et al.*, 2015), echinoderms (Harmelin *et al.*, 1980; Paul *et al.*, 1983; Azzolina *et al.*, 1985), bryozons (Harmelin, 2017a, 2017b), mapping of benthic habitats (Augier and Boudouresque, 1967, 1970a, 1970b, 1976; Belsher *et al.*, 2005; Astruch *et al.*, 2012), ecosystem functioning (Personnic *et al.*, 2014; Thibaut *et al.*, 2017), impact of human activities such as anchoring and contaminants (Boudouresque *et al.*, 1975; Ganteaume *et al.*, 2005b; Rouanet *et al.*, 2013), fisheries (Cadiou *et al.*, 2001; Cadiou and Le Diréach, 2002; Bonhomme *et al.*, 2008, 2009; Cadiou *et al.*, 2009; Bonhomme *et al.*, 2012, 2014), reserve effect (Harmelin-Vivien and Harmelin, 2012) and control of biological invasions (Cottalorda *et*

al., 1996; Boudouresque and Verlaque, 2005; Cottalorda *et al.*, 2010, 2011, 2012; Barcelo *et al.*, 2013b, 2016). Each new study thus fits into a general pattern of knowledge, in all fields of science, which provides a basis for optimal interpretation.

Materials and methods

Five habitats were sampled in the Port-Cros Archipelago MPA (Port-Cros National Park, Eastern Provence, France, northwestern Mediterranean): (i) shallow rocky reefs (0-3 m depth, 13 sites; hereafter RS); (ii) deep rocky reefs (5-15 m, 12 sites; RD); (iii) relatively shallow *Posidonia oceanica* seagrass meadows (10-15 m; 5 sites; PS); (iv) deep *P. oceanica* meadows adjacent to circalittoral soft bottoms, namely coastal detrital (CD) and coarse sands and fine gravels under the influence of bottom currents (CSBC) (30-35 m; 4 sites; PD); and (v) coralligenous (25-40 m; 6 sites; C) (Fig. 4). Within the framework of MUM management, three types of management were considered: (i) sites reserved for scuba diving, where artisanal and recreational fishing are totally prohibited; these are no-take areas (hereafter: NT); in addition, divers must give a commitment to respect, if they wish to be allowed to dive, the diving charter which prohibits, in particular, the feeding of fish; (ii) sites where longlines and trawling (artisanal fishing), spear fishing and angling (recreational fishing) are prohibited; artisanal fishers must, if they wish to be allowed to fish, give a commitment to respect the fishing charter, which is much more restrictive than general regulations and the local regulations of the *prud'homie des pêcheurs* (see Table I); these sites are restricted fishing areas (RF); and (iii) sites reserved for artisanal fishers; spear fishing, angling and trawling are prohibited; as for RF areas, artisanal fishers must commit to respecting the fishing charter (Table I); these sites are artisanal fishing areas (AF) (Table III).

Table III. Localization of the sampling sites (see Fig. 4). Habitat: RS = shallow reefs, RD = deep reefs, PS = relatively shallow *Posidonia oceanica* seagrass meadows, PD = deep *P. oceanica* meadows, C = coralligenous. Management: NT = no-take areas, RF = restricted fishing areas, AF = artisanal fishing areas. Sampling: Scuba = scuba diving, Snork. = snorkelling. Latitude and longitude: WGS 84. Dates: day/month/year (2014).

N°	Site	Habitat	Management	Sampling	Latitude	Longitude	Depth	Dates
1	Montrémian	RD	NT	Scuba	43°01.118'	6°21.744'	5-15 m	16/09/14 08/10/14
2	Bagaud West	RD	RF	Scuba	43°00.721'	6°21.620'	5-15 m	16/09/14 08/10/14
3	Bagaud South	RD	AF	Scuba	43°00.210'	6°21.792'	5-15 m	14/09/14 07/10/14

N°	Site	Habitat	Management	Sampling	Latitude	Longitude	Depth	Dates
4	Pointe du Cognet	RD	RF	Scuba	42°59.820'	6°22.321'	5-15 m	15/09/14
								08/10/14
5	Southern coast	RD	RF	Scuba	42°59.814'	6°22.855'	5-15 m	16/09/14
								08/10/14
6	Gabinière West	RD	NT	Scuba	42°59.311'	6°23.622'	5-15 m	15/09/14
								07/10/14
7	Le Vaisseau	RD	NT	Scuba	42°59.722'	6°24.390'	5-15 m	13/09/14
								07/10/14
8	Tuff	RD	RF	Scuba	43°00.161'	6°24.780'	5-15 m	13/09/14
								06/10/14
9	Pointe de Port-Man	RD	RF	Scuba	43°00.820'	6°25.280'	5-15 m	12/09/14
								06/10/14
10	Pointe de la Galère	RD	NT	Scuba	43°01.235'	6°24.551'	5-15 m	14/09/14
								06/10/14
11	Rascas	RD	RF	Scuba	43°00.884'	6°23.639'	5-15 m	14/09/14
								06/10/14
12	Fausse Monnaie	RD	RF	Scuba	43°00.325'	6°22.466'	5-15 m	15/09/14
								16/10/14
13	Montrémian	PS	NT	Scuba	43°01.082'	6°21.705'	10-15 m	16/09/14
								08/10/14
14	Bagaud Pass	PS	AF	Scuba	43°00.371'	6°22.005'	10-15 m	14/09/14
								07/10/14
15	Baie Port-Cros	PS	RF	Scuba	43°00.589'	6°22.752'	10-15 m	13/09/14
								08/10/14
16	Vallon	PS	RF	Scuba	42°59.563'	6°23.857'	10-15 m	13/09/14
								06/10/14
17	Pointe de Port-Man	PS	RF	Scuba	43°00.786'	6°25.280'	10-15 m	12/09/14
								06/10/14
18	Bagaud West	PD	AF	Scuba	43°00.684'	6°21.438'	30-35 m	16/09/14
								16/10/14
19	Bagaud Pass	PD	AF	Scuba	43°00.934'	6°22.411'	30-35 m	14/09/14
								08/10/14
20	Vallon	PD	RF	Scuba	42°59.461'	6°23.842'	30-35 m	13/09/14
								06/10/14
21	Pointe de Port-Man	PD	AF	Scuba	43°00.962'	6°25.296'	30-35 m	12/09/14
								06/10/14
22	Montrémian	C	NT	Scuba	43°01.160'	6°21.759'	25-40 m	16/09/14
								26/09/14
								16/10/14

N°	Site	Habitat	Management	Sampling	Latitude	Longitude	Depth	Dates
23	Pointe du Cognet	C	RF	Scuba	43°01.148'	6°22.513'	25-40 m	15/09/14 08/10/14
24	Roche des catalans	C	AF	Scuba	43°00.037'	6°21.789'	25-40 m	14/09/14 07/10/14
25	Gabinière East	C	NT	Scuba	42°59.241'	6°23.797'	25-40 m	15/09/14 07/10/14
26	Le Vaisseau	C	NT	Scuba	42°59.735'	6°24.462'	25-40 m	13/09/14 07/10/14
27	Pointe de la Galère	C	NT	Scuba	43°01.246'	6°24.571'	25-40 m	12/09/14 06/10/14
28	Montrémian	RS	NT	Snork.	43°01.069' 43°01.105'	6°21.720' 6°21.866'	0-3 m	16/09/14 16/10/14
29	Bagaud West	RS	RF	Snork.	43°00.705' 43°00.779'	6°21.612' 6°21.577'	0-3 m	16/09/14 20/10/14
30	Bagaud South	RS	RF	Snork.	43°00.242' 43°00.322'	6°21.809' 6°21.702'	0-3 m	14/09/14 16/10/14
31	Pointe du Cognet	RS	RF	Snork.	42°59.805' 42°59.888'	6°22.320' 6°22.303'	0-3 m	15/09/14 20/10/14
32	Southern coast	RS	RF	Snork.	42°59.857' 42°59.880'	6°23.342' 6°23.148'	0-3 m	15/09/14 20/10/14
33	Gabinière West	RS	NT	Snork.	42°59.370' 42°59.273'	6°23.709' 6°23.622'	0-3 m	15/09/14 20/10/14
34	Le Vaisseau	RS	NT	Snork.	42°59.805' 42°59.757'	6°24.424' 6°24.313'	0-3 m	13/09/14 06/10/14
35	Tuff	RS	RF	Snork.	43°00.162' 43°00.126'	6°24.803' 6°24.650'	0-3 m	13/09/14 06/10/14
36	Pointe de Port-Man	RS	RF	Snork.	43°00.701' 43°00.829'	6°25.223' 6°25.282'	0-3 m	12/09/14 06/10/14
37	Pointe de la Galère	RS	NT	Snork.	43°01.111' 43°01.209'	6°24.506' 6°24.543'	0-3 m	12/09/14 06/10/14
38	Northern coast	RS	RF	Snork.	43°00.896' 43°00.968'	6°23.842' 6°24.039'	0-3 m	14/09/14 06/10/14
39	Fausse Monnaie	RS	RF	Snork.	43°00.341' 43°00.413'	6°22.503' 6°22.614'	0-3 m	15/09/14 16/10/14
40	Bagaud East	RS	RF	Snork.	43°00.594' 43°00.693'	6°21.931' 6°21.875'	0-3 m	15/09/14 08/10/14

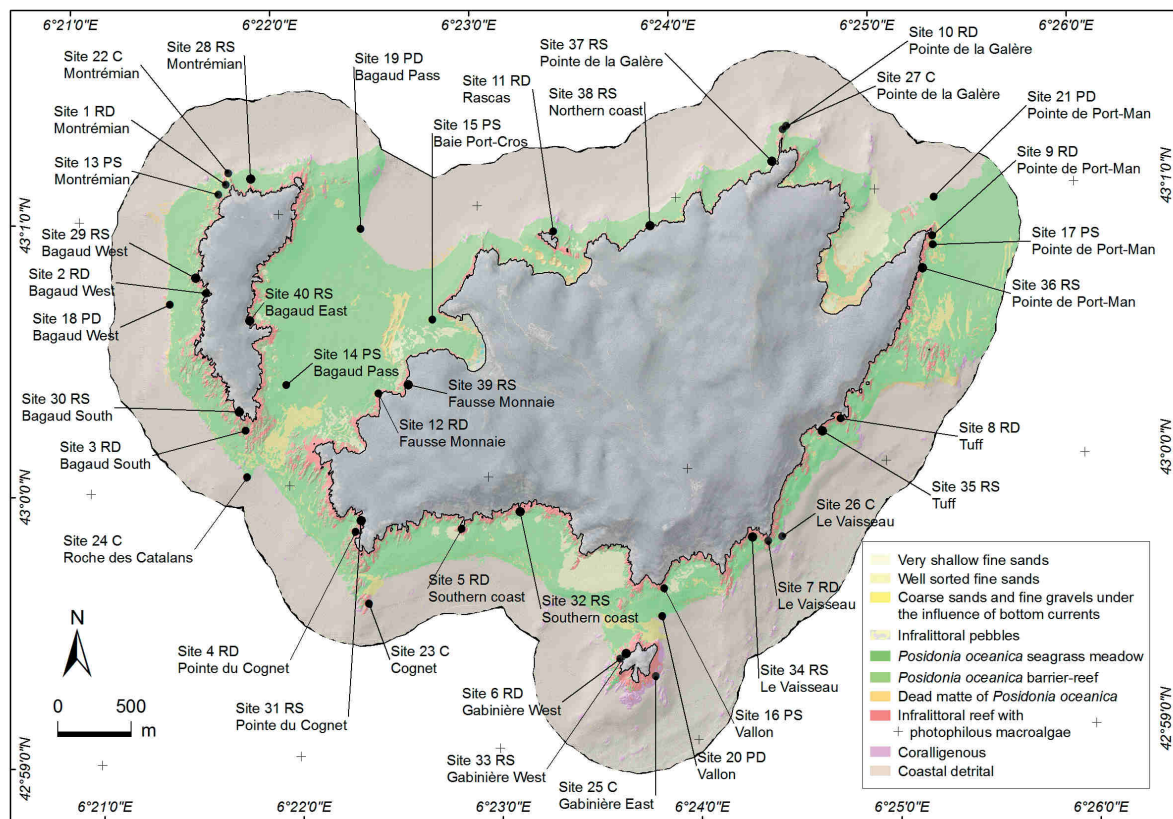


Figure 4. Localization of the sample sites (site 1 through site 40; see Table III for details). Map of the habitats: from Bonhomme *et al.* (2011) and Astruch *et al.* (2012). Name of the habitats: from Pérès and Picard (1964) and Pérès (1967, 1982).

Visual censuses were performed on transects arranged randomly. This method, developed by Harmelin-Vivien and Harmelin (1975) and Harmelin-Vivien *et al.* (1985), has been improved in particular in the framework of the European BIOMEX program (BIOMEX, 2006), and is used in most MPAs in the north-western Mediterranean (Harmelin-Vivien and Harmelin, 2013). The fish assemblage was assessed, at each site, from 10 random transects (replicates) 25 m long and 5 m wide, marked out by a graduated tape. The sampling unit is therefore a transect of 125 m². On the 10-15 m depth *Posidonia oceanica* seagrass habitats (PS), where the density of the fish visible by visual censuses is low, the surface area of the transects was 50 m long and 5 m wide, i.e. 250 m². The transects were surveyed by scuba diving (RD, PS, PD, C) or snorkelling (RS). In order to smooth the temporal variability, the 10 replicates of each site were performed in two sessions (five each session), at two close dates (Table III; see Le Diréach *et al.*, 2010; Bonhomme *et al.*, 2015). In each sample (transect, visual census), each observer identified all the fish species present, with the exception of small cryptic species (mainly Gobiidae, Blenniidae and Tripterygiidae), for which the census could be biased. Invertebrates of fisheries interest (cephalopod molluscs and decapod crustaceans) were also recorded (results not presented here). The number of individuals of each species and their total length (TL) were recorded: to the nearest 1 cm (up to 10 cm TL) and then to 2 cm (10 through 40 cm TL) and to 5 cm beyond 40 cm TL. Visual censuses were performed in September and October 2014; autumn is the period of better stability of the coastal fish population, with therefore high representativeness, before the cold season, in the Mediterranean (Table III). It is worth noting that fewer fish species are recorded by visual counts than by trawling; in contrast, more individuals and a greater biomass are recorded from visual counts (Harmelin-Vivien and Francour, 1992).

At the end of each visual census, the observer crossed the transect in the opposite direction in order to characterize the habitat by recording the following parameters on 5 m sections (10 m sections for relatively shallow *Posidonia oceanica* seagrass meadows, PS): (i) the nature of the substrate (percentage of rock, seagrass, sand and gravel, total = 100 %); (ii) number and size of blocks (small <1 m, average 1 to 2 m and large > 2 m in diameter). This criterion was not noted for the coralligenous habitat, because of the depth constraint (limited diving time); (iii) the slope, according to 4 categories (1 = sub-horizontal 0-30 °, 2 = slight slope 30-60 °, 3 = steeply sloping 60-90 °, 4 = overhang > 90 °), was only recorded on the coralligenous habitat; (iv) the dominant stratum height (only noted for the coralligenous habitat), without distinguishing plants (e.g. *Cystoseira*) from animal (e.g. gorgonians): 0-10 cm, 10-30 cm or > 30 cm; (v) the roughness of the substrate (only noted for the coralligenous habitat), with 3 categories: 1 = smooth, 2 = anfractuous and

3 = very anfractuouse. The interpretation of these data is not presented here, but can be found in Astruch *et al.*, 2015).

The metrics considered in the present study are species richness, abundance or density, and biomass. The analysis focuses on the average values of these metrics by site and habitat, for the whole fish stand and for the target species of the fishery. As far as species richness is concerned, we considered the mean number of species per sample (point diversity), the cumulative number of species per site and at the level of the habitat (alpha diversity) and at the level of the whole area, the Port-Cros Archipelago (gamma diversity) (see Sala and Knowlton, 2006 and Boudouresque, 2014, for the concept of biodiversity). The size class distribution was also explored for a number of target species (results not presented here; see Astruch *et al.*, 2015). Finally, the species have been grouped according to their diet (see below).

A treatment based on a list of 24 target species (Table IV) was carried out for each habitat. This list was prepared by Daniel *et al.* (2002) based on the work of Harmelin *et al.* (1995) and Harmelin (1999) and used by Astruch *et al.* (2009) and Bonhomme *et al.* (2015) in the Calanques National Park (near Marseille, Western Provence). As part of the present study, other target species encountered in Port-Cros, such as *Pagellus erythrinus*, *Pagrus pagrus*, *Sphyræna viridensis* and *Epinephelus costae*, were added.

From the size measured during the census and on the basis of size/mass relationships available in the literature (e.g. Bauchot and Pras, 1980; FishBase, 2015), the wet mass of each individual was estimated. On the basis of the abundance and size of individuals counted at each site, the teleost fish biomass (wet mass WM: kg WM per 100 m²) was calculated.

Table IV. Target species of the fishery, considered in the present study (in alphabetical order; common synonyms). Targeted by artisanal fishing (Art.), recreational fishing – angling (Angl.) and spear fishing (Spear). Spear fishing is prohibited within the Port-Cros Archipelago MPA.

Species	French common name	English common name	Targeted by
<i>Conger conger</i>	Congre	Conger eel	Art., Spear
<i>Coris julis</i>	Girelle	Rainbow wrasse	Angl.
<i>Dentex dentex</i>	Denté commun, denti,	Common dentex	Art., Angl., Spear
<i>Dicentrarchus labrax</i>	Loup, bar commun	European seabass	Art., Angl., Spear
<i>Diplodus cervinus</i>	Sar tambour, sar à grosses lèvres	Zebra sea bream	Art., Angl., Spear

Species	French common name	English common name	Targeted by
<i>Diplodus puntazzo</i>	Sar à museau pointu	Sharpsnout bream	Art., Angl., Spear
<i>Diplodus sargus</i>	Sar commun	White sea bream	Art., Angl., Spear
<i>Diplodus vulgaris</i>	Sar à tête noire, vérade	Common two-banded sea bream	Art., Angl.
<i>Epinephelus costae</i> (= <i>E. alexandrinus</i>)	Badèche	Golden grouper	Spear
<i>Epinephelus marginatus</i>	Mérou brun	Dusky grouper	Spear (poaching)
<i>Labrus merula</i>	Merle, labre merle	Brown wrasse	Art., Angl., Spear
<i>Labrus mixtus</i> (= <i>L. bimaculatus</i>)	Vieille coquette, labre coquette	Cuckoo wrasse	Angl.
<i>Labrus viridis</i>	Labre vert, lasagne	Green wrasse	Art., Angl., Spear
<i>Mullus surmuletus</i>	Rouget de roche	Striped red mullet	Art., Angl., Spear
<i>Muraena helena</i>	Murène de Méditerranée	Mediterranean moray	Art., Spear
<i>Pagellus erythrinus</i>	Pageot commun, pageot rose	Common pandora	Art., Angl., Spear
<i>Pagrus pagrus</i>	Pagre commun, pagre	Common sea bream	Art., Angl., Spear
<i>Phycis phycis</i>	Mostelle de roche, mostelle	Forkbeard	Art., Spear
<i>Sciaena umbra</i>	Corb noir, corb	Brown meagre	Art., Spear (poaching)
<i>Scorpaena scrofa</i>	Rascasse rouge, chapon	Red scorpionfish	Art., Spear
<i>Seriola dumerilii</i>	Sériole couronnée, sériole	Greater amberjack	Art., Angl., Spear
<i>Serranus cabrilla</i>	Serran chevrette	Comber	Angl.
<i>Serranus scriba</i>	Serran écriture	Painted comber	Angl.
<i>Sparus aurata</i>	Daurade royale	Gilt-head sea bream	Art., Angl., Spear
<i>Sphyaena viridensis</i>	Bécune bouche jaune, barracuda	Yellowmouth barracuda	Art., Angl., Spear
<i>Spondyllosoma cantharus</i>	Canthare, daurade grise	Black sea bream	Art., Angl.
<i>Symphodus mediterraneus</i>	Crénilabre méditerranéen	Axillary wrasse	Angl.
<i>Symphodus tinca</i>	Crénilabre paon	Peacock wrasse	Angl., Spear

The teleost fish species were classified, according to their diet, into 6 trophic groups. The trophic groups considered here are based on the recommendations of Mireille Harmelin-Vivien (pers. comm.). This classification has been simplified, compared to those used by Bell and Harmelin-Vivien (1982) and Ourgaud *et al.* (2015). Differences

with literature data mainly concern omnivorous and mesocarnivorous groups. The trophic groups used here are as follows: (i) Planktivorous teleosts are living in the water column and feed primarily on zooplankton in daytime, such as *Chromis chromis*, *Boops boops*, *Spicara* spp. and *Atherina* spp., or at night, such as *Anthias anthias* and *Apogon imberbis*. (ii) Piscivorous teleosts; their diet is composed mainly of teleost fishes but also sometimes of large molluscs and decapod crustaceans. The main species are *Dentex dentex*, *Sphyaena viridensis*, *Seriola dumerilii*, *Scorpaena scrofa* and *Epinephelus marginatus*. (iii) Macrocarnivorous teleosts feed on decapod crustaceans (mainly Caridae and Brachyura), large amphipods, and teleosts. The main families and species are the Congridae, Muraenidae, *Serranus cabrilla*, *S. scribea*, *Scorpaena porcus*, *S. notata* and *Pagrus pagrus*. (iv) Omnivorous teleosts have a mainly carnivorous diet, but can also consume macroalgae: e.g. *Diplodus puntazzo* and the Mugilidae. (v) Mesocarnivorous teleosts have a relatively varied diet, feeding on annelids, amphipods, small crustaceans, echinoderms and molluscs. The main families, genera and species are Labridae, Mullidae, *Diplodus* spp., *Spondyllosoma cantharus*, *Phycis phycis* and *Sciaena umbra*. (vi) Herbivorous teleosts feed exclusively on primary producers such as *Posidonia oceanica* or macroalgae. The main species is *Sarpa salpa*.

Data have been processed with STATISTICA™ software. The conditions of normality (Levene test) and homogeneity of variances (Bartlett test) were tested for species richness, densities and biomass of teleost fishes, all species combined, and just the subset of target species. When these conditions are met, ANOVAs were performed, and if applicable the Newman-Keuls post-hoc test (named NK in the results) was applied to assess the significance of differences. However, these conditions are not always met, even when the transformations $\log(x + 1)$ and $\sqrt{}$ were applied. In these cases, the nonparametric Kruskal-Wallis test (named KW in the results) was used, as well as the multiple comparisons of the post-hoc average ranks (named CMAR in the results) in order to characterize the differences. In cases where only two groups were compared, the nonparametric Mann-Whitney test (named MW in the results) was used. The probabilities (p) corresponding to the different tests are mentioned and the level of significance reported as follows: (i) * means $0.05 > p > 0.01$ and indicates that there are significant differences with a confidence level of 95 % and 99 %; (ii) ** means $0.01 > p > 0.001$ and indicates that there are significant differences with a confidence level of 99 % to 99.9 %; (iii) *** means $p < 0.001$ and indicates that there are significant differences with a confidence level $> 99.9\%$; (iv) ns means $p > 0.05$ and indicates that there are no significant differences with a confidence level of 95%.

For details regarding the data, standard deviations (SD) and statistical tests, refer to Astruch *et al.* (2015).

Results

Shallow rocky reefs (0-3 m depth)

The overall species diversity (alpha diversity for the study area) in shallow rocky reefs (0-3 m depth) was 34 species. The alpha diversity per site ranged between 17 (site 33, Gabinière West) and 23 (site 36, Pointe de Port-Man). The point-diversity generally did not significantly differ between sites, whatever the management type (NT or RF) or the species taken into account (all teleost species or just the target species) (Tables V, VI and VII). Some species were present at all sites: *Coris julis*, *Diplodus sargus*, *D. vulgaris*, *Mugil* sp., *Sarpa salpa*, *Serranus cabrilla*, *Symphodus tinca* and *Thalassoma pavo*. Other species were abundant but not present at all sites: *Chromis chromis*, *Diplodus puntazzo*, *Labrus merula*, *Oblada melanura*, *Serranus scriba*, *Symphodus ocellatus* and *S. roissali*. Only a single individual of the dusky grouper *Epinephelus marginatus* has been sighted (Site 35, Tuff) (Table VI).

Table V. Species diversity of teleost fishes of shallow rocky reefs. Mean number of species per sample (point diversity), cumulative number of species per site (alpha diversity). Target species are species targeted by artisanal fishing and/or recreational fishing (see Table IV).

Sites	All species		Target species	
	Point diversity ^a	Alpha diversity	Point diversity ^a	Alpha diversity
Site 28 Montrémian	10.9	21	4.9	11
Site 33 Gabinière West	8.4	17	4.1	9
Site 34 Le Vaisseau	9.9	19	5.2	11
Site 37 Pointe de la Galère	6.7	20	4.4	11
Site 29 Bagaud West	9.2	19	4.2	8
Site 30 Bagaud South	8.4	18	4.4	9
Site 31 Pointe du Cognet	9.5	19	5.0	10
Site 32 Southern coast	10.0	21	6.0	12
Site 35 Tuff	8.4	22	4.0	12
Site 36 Pointe de Port-Man	8.5	23	5.8	13
Site 38 Northern coast	9.2	20	5.0	10
Site 39 Fausse Monnaie	9.1	20	5.0	10
Site 40 Bagaud East	10.0	19	4.9	8

^a Standard deviation: 2-3.

Table VI. Species recorded in the visual censuses of shallow rocky reefs (0-3 m depth). Ab. (abundance) = cumulated number of individuals per site (all transects). Occ. (occurrence) = percentage of transects where the species was recorded. - = absent. * = target species (see Table IV). Management: NT = no-take areas; RF = restricted fishing areas: longlines (artisanal fishing) and angling (recreational fishing) prohibited. Total abundance: cumulative number of sighted individuals (all sites).

Family	Species	NT (no-take areas)								RF (restricted fishing areas)																Total abundance		
		Site 28 Montrémian		Site 33 Gabinière West		Site 34 Le Vaisseau		Site 37 Pointe de la Galère		Site 29 Bagaud West		Site 30 Bagaud South		Site 31 Pointe du Cognet		Site 32 Southern coast		Site 35 Tuff		Site 36 Pointe de Port-Man		Site 38 Northern coast		Site 39 Fausse Monnaie			Site 40 Bagaud East	
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.		Ab.	Occ.
Apogonidae	<i>Apogon imberbis</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	1
Atherinidae	<i>Atherina</i> sp.	52	30%	94	30%	45	20%	-	-	-	-	-	-	-	-	80	20%	56	30%	10	10%	-	-	266	80%	55	20%	658
Fistulariidae	<i>Fistularia commersonii</i>	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
Labridae	<i>Coris julis</i> *	283	100%	221	100%	156	100%	244	100%	330	100%	195	100%	250	100%	243	100%	172	100%	221	100%	209	100%	132	100%	232	100%	2 888
	<i>Labrus merula</i> *	2	10%	1	10%	2	20%	-	-	3	30%	3	20%	6	50%	7	70%	2	10%	3	30%	6	40%	2	20%	7	40%	44
	<i>Labrus viridis</i> *	1	10%	-	-	1	10%	2	10%	-	-	-	-	4	20%	2	20%	1	10%	1	10%	-	-	-	-	-	-	12
	<i>Symphodus cinereus</i>	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	<i>Symphodus doderleini</i>	-	-	-	-	-	-	1	10%	1	10%	1	10%	-	-	-	-	-	1	10%	1	10%	-	-	1	10%	6	
	<i>Symphodus mediterraneus</i> *	-	-	-	-	3	30%	1	10%	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	5
	<i>Symphodus melanocercus</i>	-	-	-	-	-	-	-	-	3	20%	3	20%	4	30%	6	50%	1	10%	-	-	1	10%	1	10%	3	30%	22
	<i>Symphodus ocellatus</i>	7	50%	11	50%	-	-	13	40%	13	40%	10	40%	2	20%	18	30%	1	10%	3	20%	2	20%	9	60%	53	70%	142
	<i>Symphodus roissali</i>	19	90%	43	100%	7	30%	1	10%	19	70%	14	70%	31	90%	14	60%	14	60%	11	60%	5	30%	25	90%	26	90%	229
	<i>Symphodus rostratus</i>	1	10%	-	-	-	-	-	-	-	-	-	-	1	10%	1	10%	-	-	1	10%	-	-	-	-	-	-	4
	<i>Symphodus tinca</i> *	33	100%	11	40%	14	50%	17	70%	39	90%	92	70%	38	70%	63	100%	30	60%	35	100%	26	80%	120	80%	90	100%	608
	<i>Thalassoma pavo</i>	53	90%	12	80%	41	100%	6	50%	66	100%	50	70%	53	100%	12	50%	57	100%	14	60%	10	70%	11	30%	8	50%	393
Moronidae	<i>Dicentrarchus labrax</i> *	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	2	20%	-	-	1	10%	-	-	1	10%	-	-	5
Mugilidae	<i>Mugil</i> sp.	321	90%	21	50%	214	100%	28	40%	187	70%	14	30%	69	70%	259	50%	151	70%	21	30%	38	60%	28	60%	49	90%	1 400

Family	Species	NT (no-take areas)								RF (restricted fishing areas)																Total abundance		
		Site 28 Montrémian		Site 33 Gabinière West		Site 34 Le Vaisseau		Site 37 Pointe de la Galère		Site 29 Bagaud West		Site 30 Bagaud South		Site 31 Pointe du Cognet		Site 32 Southern coast		Site 35 Tuff		Site 36 Pointe de Port-Man		Site 38 Northern coast		Site 39 Fausse Monnaie			Site 40 Bagaud East	
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.		Ab.	Occ.
Mullidae	<i>Mullus surmuletus</i> *	2	10%	1	10%	1	10%	-	-	-	-	-	-	2	10%	3	30%	1	10%	4	30%	-	-	6	30%	-	-	20
Muraenidae	<i>Muraena helena</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	1	
Pomacentridae	<i>Chromis chromis</i>	211	90%	70	20%	303	50%	72	20%	93	70%	460	40%	-	-	-	-	5	20%	-	-	216	30%	-	-	10	10%	1 440
Scorpaenidae	<i>Scorpaena porcus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	10%	-	-	7	
Serranidae	<i>Epinephelus marginatus</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	1	
	<i>Serranus cabrilla</i> *	5	30%	5	50%	6	50%	6	50%	4	20%	10	40%	3	30%	2	20%	5	40%	6	40%	5	40%	1	10%	1	10%	59
	<i>Serranus scriba</i> *	7	70%	-	-	3	30%	3	30%	5	40%	4	30%	4	30%	4	40%	1	10%	4	40%	9	50%	9	60%	11	60%	64
Sparidae	<i>Boops boops</i>	-	-	-	-	-	-	-	-	6	10%	-	-	-	-	-	-	10	10%	23	20%	-	-	-	-	-	-	39
	<i>Dentex dentex</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	1
	<i>Diplodus annularis</i>	2	10%	-	-	1	10%	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	9	40%	4	40%	15	50%	32
	<i>Diplodus puntazzo</i> *	3	20%	10	30%	4	40%	4	10%	4	20%	-	-	3	30%	1	10%	1	10%	3	30%	3	30%	-	-	3	30%	39
	<i>Diplodus sargus</i> *	18	80%	28	80%	34	80%	15	70%	24	90%	30	90%	42	90%	30	80%	17	80%	41	90%	22	70%	34	100%	32	90%	367
	<i>Diplodus vulgaris</i> *	10	50%	20	80%	60	100%	21	80%	5	30%	8	60%	20	70%	32	90%	26	50%	23	70%	20	70%	22	70%	15	60%	282
	<i>Oblada melanura</i>	48	80%	-	--	24	60%	56	30%	13	40%	9	50%	32	60%	23	60%	18	70%	3	20%	63	70%	2	20%	19	30%	310
	<i>Sarpa salpa</i>	46	60%	158	90%	154	100%	9	10%	78	60%	154	70%	75	60%	104	70%	97	60%	58	30%	62	80%	1	10%	92	60%	1 088
	<i>Sparus aurata</i> *	1	10%	1	10%	-	-	2	10%	-	-	2	20%	-	-	2	20%	-	-	3	20%	2	10%	2	20%	-	-	15
	<i>Spondyliosoma cantharus</i> *	-	-	-	-	-	-	2	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Alpha species diversity		21		17		19		20		19		18		19		21		22		23		20		20		19		34
Mean point species diversity		10.9		8.4		9.9		6.7		9.2		8.4		9.5		10		8.4		8.5		9.2		9.1		10		-
CV (coefficient of variation)		22.2		31.8		22.1		29.1		16		20.4		17.4		26.2		35.1		38.1		32.7		24		22.1		-

The biomass (all species) presented sharp and significant differences between sites: between 1.0 (SD = 0.8; site 37, Pointe de la Galère) and 7.2 (SD = 7.3; site 30, Bagaud South); they were due to *Sarpa salpa*, Mugilidae and plankton-feeders. In contrast, where only target species are taken into consideration, differences were non-significant (KW tests) (Table VII). The type of management (NT vs. RF) did not matter: 3.3 (SD=3.3) and 3.8 (SD=3.8) kg WM/100 m², respectively (ANOVA, F = 0.284, p = 0.595, ns).

The fish assemblages were dominated by mesocarnivorous, herbivorous and to a lesser extent omnivorous species. While the presence of mesocarnivorous species was relatively homogeneous, whatever the site, the biomass of herbivorous species, in this case *Sarpa salpa*, was very variable from one site to another. Absent from sites 37 (Pointe de la Galère) and 39 (Fausse Monnaie), it represented more than 65% of the biomass at site 30 (Bagaud South). The piscivorous species were scarce compared to the other categories; they represented, at most, 13% of the biomass at the site 32 station (Southern coast) (Fig. 5). The trophic structure did not differ significantly according to the type of management (NT vs. RF); unexpectedly, the mean biomass of piscivorous teleosts was close to 0 % for sites with NT management, vs. 3 % for sites with RF management.

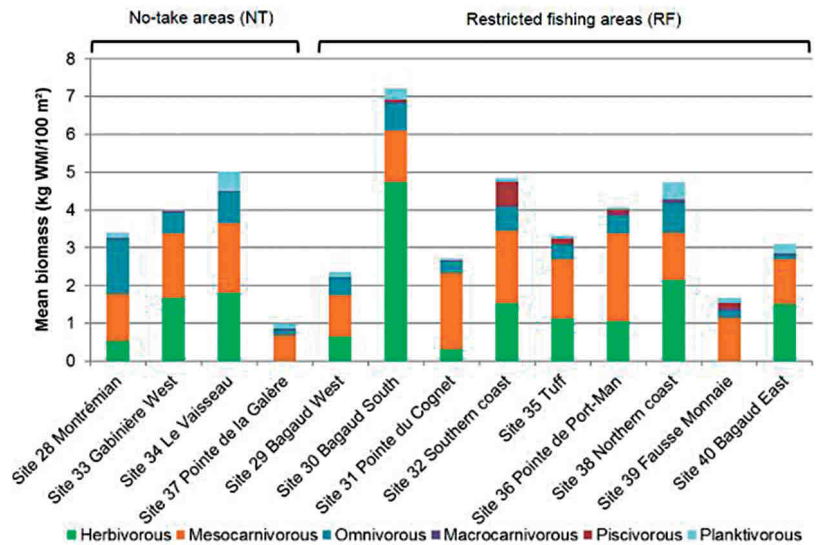


Figure 5. Mean biomass (kg WM/100 m²) of teleost fishes in shallow (0-3 m) rocky reef habitats, and its distribution between the 6 trophic groups considered.

Table VII. Main characteristics of the teleost fish stands of the infralitoral shallow rocky reefs (0-3 m depth). Port-Cros Archipelago MPA (Port-Cros National Park). Sites are ranked according to the management type, NT (no-take areas) and RF (restricted fishing areas). Biomass: wet mass.

Sites	NT (no-take areas)				RF (restricted fishing areas)								
	Site 28 Montré- mian	Site 33 Gabinère West	Site 34 Le Vaisseau	Site 37 Pointe de la Galère	Site 29 Bagaud West	Site 30 Bagaud South	Site 31 Pointe du Cognet	Site 32 Southern coast	Site 35 Tuff	Site 36 Pointe de Port-Man	Site 38 Northern coast	Site 39 Fausse Monnaie	Site 40 Bagaud East
Alpha diversity per site	21	17	19	20	19	18	19	21	22	23	20	20	19
Mean point diversity (per transect) (all species)	10.9	8.4	9.9	6.7	9.2	8.4	9.5	10	8.4	8.5	9.2	9.1	10
Mean point diversity (per transect) (target species)	4.9	4.1	5.2	4.4	4.2	4.4	5	6	4	5.8	5	5	4.9
Mean density/100 m ² (all species)	90.00	56.64	85.84	40.32	71.52	84.80	51.20	72.64	53.44	39.28	56.80	54.64	57.76
Mean density/100 m ² (target species)	29.20	23.84	22.72	25.20	33.12	27.60	29.76	31.28	20.64	27.68	24.24	26.32	31.28
Mean biomass (kg/100m ²) (all species)	3.41	4.00	5.02	1.00	2.36	7.22	2.72	4.83	3.31	4.06	4.73	1.66	3.09

Sites	NT (no-take areas)				RF (restricted fishing areas)								
	Site 28 Montré- mian	Site 33 Gabinère West	Site 34 Le Vaisseau	Site 37 Pointe de la Galère	Site 29 Bagaud West	Site 30 Bagaud South	Site 31 Pointe du Cognet	Site 32 Southern coast	Site 35 Tuff	Site 36 Pointe de Port-Man	Site 38 Northern coast	Site 39 Fausse Monnaie	Site 40 Bagaud East
Mean biomass (kg/100m ²) (target species)	1.29	2.05	1.93	0.72	1.21	1.38	2.04	2.64	1.69	2.55	1.42	1.27	1.22
Herbivorous (kg/100 m ²)	0.53	1.68	1.80	0.01	0.64	4.73	0.32	1.51	1.13	1.06	2.15	0.01	1.51
Macrocarnivorous (kg/100 m ²)	0.03	0.06	0.03	0.03	0.03	0.05	0.03	0.04	0.01	0.04	0.12	0.08	0.06
Mesocarnivorous (kg/100 m ²)	1.24	1.70	1.85	0.68	1.12	1.36	2.00	1.95	1.55	2.33	1.26	1.14	1.19
Omnivorous (kg/100 m ²)	1.46	0.54	0.81	0.14	0.44	0.73	0.31	0.61	0.39	0.46	0.75	0.18	0.10
Piscivorous (kg/100 m ²)	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.64	0.16	0.14	0.00	0.14	0.00
Planktivorous (kg/100 m ²)	0.16	0.02	0.53	0.15	0.13	0.31	0.06	0.08	0.06	0.04	0.44	0.12	0.24

Deep rocky reefs (5-15 m depth)

The overall species diversity (alpha diversity for the study area) in deep rocky reefs (5-15 m depth) was 47 species. The alpha diversity per site ranged between 23 (site 5, Southern coast) and 34 (site 10, Pointe de la Galère). The point-diversity was relatively homogenous between sites, with the exception of sites 12 (Fausse Monnaie) and 10 (Pointe de la Galère), 8.9 (SD 2.7) and 13.7 (SD 3.7) respectively (NK, $p = 0.02$). There were no differences, according to the management type (NT or RF). As far as the point diversity (mean number of species per transect) is concerned, there were no significant differences between sites (KW: $p = 0.250$, ns), but the type of management matters: point diversity was higher for NT than for RF (ANOVA: $p = 0.013$). The type of management also matters when only target species were considered, with alpha diversity higher for NT than for RF (Tables VIII, IX and X). Nine species were present at all sites: *Chromis chromis*, *Coris julis*, *Diplodus annularis*, *D. sargus*, *D. vulgaris*, *Symphodus mediterraneus*, *S. melanocercus*, *S. ocellatus*, *S. tinca*. The dusky grouper *Epinephelus marginatus* has been frequently observed; at sites 6 (Gabinière West) and 8 (Tuff), it was present on 70 % of the transects. The golden grouper *Epinephelus costae* was sighted once (site 7, Le Vaisseau). The brown meagre *Sciaena umbra* has been observed at most of the sites. Finally, an individual of the meridional species *Sparisoma cretense*, the presence of which was unexpected in Provence, swimming with a *Symphodus tinca* school of juveniles, has been sighted at site 2 (Bagaud West) (Table IX).

Table VIII. Species diversity of teleost fishes of deep rocky reefs. Mean number of species per sample (point diversity), cumulative number of species per site (alpha diversity). Target species are species targeted by artisanal fishing and/or recreational fishing (see Table IV).

Sites	All species		Target species	
	Point diversity ^a	Alpha diversity	Point diversity ^b	Alpha diversity
Site 1 Montrémian	11.8	27	6.7	15
Site 6 Gabinière West	13.1	28	7.2	17
Site 7 Le Vaisseau	10.7	30	6.6	16
Site 10 Pointe de La Galère	13.7	34	8.2	17
Site 2 Bagaud West	13.1	28	6.4	13
Site 4 Pointe du Cognet	12.4	25	6.5	12
Site 5 Southern coast	11.6	23	6.6	13
Site 8 Tuff	12..0	28	6.5	14
Site 9 Pointe de Port-Man	10.8	25	5.3	12
Site 11 Rascass	12.6	29	7.5	15
Site 12 Fausse Monnaie	8.9	28	4.7	15
Site 3 Bagaud South	11.0	25	5.9	13

^a Standard deviation: 2-3. ^b Standard deviation: 1-3.

Table IX. Species recorded in the visual censuses of deep rocky reefs (5-15 m depth). Ab. (abundance) = cumulated number of individuals per site (all transects). Occ. (occurrence) = percentage of transects where the species was recorded. - = absent. * = target species (see Table IV). Management: NT = no-take areas; RF = restricted fishing areas: longlines (artisanal fishing) and angling (recreational fishing) prohibited; AF = artisanal fishing area. Total abundance: cumulative number of sighted individuals (all sites).

Family	Species	NT (no-take areas)								RF (restricted fishing areas)												AF (artisanal fishing area)		Total abundance		
		Site 1 Montrémian		Site 6 Gabinière West		Site 7 Le Vaisseau		Site 10 Pointe de la Galère		Site 2 Bagaud West		Site 4 Pointe du Cognet		Site 5 Southern coast		Site 8 Tuff		Site 9 Pointe de Port-Man		Site 11 Rascas		Site 12 Fausse Monnaie			Site 3 Bagaud South	
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.		Ab.	Occ.
Apogonidae	<i>Apogon imberbis</i>	-	-	10	40%	16	30%	9	30%	1	10%	1	10%	-	-	30	70%	5	20%	14	50%	1	10%	10	10%	97
Atherinidae	<i>Atherina</i> sp.	22	10%	-	-	-	-	-	-	230	20%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	252
Carangidae	<i>Seriola dumerili</i> *	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Centracanthidae	<i>Spicara maena</i>	19	30%	-	-	-	-	1	10%	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	21
	<i>Spicara smaris</i>	6	20%	-	-	-	-	200	20%	-	-	-	-	-	-	1	10%	46	20%	-	-	-	-	1321	40%	1 574
Engraulidae	<i>Engraulis encrasicolus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	10%	-	-	150	10%	-	-	180
Labridae	<i>Coris julis</i> *	228	100%	247	100%	240	90%	137	100%	375	100%	330	100%	220	100%	304	100%	211	100%	413	100%	139	100%	229	100%	3 073
	<i>Labrus merula</i> *	4	30%	6	50%	3	30%	1	10%	7	50%	7	40%	10	50%	1	10%	-	-	5	40%	3	30%	2	20%	49
	<i>Labrus mixtus</i> *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	20%	-	-	-	-	2
	<i>Labrus viridis</i> *	1	10%	2	20%	1	10%	3	20%	3	20%	-	-	2	10%	3	30%	1	10%	-	-	1	10%	-	-	17
	<i>Symphodus cinereus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	1
	<i>Symphodus doderleini</i>	-	-	7	60%	5	30%	3	20%	1	10%	1	10%	1	10%	3	30%	-	-	3	20%	-	-	2	20%	26
	<i>Symphodus mediterraneus</i> *	9	50%	6	50%	5	30%	12	80%	4	30%	3	30%	8	40%	6	60%	2	20%	16	70%	1	10%	6	50%	78
	<i>Symphodus melanocercus</i>	10	80%	13	90%	31	80%	23	60%	17	100%	8	70%	8	40%	17	70%	8	60%	9	60%	8	40%	16	70%	168
	<i>Symphodus ocellatus</i>	7	30%	86	80%	160	90%	10	30%	10	60%	50	90%	43	70%	3	20%	16	40%	76	80%	6	50%	49	70%	516
	<i>Symphodus roissali</i>	-	-	3	20%	2	20%	-	-	7	40%	9	50%	5	40%	1	10%	3	30%	1	10%	1	10%	7	50%	39
	<i>Symphodus rostratus</i>	3	30%	-	-	2	20%	6	40%	1	10%	-	-	4	30%	1	10%	1	10%	3	30%	2	10%	4	30%	27
	<i>Symphodus tinca</i> *	46	100%	67	100%	76	100%	42	100%	122	100%	95	100%	99	100%	45	90%	64	100%	69	90%	57	70%	86	100%	868
	<i>Thalassoma pavo</i>	3	30%	-	-	2	10%	2	20%	5	30%	1	10%	6	20%	7	30%	21	60%	4	20%	2	10%	3	20%	56

Family	Species	NT (no-take areas)								RF (restricted fishing areas)																AF (artisanal fishing area)		Total abundance
		Site 1 Mon-trémian		Site 6 Gabinière West		Site 7 Le Vaisseau		Site 10 Pointe de la Galère		Site 2 Bagaud West		Site 4 Pointe du Cognet		Site 5 Southern coast		Site 8 Tuff		Site 9 Pointe de Port-Man		Site 11 Rascas		Site 12 Fausse Monnaie		Site 3 Bagaud South				
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.		
Mugilidae	<i>Mugil</i> sp.	-	-	9	20%	-	-	1	10%	13	30%	-	-	-	-	-	-	1	10%	4	20%	7	20%	-	-	35		
Mullidae	<i>Mullus surmuletus</i> *	1	10%	2	20%	13	60%	4	40%	4	30%	2	20%	3	20%	2	20%	-	-	4	20%	1	10%	1	10%	37		
Muraenidae	<i>Muraena helena</i> *	-	-	-	-	1	10%	3	20%	-	-	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	5		
Phycidae	<i>Phycis phycis</i> *	-	-	1	10%	-	-	1	10%	1	10%	-	-	-	-	-	-	-	-	1	10%	-	-	1	10%	5		
Pomacentridae	<i>Chromis chromis</i>	3 622	100%	409	100%	350	20%	1 496	90%	601	100%	347	90%	853	100%	623	100%	178	70%	1 964	100%	320	60%	1 787	100%	12 550		
Scaridae	<i>Sparisoma cretense</i>	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
Sciaenidae	<i>Sciaena umbra</i> *	-	-	17	20%	-	-	4	10%	-	-	9	40%	11	50%	1	10%	-	-	9	20%	2	10%	7	30%	60		
Scorpaenidae	<i>Scorpaena notata</i>	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
	<i>Scorpaena porcus</i>	-	-	-	-	-	-	-	-	-	-	1	10%	-	-	-	-	-	-	1	10%	-	-	-	-	2		
	<i>Scorpaena scrofa</i> *	1	10%	-	-	-	-	2	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3		
Serranidae	<i>Anthias anthias</i>	-	-	545	60%	50	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	595		
	<i>Epinephelus costae</i> *	-	-	-	-	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
	<i>Epinephelus marginatus</i> *	-	-	16	70%	5	30%	2	10%	-	-	4	20%	2	20%	10	70%	-	-	2	20%	-	-	4	20%	45		
	<i>Serranus cabrilla</i> *	11	60%	13	70%	12	70%	14	90%	12	60%	-	-	3	30%	5	30%	11	60%	8	50%	2	10%	15	80%	106		
	<i>Serranus scriba</i> *	8	50%	1	10%	10	50%	12	70%	17	90%	7	60%	9	70%	7	60%	6	50%	18	90%	6	50%	14	60%	115		

Family	Species	NT (no-take areas)								RF (restricted fishing areas)																AF (artisanal fishing area)		Total abundance
		Site 1 Montémrian		Site 6 Gabinière West		Site 7 Le Vaisseau		Site 10 Pointe de la Galère		Site 2 Bagaud West		Site 4 Pointe du Cognet		Site 5 Southern coast		Site 8 Tuff		Site 9 Pointe de Port-Man		Site 11 Rascas		Site 12 Fausse Monnaie		Site 3 Bagaud South				
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.		
Sparidae	<i>Boops boops</i>	120	20%	100	10%	53	30	126	30%	10	10%	5	20%	-	-	3	10%	-	-	9	10%	3	10%	-	-	-	-	429
	<i>Dentex dentex</i> *	-	-	2	20%	-	-	-	-	1	10%	-	-	-	-	2	10%	1	10%	-	-	-	-	-	-	-	-	6
	<i>Diplodus annularis</i>	23	80%	12	70%	3	20%	45	100%	7	50%	12	70%	16	50%	11	60%	13	50%	6	40%	24	70%	1	10%	-	-	173
	<i>Diplodus puntazzo</i> *	3	20%	11	40%	5	30%	12	70%	-	-	5	40%	7	10%	-	-	8	30%	7	50%	1	10%	-	-	-	-	59
	<i>Diplodus sargus</i> *	16	100%	18	60%	7	50%	24	70%	36	50%	26	80%	16	80%	33	90%	26	50%	35	70%	27	80%	9	30%	-	-	273
	<i>Diplodus vulgaris</i> *	69	100%	74	70%	28	80%	44	70%	89	90%	67	100%	66	80%	66	70%	154	90%	88	90%	26	60%	40	80%	-	-	811
	<i>Oblada melanura</i>	2	10%	-	-	1	10%	60	40%	196	80%	47	60%	77	80%	81	70%	45	80%	49	30%	40	60%	2	20%	-	-	600
	<i>Pagellus bogaraveo</i>	-	-	-	-	-	-	12	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
	<i>Pagrus pagrus</i> *	1	10%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	<i>Sarpa salpa</i>	22	50%	21	20%	31	10%	24	20%	162	80%	117	90%	43	60%	19	30%	120	50%	18	30%	137	40%	9	20%	-	-	723
	<i>Sparus aurata</i> *	-	-	1	10%	-	-	3	20%	-	-	3	20%	-	-	-	-	-	-	2	10%	1	10%	-	-	-	-	10
	<i>Spondyllosoma cantharus</i> *	7	20%	3	20%	2	20%	2	20%	6	30%	-	-	-	-	5	20%	7	40%	-	-	2	20%	9	50%	-	-	43
Sphyraenidae	<i>Sphyraena viridensis</i> *	4	20%	-	-	-	-	3	20%	-	-	-	-	--	-	-	-	1	10%	-	-	-	-	-	-	-	8	
Alpha species diversity		27		28		30		34		28		25		23		28		25		29		28		25				
Mean point species diversity		11.8		13.1		10.7		13.7		13.1		12.4		11.6		12		10.8		12.6		8.9		11				
CV (coefficient of variation)		23.9		17.8		28.6		26.7		13.7		25.6		31.0		18.4		31.1		27.8		30.2		25.0				

The mean biomass presented sharp differences between sites, both when all species, or only target species, were considered (Fig. 6 and Table X): from 19.8 (SD = 16.6) kg WM/100 m² at site 6 (Gabinière West) to 2.8 (SD = 2.5) kg/100 m² at site 12 (Fausse Monnaie) (all species; CMAR, $p = 0.01$ between these two sites). However, the type of management does not matter: no significant differences were noted between NT and RF, both for all species (ANOVA, $p = 0.31$, ns) and for only the target species (MW, $p = 0.12$, ns).

Table X. Main characteristics of the teleost fish stands of the deep rocky reefs (5-15 m depth). Port-Cros Archipelago MPA (Port-Cros National Park). Sites are ranked according to the management type, NT (no-take areas), RF (restricted fishing areas) and AF (artisanal fishery area). Biomass: wet mass.

Sites	NT (no-take areas)				RF (restricted fishing areas)							AF (artisanal fishing area)
	Site 1 Mon-trémian	Site 6 Gabinière West	Site 7 Le Vaisseau	Site 10 Pointe de la Galère	Site 2 Bagaud West	Site 4 Pointe du Cognet	Site 5 South-ern coast	Site 8 Tuff	Site 9 Pointe de Port-Man	Site 11 Rascas	Site 12 Fausse Monnaie	Site 3 Bagaud South
Alpha diversity per site	27	28	30	34	28	25	23	28	25	29	28	25
Mean point diversity (per transect) (all species)	11.8	13.1	10.7	13.7	13.1	12.4	11.6	12	10.8	12.6	8.9	11
Mean point diversity (per transect) (target species)	6.7	7.2	6.6	8.2	6.4	6.5	6.6	6.5	5.3	7.5	4.7	5.9
Mean density/100 m ² (all species)	341.4	136.2	89.4	187.4	155.1	92.6	121.0	103.3	78.3	227.2	77.7	290.7
Mean density/100 m ² (target species)	32.2	38.7	32.6	25.8	53.7	44.6	36.5	38.8	38.8	54.3	21.4	33.1
Mean biomass (kg/100m ²) (all species)	4.40	17.77	5.02	5.43	7.12	7.24	4.60	8.29	5.93	4.62	2.76	5.76
Mean biomass (kg/100m ²) (target species)	2.06	16.54	4.66	3.51	3.56	3.95	3.61	7.30	3.23	2.98	1.49	3.95
Herbivorous (kg/100 m ²)	0.40	0.17	0.14	0.09	2.28	2.93	0.43	0.28	2.13	0.07	0.53	0.27
Macrocarcivorous (kg/100 m ²)	0.07	0.04	0.27	0.81	0.10	0.02	0.04	0.05	0.04	0.11	0.12	0.07
Mesocarcivorous (kg/100 m ²)	1.62	3.05	1.34	1.74	3.35	2.03	2.03	2.44	2.82	2.29	1.43	1.23
Omnivorous (kg/100 m ²)	0.12	0.66	0.20	0.45	0.61	0.14	0.31	0.06	0.24	0.24	0.40	0.03
Piscivorous (kg/100 m ²)	0.30	13.07	2.93	0.73	0.10	1.83	1.31	4.82	0.22	0.49	0.00	2.64
Planctivorous (kg/100 m ²)	1.88	0.77	0.14	1.61	0.69	0.29	0.47	0.66	0.49	1.43	0.29	1.52

The fish assemblages were dominated by piscivorous (mainly the dusky grouper *Epinephelus marginatus*) and mesocarnivorous species (mainly the sea bream *Diplodus sargus* and *D. vulgaris*). Herbivorous species (*Sarpa salpa*) were abundant at some sites, such as site 4 (Pointe du Cognet), where they accounted for 40 % of the biomass. The type of management matters: piscivorous were dominant and herbivorous negligible under NT management (no-take areas), while herbivorous and mesocarnivorous species were dominant under RF management (restricted fishing areas) (Fig. 6).

Relatively shallow *Posidonia oceanica* seagrass meadows (10-15 m depth)

The overall species diversity (alpha diversity for the study area) in relatively shallow *Posidonia oceanica* seagrass meadows (10-15 m depth) was 30 species. The alpha diversity per site ranged between 18 (site 17, Pointe de Port-Man) and 28 (site 16, Vallon). The point diversity significantly differed between sites (KW, $p = 0.001$), between 7.0 (SD 1.9; site 17, Pointe de Port-Man) and 12.2 (SD 4.1; site 15, Baie de Port-Cros) (Table XI). Twelve species were present at all sites: *Boops boops*, *Chromis chromis*, *Coris julis*, *Diplodus annularis*, *Sarpa salpa*, *Serranus scriba*, *Spicara smaris*, *Spondyllosoma cantharus*, *Symphodus mediterraneus*, *S. melanocercus*, *S. ocellatus* and *S. tinca*. The damselfish *Chromis chromis* was by far the most common species, followed by the picarel *Spicara smaris* and the Mediterranean rainbow wrasse *Coris julis* (Table XII).

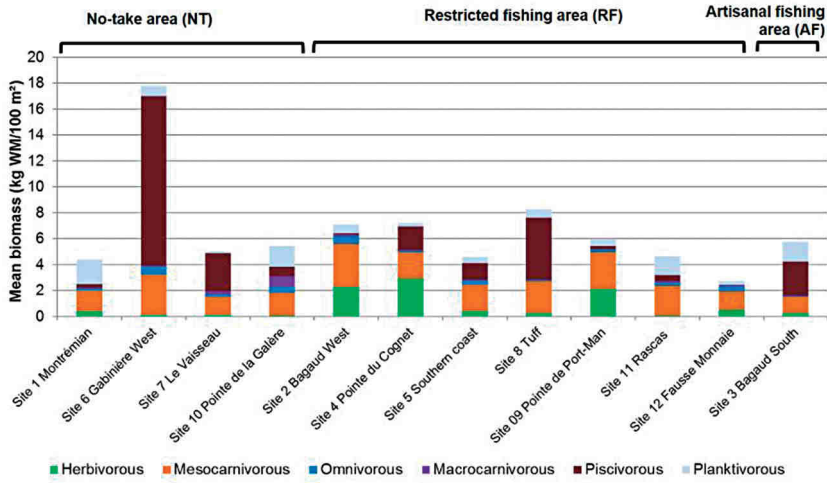


Figure 6. Mean biomass (kg WM/100 m²) of teleost fishes in deep (5-15 m) rocky reef habitats, and its distribution between the 6 trophic groups considered.

Table XI. Species diversity of teleost fishes of relatively shallow *Posidonia oceanica* seagrass meadows. Mean number of species per sample (point diversity), cumulative number of species per site (alpha diversity). Target species are species targeted by artisanal fishing and/or recreational fishing (see Table IV).

Sites	All species		Target species	
	Point diversity ^a	Alpha diversity	Point diversity ^b	Alpha diversity
Site 13 Montrémian	7.4	20	3.0	9
Site 15 Baie de Port-Cros	12.2	25	4.3	11
Site 16 Vallon	9.3	28	4.2	15
Site 17 Pointe de Port-Man	7.0	18	2.2	8
Site 14 Bagaud Pass	10.5	23	4.1	9

^a Standard deviation: 2-3. ^b Standard deviation: 1-2.

Table XII. Species recorded in the visual censuses of relatively shallow *Posidonia oceanica* seagrass meadows (10-15 m depth). Ab. (abundance) = cumulated number of individuals per site (all transects). Occ. (occurrence) = percentage of transects where the species was recorded. - = absent. * = target species (see Table IV). Management: NT = no-take area; RF = restricted fishing areas: longlines (artisanal fishing) and angling (recreational fishing) prohibited; AF = artisanal fishing area. Total abundance: cumulative number of sighted individuals (all sites).

Family	Species	NT (no-take area)		RS (restricted fishing areas)						AF (artisanal fishing area)		Total abundance
		Site 13 Mon-trémian		Site 15 Baie de Port-Cros		Site 16 Vallon		Site 17 Pointe de Port-Man		Site 14 Bagaud Pass		
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	
Atherinidae	<i>Atherina</i> sp.	-	-	100	10 %	48	20 %	16	10 %	-	-	164
Centracanthidae	<i>Spicara maena</i>	7	20 %	31	40 %	14	20 %			113	40 %	165
	<i>Spicara smaris</i>	120	30 %	227	40 %	5	30 %	47	60 %	436	80 %	835
Labridae	<i>Coris julis</i> *	91	100 %	210	100 %	62	90 %	160	100 %	189	100 %	712
	<i>Labrus merula</i> *	-	-	2	20 %	4	30 %	2	20 %	3	30 %	11
	<i>Labrus viridis</i> *	1	10 %	-	-	3	20 %	-	-	-	-	4
	<i>Symphodus cinereus</i>	-	-	11	50 %	-	-	-	-	1	10 %	12
	<i>Symphodus doderleini</i>	-	-	4	20 %	-	-	30	30 %	3	20 %	37
	<i>Symphodus mediterraneus</i> *	4	40 %	10	70 %	3	30 %	1	10 %	11	50 %	29
	<i>Symphodus melanocercus</i>	6	40 %	18	80 %	12	50 %	13	70 %	11	60 %	60
	<i>Symphodus ocellatus</i>	27	60 %	85	100 %	7	40 %	1	10 %	9	40 %	129
	<i>Symphodus roissali</i>	1	10 %	3	20 %	1	10 %	-	-	1	10 %	6
	<i>Symphodus rostratus</i>	7	50 %	8	60 %	1	10 %	-	-	1	10 %	17
	<i>Symphodus tinca</i> *	8	60 %	46	90 %	8	30 %	5	30 %	19	90%	86
	<i>Thalassoma pavo</i>	1	10 %	-	-	1	10%	-	-	1	10 %	3
Mullidae	<i>Mullus surmuletus</i> *	-	-	3	20 %	3	30%	-	-	1	10 %	7
Pomacentridae	<i>Chromis chromis</i>	140	70%	910	90 %	1 102	100 %	794	100 %	1 271	100 %	4 217
Serranidae	<i>Serranus cabrilla</i> *	4	40 %	5	40 %	4	40 %	1	10 %			14
	<i>Serranus scriba</i> *	5	30 %	10	40 %	11	60 %	7	40 %	15	90 %	48

The mean biomass presented sharp and significant differences between sites, especially when all species were considered (KW, $p = 0.002$): from 2.4 (SD = 3.1) kg WM/100 m² at site 16 (Vallon) to 0.3 (SD = 0.4) kg WM/100 m² at site 13 (Montrémian) (Fig. 7 and Table XIII).

The fish assemblages were dominated by herbivorous (*Sarpa salpa*; up to 40 % of the biomass) and planktivorous (up to 70 %) species. Piscivorous and macrocarnivorous teleosts seem poorly represented, but this is an artefact, as most of the species belonging to these trophic groups (e.g. *Conger conger* and *Scorpaenidae*) have a nocturnal behaviour pattern, while visual censuses were done in daytime (Fig. 7, Table XIII).

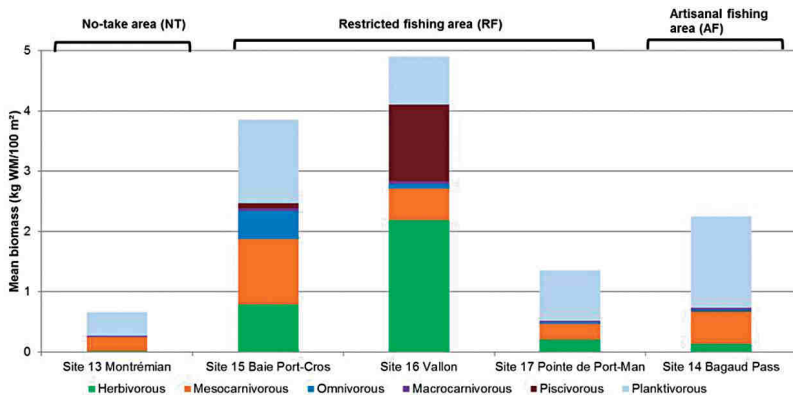


Figure 7. Mean biomass (kg WM/100 m²) of teleost fishes in relatively shallow (10-15 m depth) *Posidonia oceanica* seagrass meadows, and its distribution between the 6 trophic groups considered.

Table XIII. Main characteristics of the teleost fish stands of the relatively shallow *Posidonia oceanica* seagrass meadows (10-15 m depth). Port-Cros Archipelago MPA (Port-Cros National Park). Sites are ranked according to the management type, NT (no-take areas), RF (restricted fishing areas) and AF (artisanal fishing areas). Biomass: wet mass.

	NT (no-take area)	RF (restricted fishing areas)			AF (ar- tisanal fishing area)
Sites	Site 13 Mon- trémian	Site 15 Baie Port- Cros	Site 16 Vallon	Site 17 Pointe de Port-Man	Site 14 Bagaud Pass
Alpha diversity per site	20	25	28	18	23
Mean point diversity (per transect) (all species)	7.4	12.2	9.3	7.0	10.5
Mean point diversity (per transect) (target species)	3.0	4.3	4.2	2.2	4.1
Mean density/100 m ² (all spe- cies)	25.72	77.12	60.84	47.08	91.28

	NT (no-take area)	RF (restricted fishing areas)			AF (ar- tisanal fishing area)
Sites	Site 13 Mon- trémian	Site 15 Baie Port- Cros	Site 16 Vallon	Site 17 Pointe de Port-Man	Site 14 Bagaud Pass
Mean density/100 m ² (target species)	4.60	12.16	7.60	7.08	9.68
Mean biomass (kg/100m ²) (all species)	0.33	1.93	2.45	0.67	1.13
Mean biomass (kg/100m ²) (tar- get species)	0.09	0.77	0.92	0.14	0.25
Herbivorous (kg/100 m ²)	0.01	0.39	1.09	0.10	0.06
Macrocarcivorous (kg/100 m ²)	0.01	0.02	0.02	0.01	0.02
Mesocarcivorous (kg/100 m ²)	0.12	0.54	0.26	0.13	0.27
Omnivorous (kg/100 m ²)	~0.00	0.23	0.04	0.02	0.01
Piscivorous (kg/100 m ²)	0.00	0.04	0.64	~0.00	0.00
Planktivorous (kg/100 m ²)	0.12	0.70	0.40	0.42	0.76

Deep *Posidonia oceanica* seagrass meadows

Deep *Posidonia oceanica* seagrass meadows are meadows adjacent to circalittoral soft bottoms, namely coastal detrital (CD) and coarse sands and fine gravels under the influence of bottom currents (CSBC) (30-35 m depth). The overall species diversity (alpha diversity for the study area) was 22 species, of which 9 are target species of fishery (artisanal and recreational). The alpha diversity per site ranged between 5 (site 21, Pointe de Port-Man) and 15 (site 18, Bagaud West). The point diversity (number of species per transect) was conspicuously low: 1.5 through 5.6. Four species were present at all sites: *Boops boops*, *Coris julis*, *Mullus surmuletus* and *Serranus cabrilla*. There were no differences, according to the management type (RF or AF) (Tables XIV, XV).

Table XIV. Species diversity of teleost fishes of deep *Posidonia oceanica* seagrass meadows. Mean number of species per sample (point diversity), cumulative number of species per site (alpha diversity). Target species are species targeted by artisanal fishing and/or recreational fishing (see Table IV).

Sites	All species		Target species	
	Point diversity ^a	Alpha diversity	Point diversity ^b	Alpha diversity
Site 20 Vallon	2.9	9	2.1	5
Site 18 Bagaud West	5.6	15	2.7	7
Site 19 Bagaud Pass	2.9	10	2.0	3
Site 21 Pointe de Port-Man	1.5	5	1.3	3

^a Standard deviation: 1-3. ^b Standard deviation: 1-2.

Table XV. Species recorded in the visual censuses of deep *Posidonia oceanica* seagrass meadows (30-35 m depth). Ab. (abundance) = cumulated number of individuals per site (all transects). Occ. (occurrence) = percentage of transects where the species was recorded. - = absent. * = target species (see Table IV). Management: RF = restricted fishing area: longlines (artisanal fishing) and angling (recreational fishing) prohibited; AF = artisanal fishing areas. Total abundance: cumulative number of sighted individuals (all sites).

Family	Species	RF (restricted fishing area)		AF (artisanal fishing areas)						Total abundance
		Site 20 Vallon		Site 18 Bagaud West		Site 19 Bagaud Pass		Site 21 Pointe de Port-Man		
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.
Centracanthidae	<i>Spicara maena</i>	-	-	225	70%	-	-	-	-	225
	<i>Spicara smaris</i>	680	10%	83	40%	130	10%	-	-	893
Labridae	<i>Coris julis</i> *	506	100%	292	100%	419	100%	251	100%	1 468
	<i>Ctenolabrus rupestris</i>	-	-	-	-	1	10%	-	-	1
	<i>Symphodus cinereus</i>	-	-	5	20%	2	20%	-	-	7
	<i>Symphodus doderleini</i>	-	-	-	-	2	10%	-	-	2
	<i>Symphodus mediterraneus</i> *	-	-	1	10%	-	-	-	-	1
	<i>Symphodus melanocercus</i>	1	10%	2	10%	-	-	-	-	3
	<i>Symphodus ocellatus</i>	-	-	-	-	-	-	2	10%	2
	<i>Symphodus roissali</i>	1	10%	-	-	-	-	-	-	1
	<i>Symphodus rostratus</i>	-	-	1	10%	-	-	-	-	1
	<i>Symphodus tinca</i> *	-	-	2	20%	-	-	-	-	2
Mugilidae	<i>Mugil</i> sp.	-	-	-	-	1	10%	-	-	1
Mullidae	<i>Mullus surmuletus</i> *	3	30%	31	70%	4	30%	8	20%	46
Pomacentridae	<i>Chromis chromis</i>	-	-	60	20%	20	10%	-	-	80
Serranidae	<i>Serranus cabrilla</i> *	10	60%	6	50%	9	70%	1	10%	26
	<i>Serranus scriba</i> *	-	-	1	10%	-	-	-	-	1
Sparidae	<i>Boops boops</i>	1 950	50%	1 509	100%	500	20%	100	10%	4 059
	<i>Dentex dentex</i> *	1	10%	-	-	-	-	-	-	1
	<i>Diplodus annularis</i>	-	-	5	20%	-	-	-	-	5
	<i>Diplodus vulgaris</i> *	-	-	1	10%	-	-	-	-	1
Sphyraenidae	<i>Sphyraena viridensis</i> *	1	10%	-	-	-	-	-	-	1
Alpha species diversity		9		15		10		5		22
Mean point species diversity		2.9		5.6		2.9		1.5		-
CV (coefficient of variation)		47.3		43.9		50		47.1		-

The mean biomass presented sharp and significant differences between sites, especially when all species were considered (CMAR, $p = 0.01$): from 0.5 (SD = 1.0) kg WM/100 m² at site 21 (Pointe de Port-Man) to 3.7 (SD = 4.2) kg WM/100 m² at site 20 (Vallon) (Fig. 8 and Table XVI). The type of management (RF vs. AF) did not matter (MW, $p = 0.20$).

The fish assemblages were dominated by planktivorous (*Boops boops* and *Chromis chromis*) and to a lesser extent by mesocarnivorous (*Coris julis*) species. Piscivorous species were uncommon and macrocarnivorous species absent. Differences in average biomass values between sites are due to planktivorous species, which have an aggregative behaviour pattern and are highly dependent on currents, which provides them with food (Fig. 8).

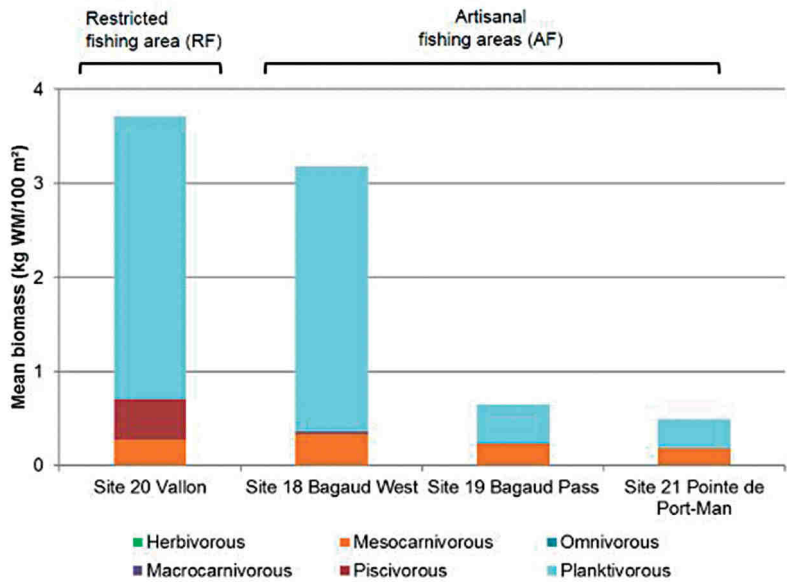


Figure 8. Mean biomass (kg WM/100 m²) of teleost fishes in deep (30-35 m depth) *Posidonia oceanica* seagrass meadows, and its distribution between the 6 trophic groups considered.

Table XVI. Main characteristics of the teleost fish stands of the deep *Posidonia oceanica* seagrass meadows (30-35 m depth). Port-Cros Archipelago MPA (Port-Cros National Park). Sites are ranked according to the management type, RF (restricted fishing area) and AF (artisanal fishing area). Biomass: wet mass.

	RF (restricted fishing area)	AF (artisanal fishing areas)		
Site	Site 20 Vallon	Site 18 Bagaud West	Site 19 Bagaud Pass	Site 21 Pointe de Port-Man
Alpha diversity per site	9	15	10	5
Mean point diversity (per transect) (all species)	2.9	5.6	2.9	1.5
Mean point diversity (per transect) (target species)	2.1	2.7	2.0	1.3
Mean density/100 m ² (all species)	252.2	17.9	87.0	29.0
Mean density/100 m ² (target species)	41.7	26.7	34.6	20.8
Mean biomass (kg/100m ²) (all species)	3.71	3.18	0.65	0.49
Mean biomass (kg/100m ²) (target species)	0.69	0.35	0.23	0.18
Herbivorous (kg/100 m ²)	0.00	0.00	0.00	0.00
Macrocarcivorous (kg/100 m ²)	0.01	0.02	0.01	0.00
Mesocarcivorous (kg/100 m ²)	0.27	0.33	0.23	0.18
Omnivorous (kg/100 m ²)	0.00	0.00	0.00	0.00
Piscivorous (kg/100 m ²)	0.42	0.00	0.00	0.00
Planctivorous (kg/100 m ²)	3.01	2.82	0.42	0.31

Coralligenous habitat

The overall species diversity (alpha diversity for the study area) in coralligenous habitats (25-40 m depth) was 36 species, of which 20 are target species of fishery (artisanal and recreational). The alpha diversity per site ranged between 10 (site 24, Roche des Catalans) and 28 (site 16, Vallon). The point diversity (number of species per transect) differed significantly between sites, both when all species (KW, $p < 0.001$) and only target species (KW, $p < 0.001$) were considered. Seven species were present at all sites: *Anthias anthias*, *Chromis chromis*, *Coris julis*, *Serranus cabrilla*, *Symphodus doderleini*, *S. mediterraneus* and *S. melanocercus*. There were no differences, according to the management type (NT, RF or AF), in mean point diversity, if all species are considered (KW, $p = 0.06$); in contrast, the type of management mattered if only target species are considered, with a mean point diversity higher with NT than with RF and AF (KW, $p = 0.0004$; CMAR, $p = 0.018$ and $p = 0.002$, respectively) (Table XVII, XVIII).

Table XVII. Species diversity of teleost fishes in the coralligenous habitat. Mean number of species per sample (point diversity), cumulative number of species per site (alpha diversity). Target species are species targeted by artisanal fishing and/or recreational fishing (see Table IV). Note that an elasmobranch species was present at site 25 (Gabinière East), so that the teleost point diversity and alpha diversity are actually 6.1 (not 6.2) and 17 (not 18), respectively (see Table XVIII).

Sites	All species		Target species	
	Point diversity ^a	Alpha diversity	Point diversity ^b	Alpha diversity
Site 22 Montrémian	10.7	29	6.7	17
Site 25 Gabinière East	7.6	18	5.6	13
Site 26 Le Vaisseau	6.2	17	4.1	11
Site 27 Pointe de la Galère	10.2	20	6.7	12
Site 23 Cognet	7.1	16	3.9	9
Site 24 Roche des Catalans	6.9	10	3.6	5

^a Standard deviation: 1-3. ^b Standard deviation: 1-2.

Family	Species	NT (no-take areas)								RF (restricted fishing area)		AF (artisanal fishing area)		Total abundance
		Site 22 Mon-trémian		Site 25 Gabinière East		Site 26 Le Vaisseau		Site 27 Pointe de la Galère		Site 23 Cognet		Site 24 Roche des Catalans		
		Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	Ab.	Occ.	
Phycidae	<i>Phycis phycis</i> *	1	10%	-	-	-	-	-	-	-	-	-	-	1
Pomacentridae	<i>Chromis chromis</i>	1 410	100%	1 570	40%	43	30%	4 972	100%	2 040	90%	444	90%	10 479
Scorpaenidae	<i>Scorpaena scrofa</i> *	-	-	1	10%	-	-	-	-	-	-	-	-	1
Serranidae	<i>Anthias anthias</i>	217	60%	6 503	100%	13 053	100%	3 298	90%	4 469	100%	3 007	100%	30 547
	<i>Epinephelus marginatus</i> *	1	10%	9	60%	9	70%	7	30%	4	20%			30
	<i>Serranus cabrilla</i> *	26	80%	17	90%	16	90%	29	90%	56	100%	30	100%	174
	<i>Serranus scriba</i> *	3	20%	-	-	-	-	-	-	-	-	-	-	3
Sparidae	<i>Boops boops</i>	100	10%	-	-	-	-	30	20%	-	-	-	-	130
	<i>Dentex dentex</i> *	-	-	26	90%	5	40%	6	30%	3	10%	-	-	40
	<i>Diplodus annularis</i>	1	10%	-	-	-	-	-	-	-	-	-	-	1
	<i>Diplodus puntazzo</i> *	32	80%	-	-	-	-	-	-	-	-	-	-	32
	<i>Diplodus sargus</i> *	13	80%	-	-	1	10%	60	70%	-	-	-	-	74
	<i>Diplodus vulgaris</i> *	19	60%	-	-	4	30%	453	80%	-	-	-	-	476
	<i>Oblada melanura</i>	-	-	-	-	8	10%	-	-	-	-	-	-	8
	<i>Pagrus pagrus</i> *	-	-	1	10%	-	-	-	-	-	-	-	-	1
	<i>Sarpa salpa</i>	4	20%	-	-	-	-	-	-	-	-	-	-	4
	<i>Sparus aurata</i> *	11	20%	2	20%	-	-	-	-	-	-	-	-	13
	<i>Spondyliosoma cantharus</i> *	28	50%	-	-	1	10%	86	30%	-	-	-	-	115
	Sphyraenidae	<i>Sphyraena viridensis</i> *	1	10%	61	20%	53	30%	47	70%	-	-	-	-
Alpha species diversity		29		18		17		20		16		10		36
Mean point species diversity		10.7		7.6		6.2		10.2		7.1		6.9		
CV (coefficient of variation)		22.1		25.7		37.1		23.9		26.1		14.4		

The biomass (all species) presented sharp differences (one order of magnitude) between sites, from 3.1 (SD = 2.2) (site 24, Roche des Catalans) to 31.8 (SD = 29.8) kg WM/100 m² (Site 27, Pointe de la Galère), with a significant difference between these two sites (KW, $p < 0.001$; CMAR, $p = 0.0015$). The type of management matters: the biomass was significantly higher with NT than with AF (CMAR, $p = 0.0003$). The difference was even more marked if only target species are taken into consideration.

The trophic structure of fish assemblages exhibited sharp differences between sites. While the stand was strongly dominated (in biomass) by piscivorous species at some sites (e.g. site 25, La Gabinière), the latter were uncommon at others (e.g. site 22, Montrémian) (Fig. 9, Table XIX). The trophic structure was strongly linked to the management type: (i) piscivorous (51 %), planktivorous (24 %) and mesocarnivorous (20 %) were dominant with NT management; (ii) planktivorous (49 %), piscivorous (38 %) and macrocarnivorous (10 %) were dominant with RF management; (iii) planktivorous (78 %), macrocarnivorous (13 %) and mesocarnivorous (10 %) were dominant with AF management (Fig. 9, Table XIX).

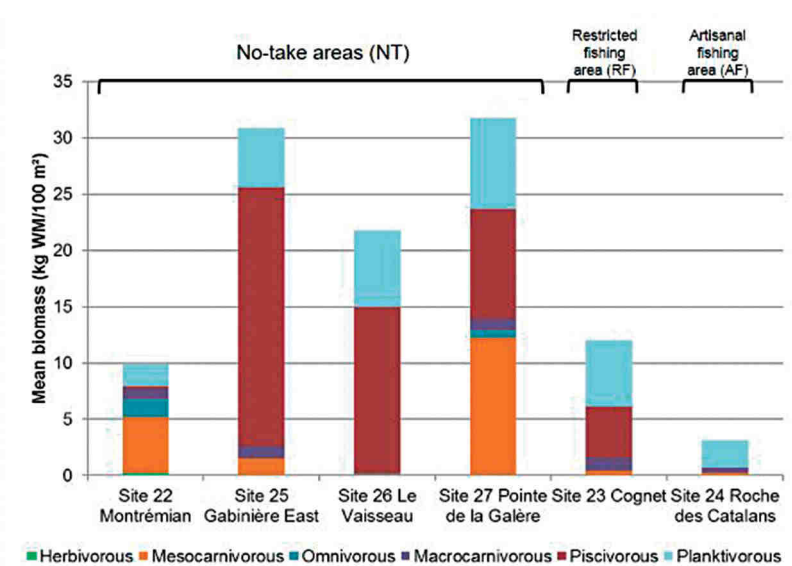


Figure 9. Mean biomass (kg WM/100 m²) of teleost fishes in the coralligenous habitat (25-40 m depth), and its distribution between the 6 trophic groups considered. At site 25, an elasmobranch species (*Myliobatis aquila*) was taken into consideration

Table XIX. Main characteristics of the teleost fish stands of the coralligenous habitat (25-40 m depth). Port-Cros Archipelago MPA (Port-Cros National Park). Sites are ranked according to the management type, NT (no-take areas), RF (restricted fishing area) and AF (artisanal fishing area). Biomass: wet mass. Note that, at site 25, an elasmobranch species was taken into consideration.

Sites	NT (no-take areas)				RF (restricted fishing area)	AF (artisanal fishing area)
	Site 22 Mon-trémian	Site 25 Gabinière East	Site 26 Le Vaisseau	Site 27 Pointe de la Galère	Site 23 Cognet	Site 24 Roche des catalans
Alpha diversity per site	29	18	17	20	16	10
Mean point diversity (per transect) (all species)	10.7	7.6	6.2	10.2	7.1	6.9
Mean point diversity (per transect) (target species)	6.7	5.6	4.1	6.7	3.9	3.6
Mean density/100 m ² (all species)	185.6	690.1	1 073.6	753.0	571.9	298.9
Mean density/100 m ² (target species)	29.6	43.6	24.3	64.8	33.5	20.1
Mean biomass (kg/100m ²) (all species)	9.87	30.86	21.79	31.81	12.03	3.08
Mean biomass (kg/100m ²) (target species)	7.76	24.95	14.95	23.70	6.11	0.68
Herbivorous (kg/100 m ²)	0.18	0.00	0.00	0.00	0.00	0.00
Macrocarcivorous (kg/100 m ²)	0.86	1.15	0.07	0.97	1.21	0.40
Mesocarcivorous (kg/100 m ²)	5.06	1.49	0.17	12.26	0.37	0.29
Omnivorous (kg/100 m ²)	1.56	0.00	0.00	0.67	0.00	0.00
Piscivorous (kg/100 m ²)	0.28	22.97	14.71	9.81	4.54	0.00
Planktivorous (kg/100 m ²)	1.93	5.26	6.83	8.11	5.92	2.39

The differences between sites may be due to the management type, but also to the complexity of the habitat and exposure to currents. Some rocky habitat sites with high average biomass were distinguished by a more complex, more chaotic habitat configuration (site 26, Le Vaisseau and site 27, Pointe de la Galère). However, site 25 (Gabinière East), although harbouring a very high average biomass, did not consist of a habitat different from the sites where density and biomass of fish were lower (e.g. site 24, Roche des Catalans). Sites 25 (Gabinière East), 26 (Le Vaisseau) and 27 (Pointe de la Galère), with exceptionally high biomass, are highly exposed to currents.

Discussion and conclusion

The gamma species diversity (all studied sites and habitats) was 53 species. This value is highly dependent upon the sampling method (see e.g. Harmelin-Vivien and Francour, 1992) and the sampling effort, so that comparisons with other Mediterranean MPAs are meaningless. It is worth pointing out that, contrary to the beliefs of most 'green' party supporters,

managers and some scientists, rooted in the ecology of the 1950s, the value of a habitat, or an area, does not depend on the number of species. In the majority of cases, disturbances do not decrease the number of species, but rather increase it; garbage dumps are richer in species than many natural habitats of high heritage value (Lubchenco and Menge, 1978; Hastwell and Huston, 2001; Boudouresque, 2014). Species sighted in this study represent only a small portion of the 215 species reported in the Port-Cros Archipelago (Francour and Harmelin, 1988; Dufour *et al.*, 2007). Two species hitherto unreported in the Port-Cros Archipelago were observed: the parrot fish *Sparisoma cretense* and the cornet fish *Fistularia commersonii* (Astruch *et al.*, 2016). *Sparisoma cretense* is a Mediterranean herbivorous fish of warm water affinities, which was previously confined to eastern and southern regions; because of the sea water warming, it is spreading northwards (Bauchot and Pras, 1980; Astruch *et al.*, 2016; Bianchi *et al.*, 2018a). *Fistularia commersonii* is a lessepsian species, i.e. a Red Sea species which entered the Mediterranean *via* the Suez Canal (Por, 1990; Boudouresque, 1999; Golani *et al.*, 2007; Por, 2009; Deidun and Germanà, 2011; Tsiamis *et al.*, 2015).

The fish biomass is generally higher along the southern and eastern coasts of the Port-Cros Archipelago than in the north and west (Fig. 10). The Northern Mediterranean Current, flowing from east to west, which provides nutrients and plankton, may partly explain this dissymmetry (Millot and Taupier-Letage, 2005; Taupier-Letage *et al.*, 2013). There are only 2 NTs areas on the western coast and the NTs are contributing to the major part of the fish biomass observed on the eastern coast of the Port-Cros Archipelago. The NTs have been implemented on capes and rocky bottoms, which are especially favorable to fish (piscivorous and carnivorous species); these sites are therefore cumulating a habitat and a protection effect. For this reason, as compared to the NTs, the censused fish biomass and the proportion of fish of high trophic levels may be relatively low in the artisanal fishing areas (AFs). The biomass is greater than 10 kg WM/100 m² (up to 32 kg; site 27, Pointe de la Galère) at 5 sites. Four of these sites are located in the coralligenous habitat, the last in the deep rocky reefs. Four of these sites are located in NT managed areas. Increasing fish biomass at sites where any form of fishing is prohibited is a well-documented process (e.g. García Charton and Pérez-Ruzafa, 1998, 1999; García Charton *et al.*, 2000; García Charton and Pérez-Ruzafa, 2001; Boudouresque *et al.*, 2005; García-Charton *et al.*, 2008; Harmelin-Vivien *et al.*, 2015). Piscivorous fishes are abundant, often dominant in NT managed sites, which was expected (García-Charton *et al.*, 2008; Sala *et al.*, 2012; Valls *et al.*, 2012; Prato *et al.*, 2013), but also in RF- and AF-managed sites, which supports the overall management strategy of the Port-Cros Archipelago MPA, Multi-Use Management (MUM) initiated ~55 years ago.

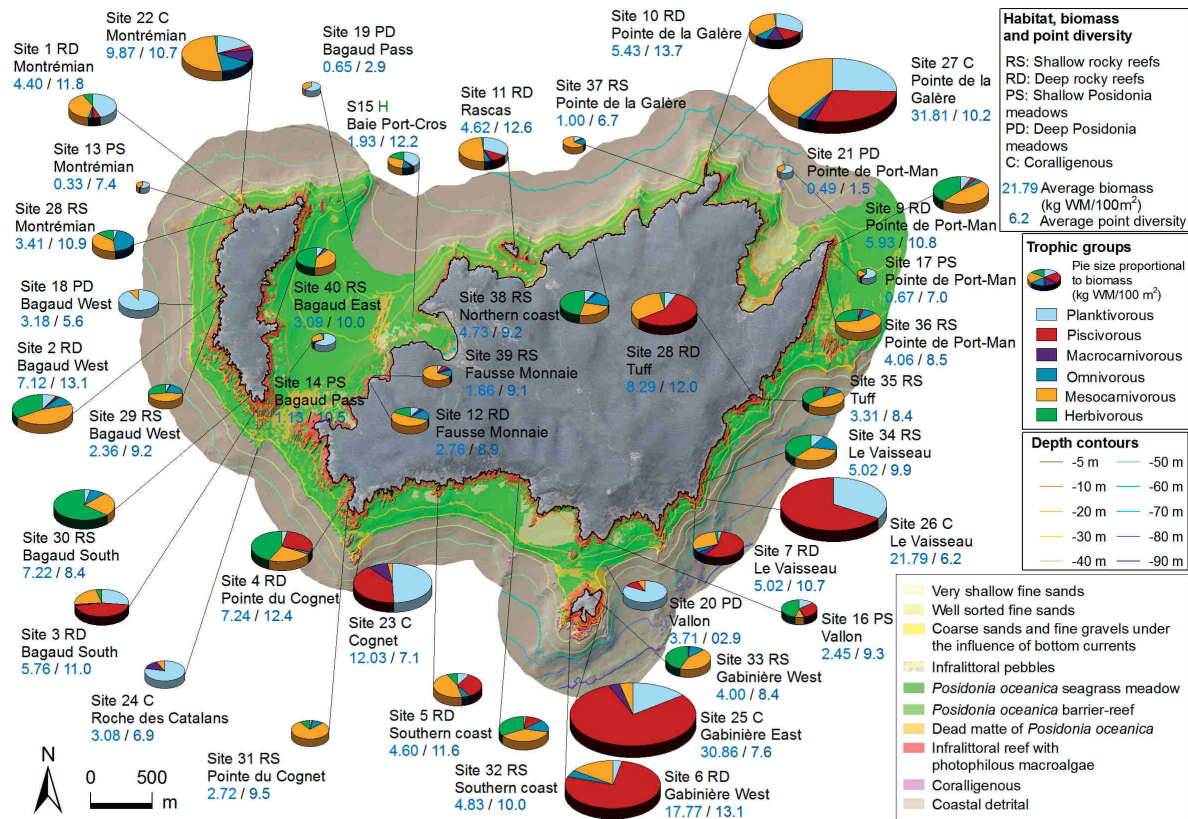


Figure 10. Trophic structure of the fish assemblages at the 40 sampled sites. The size of the pie charts is proportional to the average biomass at each site.

Mean abundance and biomass of fish differ sharply between habitats (Table XX). Within a given habitat, the variability between sites is generally high, with significant differences, especially if all species are taken into consideration (Table XXI). Such variability was to be expected; Mediterranean habitats of the infralittoral zone exhibit a high topographical diversity (slope, orientation, anfractuosity, absence or presence and size of boulders) together with a great variety of flora and fauna communities (e.g. Molinier, 1960; Pérès and Picard, 1964; Bellan-Santini, 1968, 1969; Boudouresque, 1971; Ballesteros I Sagarra, 1992; Mangialajo *et al.*, 2008; Thiriet *et al.*, 2016; Boudouresque *et al.*, 2017); this variability is also linked to the number of strata and the height of the canopy-forming species (Thibaut *et al.*, 2017; Thiriet *et al.*, 2017). Despite the high variability among sites, the assessment of a mean abundance and biomass per habitat will be useful for further comparisons within N-PCNP and as a reference for Mediterranean MPA and coastal studies.

The type of management (NT, RF and AF) generally does not matter, with the exception of the coralligenous habitat, especially when only target species are considered (Table XXII). This result may seem surprising for researchers who oppose, dogmatically, the so-called 'real' MPAs, where any form of fishing is prohibited (No-Take Zones, NTZ), and MPAs closer to the ecological reality and the notion of a socio-ecosystem, where fishing is allowed, but managed strictly and scientifically. This last type of management, called Multi-Use Management (MUM), which is that adopted by the PCNP for the Port-Cros Archipelago MPA, and gradually developed over a period of ~55 years, is clearly preferred by the authors of the present article. It takes into account, in particular, that, in the absence of most top predators (the monk seal *Monachus monachus*, sharks, etc.) (Marchessaux, 1989a, 1989b; Ferretti *et al.*, 2008), artisanal fishing constitutes a surrogate of these predators and that ecosystems are more 'natural', with artisanal fishing well in hand (scientifically managed, with regulations strictly enforced), than in the absence of both artisanal fisheries and top predators (Boudouresque *et al.*, 2004, 2005). It is interesting to note that this 'ecosystem-based' management is validated by the EBQI (Ecosystem-based Quality Index): *Posidonia oceanica* and reef ecosystems of the Port-Cros Archipelago (PCNP) rank first in the Mediterranean from the point of view of the functioning of the ecosystem, equally or even above the ecosystems of MPAs of the NTZ type (Ruitton *et al.*, 2013; Personnic *et al.*, 2014; Boudouresque *et al.*, 2015; Thibaut *et al.*, 2017). In fact, the three types of management that we have considered in Port-Cros Archipelago, NT, RF and AF, are just facets of the same type of management, MUM management; they constitute a spatial mosaic, with areas between which most of the fish considered here are constantly moving; it is therefore logical that the differences between these facets of MUM management are rarely significant.

Table XX. Alpha diversity (study area and, in parentheses, per site), mean point diversity, mean abundance (number of individuals) per 100 m² and mean biomass (wet mass) per 100 m², $\pm$ SD, in the five studied habitats, for all species and for only target species.

	Alpha diversity: study area (min-max per site)	Mean point diversity ($\pm$ SD)	Mean abundance /100m ² ($\pm$ SD)	Mean biomass kg/100 m ² ($\pm$ SD)
All species				
Shallow rocky reefs (0-3 m)	34 (17 to 23)	9.1 $\pm$ 2.5	62.7 $\pm$ 40.2	3.7 $\pm$ 4.1
Deep rocky reefs (5-15 m)	47 (23 to 30)	11.8 $\pm$ 3.1	158.4 $\pm$ 217.7	6.6 $\pm$ 8.0
Shallow <i>Posidonia</i> meadow (10-15 m)	30 (18 to 28)	9.3 $\pm$ 3.4	60.4 $\pm$ 48.5	1.3 $\pm$ 1.8
Deep <i>Posidonia</i> meadow (30-35 m)	22 (5 to 10)	3.2 $\pm$ 2.2	136.5 $\pm$ 164.1	2.0 $\pm$ 2.8
Coralligenous (25-40 m)	36 (10 to 29)	8.1 $\pm$ 2.6	595.5 $\pm$ 603.8	18.2 $\pm$ 20.9
Target species				
Shallow rocky reefs (0-3 m)	16 (8 to 13)	4.8 $\pm$ 1.6	27.1 $\pm$ 11.2	1.6 $\pm$ 1.4
Deep rocky reefs (5-15 m)	24 (12 to 19)	6.5 $\pm$ 1.9	37.6 $\pm$ 20.6	4.7 $\pm$ 7.5
Shallow <i>Posidonia</i> meadow (10-15 m)	15 (8 to 15)	3.6 $\pm$ 1.7	8.2 $\pm$ 6.5	0.4 $\pm$ 0.8
Deep <i>Posidonia</i> meadow (30-35 m)	9 (3 to 7)	2.0 $\pm$ 1.1	30.9 $\pm$ 21.9	0.4 $\pm$ 0.8
Coralligenous (25-40 m)	21 (5 to 17)	5.1 $\pm$ 2.1	36.0 $\pm$ 26.7	13.0 $\pm$ 17.3

Table XXI. Comparison between sites, within each habitat, for all species and for only target species. Statistical tests: *: significant differences ($p < 0.05$); **: highly significant ($p < 0.01$); ***: very highly significant ($p < 0.001$); ns: non-significant.

	Mean point diversity	Mean abundance per 100m ²	Mean biomass kg/100 m ²
All species			
Shallow rocky reefs (0-3 m)	*	ns	*
Deep rocky reefs (5-15 m)	*	*	**
Shallow <i>Posidonia</i> meadow (10-15 m)	***	*	**
Deep <i>Posidonia</i> meadow (30-35 m)	*	**	*
Coralligenous (25-40 m)	***	**	***
Target species			
Shallow rocky reefs (0-3 m)	ns	ns	ns
Deep rocky reefs (5-15 m)	ns	*	*
Shallow <i>Posidonia</i> meadow (10-15 m)	**	*	*
Deep <i>Posidonia</i> meadow (30-35 m)	ns	ns	ns
Coralligenous (25-40 m)	***	**	***

Table XXII. Comparison between the types of management, NT (no-take area), RF (restricted fishery) and AF (artisanal fishery), for three parameters (point diversity, mean abundance and mean fish biomass), within each habitat, for all species or for only target species. Statistical tests: *: significant differences ($p < 0.05$); **: highly significant ($p < 0.01$); ***: very highly significant ($p < 0.001$); ns: non-significant. md: missing data.

	Mean point diversity	Mean abundance per 100m ²	Mean biomass kg/100 m ²
All species			
Shallow rocky reefs (0-3 m)	ns	ns	ns
Deep rocky reefs (5-15 m)	ns	ns	ns
Shallow <i>Posidonia</i> meadow (10-15 m)	md	**	md
Deep <i>Posidonia</i> meadow (30-35 m)	ns	ns	ns
Coralligenous (25-40 m)	ns	ns	***
Target species			
Shallow rocky reefs (0-3 m)	ns	ns	ns
Deep rocky reefs (5-15 m)	*	ns	ns
Shallow <i>Posidonia</i> meadow (10-15 m)	-	-	-
Deep <i>Posidonia</i> meadow (30-35 m)	ns	ns	ns
Coralligenous (25-40 m)	***	*	***

However, it is important to note that this success of MUM management in the MPA of the Archipelago of Port-Cros is partly due its early establishment, the rigor and the sustainability of the management, the intelligence of a particular generation of artisanal fishers, the prohibition of recreational fishing and the resolution of conflicts of use between bathers, boat users, scuba divers and artisanal fishers. But the balance that has been achieved could be compromised tomorrow. The current generation of intelligent fishers is, because of its age, being replaced. Will the new fishers have the wisdom of their elders? Will they wish to have their cake and eat it, that is to say, take advantage of the ban on recreational fishing while themselves fishing without constraint? The incredible biological capital that an MPA represents is a sort of safe that fuels greed; it is easy to dream of a robbery: take the fish and run! We know that it only takes a few months of unrestricted fishing to empty an MPA of its fish and destroy decades of effort (see e.g. Williams *et al.*, 2006). Some new fishers (fortunately not those of the area) say more or less openly that they want to get rich quick, that the future of their children is not in the fishery and that the sustainability of the fishery is not a goal for them. But the law is on the side of the PCNP; it arms the Park with powerful weapons, and it is up to the PCNP to ensure that the general interest prevails, that of all current and future users, that of the natural and cultural heritage, against the possible depredations of people seeking quick but non-sustainable profits.

The comparison of the present data with those from previous studies, available for the Port-Cros Archipelago (e.g. Harmelin, 1987, 1991; Francour, 1992), is difficult because the latter studies were more specific (just one habitat, or only a part of the species) or concerned another season. The comparison with other sectors of the Mediterranean is difficult for the same reasons. However, these comparisons, which are beyond the scope of the present article, will be the subject of a separate article.

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