

Mapping and state of conservation of benthic marine habitats and assemblages of Port-Cros national Park (Provence, France, northwestern Mediterranean Sea)

Patrick ASTRUCH¹*, Charles F. BOUDOURESQUE^{1-2*},
Denis BONHOMME¹, Adrien GOUJARD¹, Paul-Arthur ANTONIOLI¹,
Patrick BONHOMME¹, Thierry PEREZ¹⁻³, Sandrine RUITTON¹⁻²⁻⁴,
Thibault de SAINT-MARTIN¹, Marc VERLAQUE¹⁻²

¹GIS Posidonie, Groupement d'Intérêt Scientifique pour l'étude de l'environnement marin, Aix-Marseille University, campus universitaire de Luminy, case 901, 13288 Marseille cedex 09, France.

²Mediterranean Institute of Oceanography (MIO), Aix-Marseille University, UMR CNRS 7294, campus universitaire de Luminy, case 901, 13288 Marseille cedex 09, France.

³Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Aix-Marseille University, UMR CNRS 7263, Station Marine d'Endoume, rue de la Batterie des Lions, 13007 Marseille, France.

⁴Institut Universitaire de Technologie HSE, Aix-Marseille University, Avenue Maurice Sandral, BP 156, 13708 La Ciotat, France.

*Corresponding authors: patrick.astruch@univ-amu.fr and charles.boudouresque@univ-amu.fr

Résumé. Cartographie et état de conservation des habitats et assemblages marins benthiques du Parc national de Port-Cros (Provence, France, Nord-Ouest de la Méditerranée). Les habitats et assemblages benthiques, ainsi que la bathymétrie, ont été cartographiés en 2010 au moyen d'un sondeur multifaisceaux interféromètre, d'un sonar latéral et d'orthophotographies, complétés par des observations en ROV (véhicule sous-marin télécommandé) et en plongée. La comparaison des données acquises en 2010 avec les cartes dressées dans les années 1960s-1970s, puis avec une carte levée en 1999, ainsi qu'avec l'ensemble des données disponibles sur Port-Cros, ne permet pas de conclure à une dégradation importante des habitats. La surface occupée par l'herbier à *Posidonia oceanica* n'a pas diminué et la vitalité de l'herbier est bonne à très bonne. Les grandes 'macroalgues' des Substrats durs infralittoraux à macroalgues photophiles et du Coralligène sont toujours présentes et abondantes. Le Détritique côtier se présente sous l'aspect qu'il avait peut-être en Méditerranée, avant que ses fragiles espèces calcifiées et concrétionnantes ne soient broyées par les chaluts. La gestion efficace de la pêche artisanale a permis de juxtaposer une pêche économiquement rentable avec des stocks élevés de téléostéens. En revanche, le récif-barrière de *P. oceanica* de la baie de Port-Cros continue à régresser ; la limite inférieure de l'herbier à *P. oceanica* remonte ; dans ce cas, la cause n'est pas à rechercher dans des impacts locaux, mais plus probablement dans des phénomènes climatiques. Des épisodes chauds, dont la fréquence s'accroît en

liaison avec le réchauffement climatique, ont causé des mortalités massives d'espèces emblématiques, telles que les gorgones. Les forêts superficielles à *Cystoseira brachycarpa* var. *balearica* ont fortement régressé. Des 'macroalgues' introduites, envahissent la plupart des habitats ; leur impact sur la biodiversité, la structure et le fonctionnement des écosystèmes est encore mal connu. Cet impact peut s'accroître avec le temps, de telle sorte que, sur le long terme, il peut s'avérer dramatique. Au total, nos résultats traduisent d'une part le succès durable de la politique de protection du patrimoine naturel dans le Parc national de Port-Cros, mais aussi sa vulnérabilité à des impacts locaux ou venus d'ailleurs.

Mots-clés : cartographie des habitats, Substrats durs infralittoraux à macroalgues photophiles, Herbier à *Posidonia oceanica*, Coralligène, Détritique côtier, état de conservation.

Abstract. Benthic habitats and assemblages as well as bathymetric data of the Port-Cros national Park (PCNP) were mapped in 2010 using an Interferometric Multibeam Echo-Sounder, a Side-Scan Sonar and the interpretation of orthophotos, completed by ROV (Remotely Operated Vehicle) and SCUBA dives. Comparison of the 2010 data with the 1960s-1970s maps and a 1999 map, combined with all of the available literature data regarding PCNP, does not evidence any major environmental degradation. The surface area of the *Posidonia oceanica* seagrass meadows has not diminished and their state of conservation is, as a whole, 'good' to 'very good'. The large 'macroalgae' of the Sublittoral reef with photophilous macroalgae and of the Coralligenous assemblages are still present and abundant. The Coastal detritic assemblage in PCNP appears as it may once have been throughout the Mediterranean, before their fragile calcified and bio-constructive species were crushed by trawling. Efficient artisanal fishery management has allowed economically-sound fishing and high stocks of teleosts to coexist. However, the Port-Cros Bay *P. oceanica* barrier-reef inexplicably continues to regress, as does the lower meadow limit. The cause of the latter regression might be related to climatic processes rather than to local impact. A higher frequency of positive temperature anomalies linked to global warming has inflicted mass mortality episodes on some charismatic species such as the gorgonians. Shallow sublittoral forests of *Cystoseira brachycarpa* var. *balearica* have conspicuously regressed. Introduced 'macroalgae' are invading most habitats; their impact on ecosystem biodiversity, structure and functioning remains uncertain. Their impact may increase over time, so this must be monitored as in the long-run it may be potentially dramatic. To conclude, the results of this study reflect on the one hand the long-lasting success of the protection policies of the PCNP's natural heritage, but on the other hand its vulnerability to local or global impact.

Keywords: mapping of habitats, Sublittoral reef with photophilous macroalgae, *Posidonia oceanica* seagrass meadows, Coralligenous, Coastal detritic, state of conservation.

Introduction

Port-Cros national Park (hereafter referred to as PCNP) was founded in December 1963. It comprises the Isles of Port-Cros and Bagaud and the Islets of Gabinière and Rascas, as well as a 600-metre-wide surrounding sea strip (1 297 ha) (Fig. 1).

Since its foundation, PCPN has been the subject of over 1 100 studies, dealing with marine and terrestrial primary producers, Metazoa, ecology, habitat mapping, fishing, earth sciences, social studies, management, etc. Its benthic habitats have been more particularly mapped by Molinier and Picard (1952), Pérès and Picard (1963), Augier and Boudouresque (1967, 1970a, 1970b, 1976), Bourcier (1982, 1985), Augier and Nieri (1988), Meinesz *et al.* (2000a, 2000b, 2001b, 2001c, 2004), Cottalorda *et al.* (2004), Belsher *et al.* (2005) and Goujard *et al.* (2010).

The purpose of this study is **(i)** to update the map of benthic habitats and assemblages, **(ii)** to evaluate the state of conservation of these habitats and assemblages and **(iii)** to establish a categorisation of conservation priorities with regard to environmental threats and the heritage value of these habitats and assemblages. To this end, literature data were analysed, benthic acoustic data were acquired, field observations were completed and an up-to-date map was produced.

Materials and methods

Literature review

The literature review included *ca.* 400 references (scientific publications and unpublished reports) together with unpublished data. The information gathered was integrated to a Database Management System (DBMS) coupled to a Geographical Information System (GIS).

Habitats and mapping

The commonly used term of 'algae' refers neither to a specific taxon (as it is a polyphyletic group), nor to a particular morphology (as it includes unicellular or multicellular species, with thallus or cormus), nor to a functional group (as it encompasses photosynthetic, mixotrophic or heterotrophic species, including predatory species). The term 'macroalgae', found in 'Sublittoral reef with photophilous macroalgae', refers to Multicellular Photosynthetic Organisms (MPOs) belonging to the Chlorobionta, Rhodobionta (kingdom Archaeplastida) and Phaeophyceae (kingdom Stramenopiles) (Table I).

The habitats and assemblages considered are first of all five Mediterranean habitats as defined by the 1992 Habitats Directive (Cahiers d'habitats Natura 2000, 2004; Bonacorsi *et al.*, 2011) to which is added the Coastal detritic assemblage. **(i) *Posidonia oceanica* seagrass meadows** (code 1120) are both 'Priority Habitats' and 'Habitats of Community Interest' (see Table I for taxonomy and species authority). They may occur as barrier-reefs (Boudouresque *et al.*, 2006).

(ii) Reefs (code 1170): these ‘Habitats of Community Interest’ are comprised of several elementary habitats (i.e. assemblages): the Supralittoral rock assemblage (code 1170-10), the Upper midlittoral rock assemblage (code 1170-11), the Lower midlittoral rock assemblage (code 1170-12) (not mapped), as well as Sublittoral reef with photophilous macroalgae (code 1170-13) and the Coralligenous assemblage (code 1170-14). **(iii) Sandbanks which are slightly covered by sea water all the time** (code 1110). These ‘Habitats of Community Interest’ are comprised of several elementary habitats: the Very shallow fine sand assemblage (code 1110-5), the Well-sorted fine sand assemblage (code 1110-6), the Coarse sand and fine gravel under the influence of bottom currents assemblage (1110-7) and the Sublittoral pebble assemblage (code 1110-9) (Pérès and Picard, 1964). **(iv) Large shallow inlets and bays** (code 1160) are ‘Habitats of Community Interest’ represented by a single elementary habitat: the Shallow and sheltered muddy sand assemblage (code 1160-3) (Pérès and Picard, 1964). **(v) Submerged or partly submerged sea caves** (code 8330) are ‘Habitats of Community Interest’ represented by Semi-dark underwater caves (code 8330-3) and Dark underwater caves (code 8330-4). **(vi)** Finally, the **Coastal detritic assemblage** (Pérès and Picard, 1964), although not ‘Habitats of Community Interest’, was nonetheless mapped, as it occupies important surface areas in PCNP, and may furthermore be close to a pristine ecological state because unaffected by trawling or terrigenous sediment deposits, in contrast to its mainland counterpart.

Bathymetric data were acquired using a Geoswath+NG® Interferometric Multibeam Echo- Sounder (IMES). The nature of the sea-floor was mapped using: **(i)** the IMES for depths of 1 to 20 metres, **(ii)** a Klein 3900® Side-Scan Sonar (SSS) for habitats ranging from 18 to 100 metres depth. **(iii)** Orthophotographs from the French ‘Institut Géographique National’ (IGN) taken in 2003 and 2008, as well as Google Earth® images dated 13th July 2007, enabled some uncertainties for zones between the sea surface and ca. 10 m depth to be resolved. Data acquisition field campaigns using the IMES and SSS took place in March and April 2010.

Additionally, information was acquired from May to October 2010 using SCUBA diving and a Remotely Operated Vehicle (ROV), either selectively or along linear transects. The analysis of these data permitted **(i)** the interpretation of IMES and SSS images and the delineation of habitats, **(ii)** the localisation of sites featuring outstanding species, **(iii)** the evaluation of the conservation state of *Posidonia oceanica* seagrass meadows and coralligenous assemblages, **(iv)** the identification of environmental threats to species and habitats and **(v)** the categorisation of conservation priorities to be established.

When two habitats and/or assemblages blend into one another to form a mosaic to the extent that they cannot be mapped separately, it is that mosaic that was therefore mapped. In the map caption (Fig. 2), the habitat labelled in first position is the most abundant within the mosaic. Arbitrarily, to calculate the surface occupied by each habitat within the mosaic, 2/3 of the total surface were attributed to the first habitat, and the remaining 1/3 to the second. For example, when considering the surface area of the mosaic ‘*Posidonia oceanica* seagrass meadow with dead matte’, 2/3 was attributed to ‘*Posidonia oceanica* seagrass meadow’ and 1/3 to ‘Dead matte of the seagrass *Posidonia oceanica*’. Belsher *et al.* (2005) omitted to map ca. 23 ha of benthos within the PCNP boundaries; in order to compare the surface area of habitats and/or assemblages on their map with ours, we labelled the missing areas with the habitats and/or assemblages found on our 2010 map.

Table I. Cited species, with their authority and the higher taxa they belong to. For classification, see Lecointre and Le Guyader (2006) and Boudouresque (2011).

Kingdom	Subkingdom and lower taxa	Species and authority	
Archaeplastida (= Plantae)	Rhodobionta	<i>Acrothamnion preissii</i> (Sonder) E.M. Wollaston	
		<i>Chrysymenia ventricosa</i> (J.V. Lamouroux) J. Agardh	
		<i>Lithophyllum byssoides</i> (Lamarck) Foslie	
		<i>Lithophyllum racemus</i> (Lamarck) Foslie	
		<i>Lithophyllum stictaeformis</i> (Areschoug) Hauck (= <i>Pseudolithophyllum cabiochiae</i> Boudouresque <i>et</i> Verlaque)	
		<i>Lithothamnion corallioides</i> (P.L. Crouan <i>et</i> H.M. Crouan) P.L. Crouan <i>et</i> H.M. Crouan	
		<i>Lithothamnion fruticulosum</i> (Kützing) Foslie	
		<i>Lithothamnion valens</i> Foslie	
		<i>Lophocladia lallemandii</i> (Montagne) F. Schmitz. Not observed	
		<i>Mesophyllum expansum</i> (Philippi) Cabioc <i>et</i> Mendoza	
		<i>Osmundaria volubilis</i> (Linnaeus) R.E. Norris	
		<i>Peyssonnelia rosa-marina</i> Boudouresque <i>et</i> Denizot	
		<i>Phymatolithon calcareum</i> (Pallas) W.H. Adey <i>et</i> D.L. McKibbin	
		<i>Rissoella verruculosa</i> (Bertoloni) J. Agardh	
		<i>Sebdenia dichotoma</i> Berthold	
		<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	
		Viridiplantae, Chlorobionta	<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva <i>Caulerpa cylindracea</i> Sonder (= <i>C. racemosa</i> (Forsskål) J. Agardh var. <i>cylindracea</i> (Sonder) Verlaque, Huisman <i>et</i> Boudouresque

		<i>C. prolifera</i> (Forsskål) J.V. Lamouroux
		<i>C. taxifolia</i> (Vahl) C. Agardh
		<i>Codium effusum</i> (Rafinesque) Delle Chiaje
		<i>Flabellia petiolata</i> (Turra) Nizamuddin
		<i>Halimeda tuna</i> (J. Ellis et Solander) J.V. Lamouroux
		<i>Palmophyllum crassum</i> (Naccari) Rabenhorst
		<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen
		<i>Ulva olivascens</i> P.J.L. Dangeard
	Viridiplantae, Magnoliophyta	<i>Cymodocea nodosa</i> (Ucria) Ascherson
		<i>Posidonia oceanica</i> (Linnaeus) Delile
Stramenopiles	Chromobionta, Phaeophyceae	<i>Carpomitra costata</i> (Stackhouse) Batters
		<i>Cystoseira amentacea</i> (C. Agardh) Bory de Saint-Vincent var. <i>stricta</i> Montagne
		<i>C. barbata</i> (Stackhouse) C. Agardh
		<i>C. brachycarpa</i> J. Agardh var. <i>balearica</i> (Sauvageau) Giaccone
		<i>C. elegans</i> Sauvageau
		<i>C. foeniculacea</i> (Linnaeus) Greville
		<i>C. funkii</i> Schiffner ex Gerloff et Nizamuddin
		<i>C. jabukae</i> Ercegović
		<i>C. spinosa</i> Sauvageau
		<i>C. zosteroides</i> C. Agardh
		<i>Dictyopteris polypodioides</i> (A.P. De Candolle) J.V. Lamouroux
		<i>Padina pavonica</i> (Linnaeus) Thivy
		<i>Phyllariopsis brevipes</i> (C. Agardh) E.C. Henry et G.R. South
		<i>Sargassum vulgare</i> C. Agardh
		<i>Spatoglossum solieri</i> (Chauvin ex Montagne) Kützing
Opisthokonts	Metazoa, Bryozoa	<i>Adeonella calveti</i> (Canu et Bassler, 1930)
		<i>Myriapora truncata</i> (Pallas, 1766)
		<i>Pentapora fascialis</i> (Pallas, 1766)
		<i>Turbicellepora avicularis</i> (Hincks, 1860)
	Metazoa, Cnidaria	<i>Caryophyllia inornata</i> (Duncan, 1878)
		<i>Corallium rubrum</i> (Linnaeus, 1758)
		<i>Eunicella cavolini</i> Koch, 1887
		<i>Eunicella singularis</i> (Esper, 1794)
		<i>Leptopsammia pruvoti</i> Lacaze-Duthiers, 1897
		<i>Paramuricea clavata</i> (Risso, 1826)
		<i>Parazoanthus axinellae</i> (Schmidt, 1862)
		<i>Pennatula rubra</i> (Ellis, 1781)
		<i>Pteroeides spinosum</i> Ellis, 1764
	Metazoa, Crustacea	<i>Palinurus elephas</i> (Fabricius, 1787)
		<i>Scyllarides latus</i> (Latreille, 1803)
		<i>Scyllarus arctus</i> (Linnaeus, 1758)
	Metazoa, Echinodermata	<i>Arbacia lixula</i> (Linnaeus, 1758)
		<i>Paracentrotus lividus</i> (Lamarck, 1816)
	Metazoa, Mollusca	<i>Lithophaga lithophaga</i> (Linnaeus, 1758)
		<i>Patella ferruginea</i> Gmelin, 1791
		<i>Pinna nobilis</i> Linnaeus, 1758
	Metazoa, Porifera (sponges)	<i>Agelas oroides</i> Schmidt, 1864
		<i>Aplysina cavernicola</i> (Vacelet, 1859)

		<i>Axinella damicornis</i> (Esper, 1794)
		<i>A. polypoides</i> Schmidt, 1862
		<i>A. verrucosa</i> (Esper, 1794)
		<i>Clathrina clathrus</i> (Schmidt, 1864)
		<i>Haliclona poecillastroides</i> Vacelet, 1969)
		<i>H. mediterranea</i> Griessinger, 1971
		<i>Hexadella racovitzai</i> Topsent, 1896
		<i>Petrosia ficiformis</i> (Poiret, 1789)
		<i>Spongia lamella</i> (Schulze, 1879)
		<i>S. officinalis</i> Linnaeus, 1759
	Metazoa, Teleostei	<i>Apogon imberbis</i> (Linnaeus, 1758)
		<i>Conger conger</i> (Linnaeus, 1758)
		<i>Coris julis</i> (Linnaeus, 1758)
		<i>Epinephelus marginatus</i> (Lowe, 1834)
		<i>Muraena helena</i> Linnaeus, 1758
		<i>Phycis phycis</i> (Linnaeus, 1766)
		<i>Sarpa salpa</i> (Linnaeus, 1758)
		<i>Sciaena umbra</i> Linnaeus, 1758
		<i>Scorpaena scrofa</i> Linnaeus, 1758
		<i>Thalassoma pavo</i> (Linnaeus, 1758)
		<i>Thorogobius ephippiatus</i> (Lowe, 1839)

Outstanding species

Close consideration was given to a certain number of species of special interest for a variety of reasons: protected species, ecosystem engineers, key species, species of charismatic value, species of economic value, environmental quality indicator species, invasive species, etc. Some of these species may belong to several of the categories listed above and detailed hereafter.

Species may be protected at French, European or international level. *Posidonia oceanica* and *Cymodocea nodosa* are protected in France under the 19th July 1998 Order. The 26th November 1992 Order establishes a complementary list of marine species protected in France which includes the crustacean *Scyllarides latus* and the molluscs *Lithophaga lithophaga*, *Patella ferruginea* and *Pinna nobilis*. The 18th July 1999 Decree establishes a list of species protected in France which includes the Rhodobionta *Lithophyllum byssoides* (as *L. lichenoides*) and the Chromobionta *Cystoseira amentacea*, *C. spinosa*, *C. zosteroides*. These species are also listed in the 21st May 1992 EU Habitats Directive 92/43 Appendices and/or in the Appendices of the Bern and Barcelona Conventions.

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials (Lawton, 1994). *Posidonia oceanica* is an ecosystem engineer in the eponymous ecosystem. In the Coralligenous assemblage, the

ecosystem engineer is the functional group of bio-constructive species, mainly Rhodobionta such as *Lithophyllum stictaeformis* and *Mesophyllum expansum*.

A key species (often erroneously named keystone species) is a species whose impact on its community or ecosystem is broad, and further-reaching than would be expected by its abundance (Power and Mills, 1995). In the *Posidonia oceanica* ecosystem, apart from the eponymous species, the sea urchin *Paracentrotus lividus* and the teleosts *Sarpa salpa* and *Scorpaena* spp., are key species.

Charismatic species: the dusky grouper *Epinephelus marginatus* is considered a charismatic species for it is rare (outside Marine Protected Areas) and attracts SCUBA divers. Hooking and spearfishing this species is illegal in the French Mediterranean under the 19th December 2007 Order. Some species are charismatic for their seascape value, such as the gorgonians *Paramuricea clavata*, *Eunicella singularis* and *E. cavolini*, and the yellow incrusting anemone *Parazoantus axinellae*.

Species of economic value are targeted by artisanal fishermen in the PCNP; the list of these species comes from the monitoring of fisheries undertaken by Bonhomme *et al.* (2009; Cadiou *et al.*, 2009): e.g. the spiny lobster *Palinurus elephas*, the scorpionfish *Scorpaenea scrofa*, the brown meagre (corb fish) *Sciaena umbra* and the seabreams *Diplodus* spp.

Indicators of good environmental quality are e.g. the Rhodobionta *Lithophyllum byssoides* and *Rissoella verruculosa*, the Chromobionta *Cystoseira* spp. and the Magnoliophyta *Posidonia oceanica*. In contrast, most species of the genus *Ulva* (including enteromorpha-like *Ulva*) are indicators of environmental stress. Finally, some species sensitive to positive thermal anomalies are indicators of global warming; e.g. the Chlorobionta *Caulerpa prolifera*, whose expansion is favoured by the warming, and in contrast the gorgonians *Paramuricea clavata* and *Eunicella singularis*, and the sponge *Spongia officinalis* which are negatively affected by warm episodes (Perez *et al.*, 2000; Romano *et al.*, 2000; Garrabou *et al.*, 2002).

Invasive species are introduced (i.e. transported by humans and naturalised) and have a very negative ecological and/or economic impact (Boudouresque and Verlaque, 2002). In PCNP, 3 species of 'macroalgae' are particularly abundant: the Chlorobionta *Caulerpa cylindracea* (Verlaque *et al.*, 2000, 2003) and Rhodobionta *Womersleyella setacea* and *Acrothamnion preissii*. Another species, *Caulerpa taxifolia*, abundant along the French Riviera coast and in some Provence localities (Meinesz and Hesse, 1991; Meinesz *et al.*, 2001a),

has been successfully eradicated from Port-Cros (or more exactly maintained at a very low abundance) (Cottalorda *et al.*, 2010, 2011).

ZNIEFF species: in France, the Ministry of Environment has established Natural Zones of Ecological, Faunistic and Floristic Interest (ZNIEFF in French). ZNIEFFs are geographical sectors which display particularly interesting ecological features, participate in maintaining important natural equilibria or are home to rare species of primary producers and Metazoa, enhancing local natural heritage. In Provence and the French Riviera, a list of species justifying the implementation of a ZNIEFF has been established (Bellan-Santini *et al.*, 2002, 2003; Elissalde-Videment *et al.*, 2004).

Altogether, the aforementioned categories of outstanding species, combined with observations of habitat ecological state and evolution, in comparison to prior observations, has enabled the natural heritage value of the considered habitats and assemblages to be established.

Conservation state of habitats and assemblages

The conservation state of the *Posidonia oceanica* seagrass meadow and the Coralligenous assemblage was based on the conservation state defined in the SDF (Standard Data-Entry Form for National Inventories of Natural Sites of Conservation Interest; UNEP/MAP, 1999) produced by the Regional Activity Centre for Specially Protected Areas (RAC/SPA), and used in DREAL PACA (French Ministry of Environment Regional Agency) specifications for the inventory and mapping of Natura 2000 sites.

The conservation state of habitats and assemblages was established on the basis of 3 criteria: **(i)** conservation of the spatial structure (both horizontally and vertically), **(ii)** conservation of the functions of the habitat or assemblage (resource supply for other habitats, ecosystem services) and, **(iii)** restoration potential for impacted habitats and assemblages. A combination of these criteria allows the conservation state of the considered habitat and/or assemblage to be established: pristine (A), good (B) or moderate to low (C).

Table II. Categorisation of conservation priorities by crossing heritage value and severity of natural and/or human threats.

		Natural heritage value				
		Null	Low	Moderate	High	Very high
Threats	Null	Null	Null	Low	Moderate	High
	Low	Null	Low	Low	Moderate	High
	Moderate	Low	Low	Moderate	High	High
	High	Moderate	Moderate	High	High	Very high
	Very high	High	High	High	Very high	Very high

The categorisation of conservation priorities was based on natural heritage value vs. severity of natural and/or human threats (Table II). The Port-Cros area was subdivided into 10 zones (as defined by Bonhomme *et al.*, 2009; Fig. 1) for the purpose of the ecological analysis.

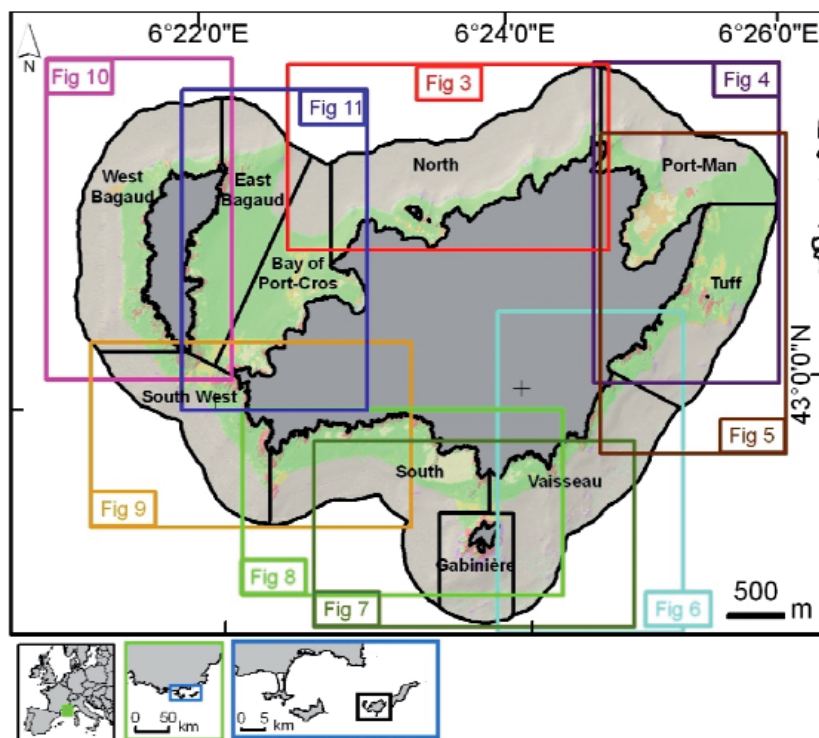


Figure 1. The 10 zones of PCNP marine area, according to Bonhomme *et al.* (2009). Refer to Fig. 3 through Fig. 11 for detailed maps corresponding to each zone.

Results and discussion

Mapping the habitats and assemblages

A map of PCNP benthic habitats was based on the original data acquired in 2010 (Fig. 3 through 11; a more accurate version of this map is available at www.portcrosparcnational.fr). When compared to the benthos map of Belsher *et al.* (2005), which is based on data acquired in 1999, two types of differences are revealed.

These differences concern first of all the position of boundaries between habitats or assemblages. The possibility cannot be ruled out that some boundaries may have been displaced over the course of a decade. However, even if map accuracy for the present study is ca. 1 m, the same cannot be said about the map produced by Belsher *et al.* (2005) where precision is not specified; on the basis of the techniques used in the latter study, we estimated precision to be between 10 and ca. 30 m. Furthermore, our interpretation of the 2010 IMES and SSS images may be uncertain. Therefore the differences between the two maps must not be interpreted as a variation over time.

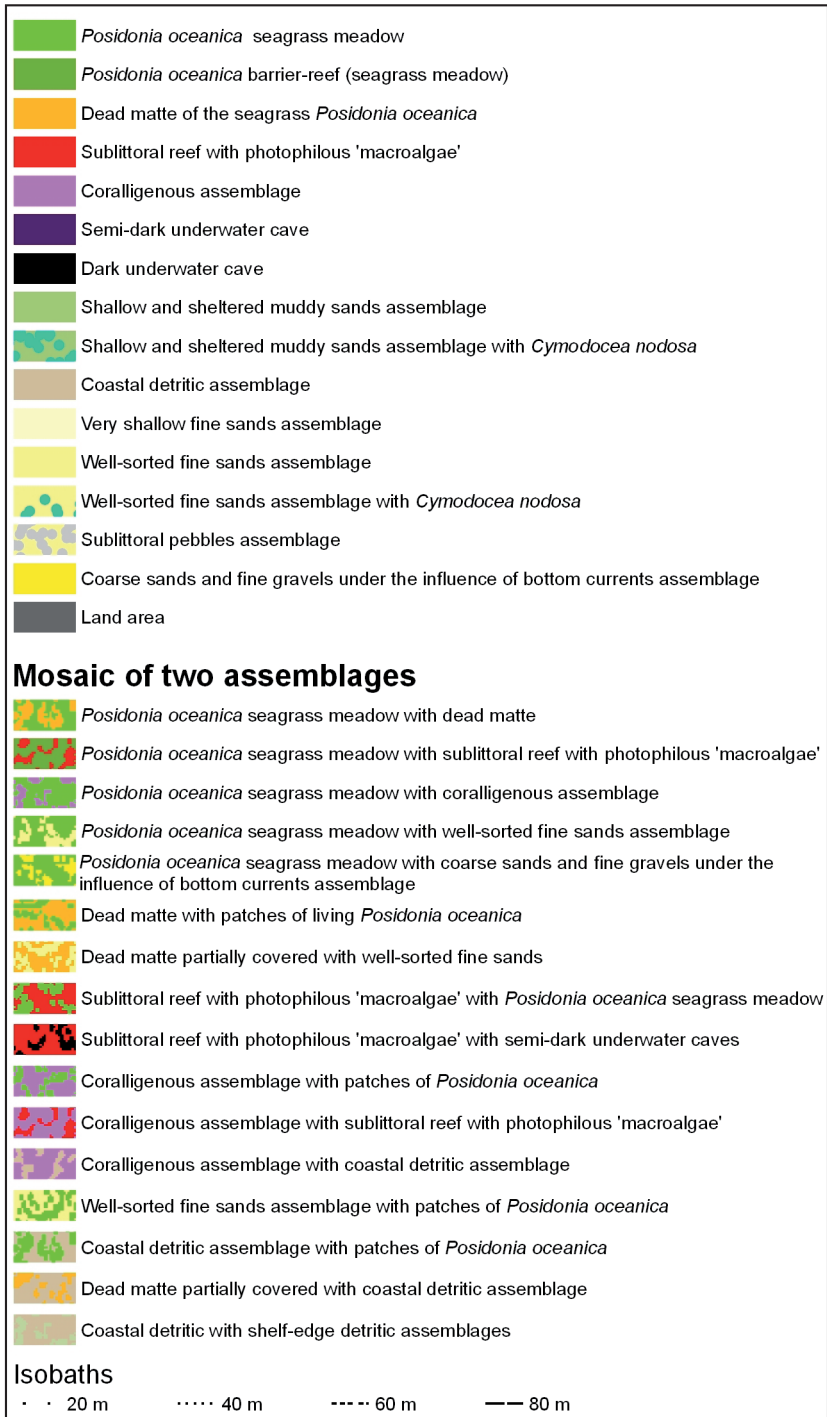


Figure 2. Key for Fig. 3 through 11.

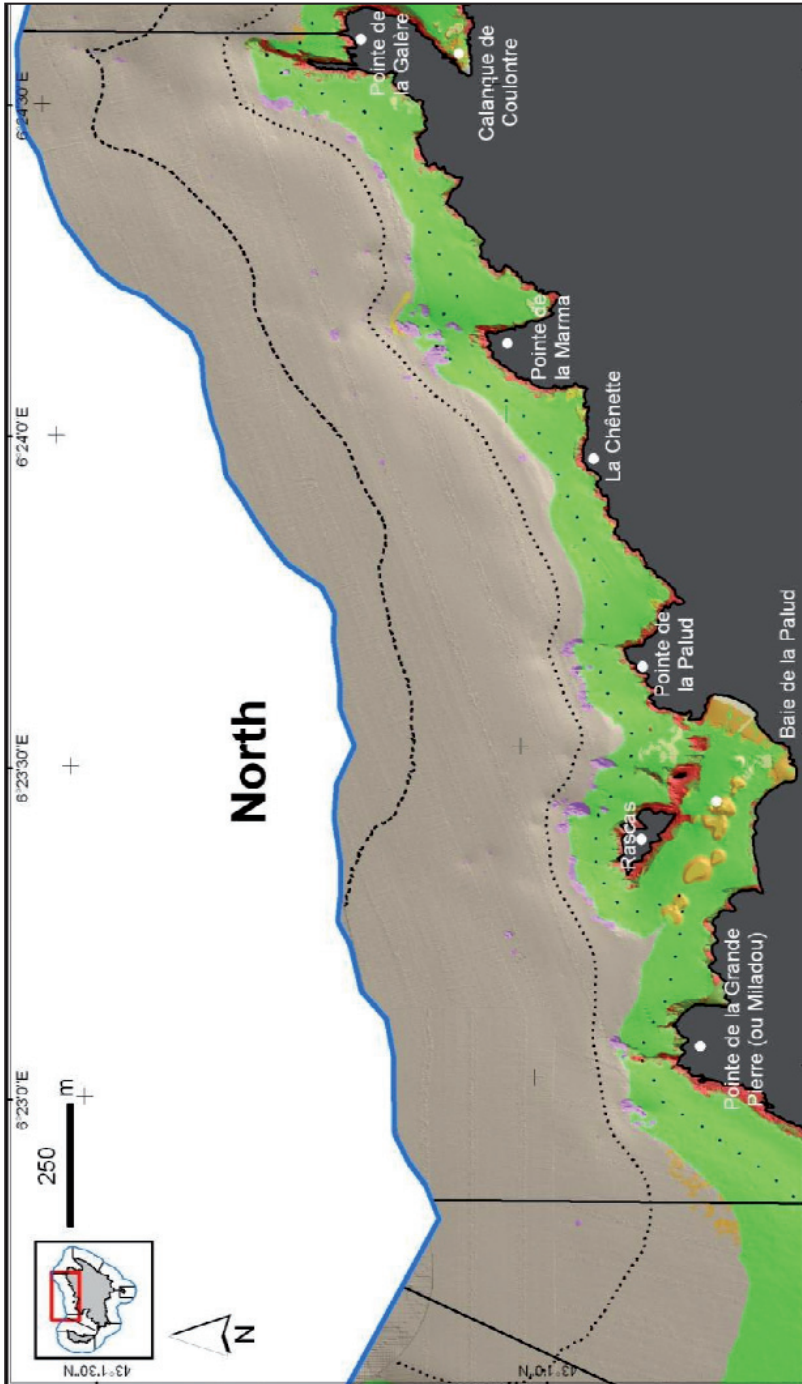


Figure 3. Map of benthic habitats and assemblages: North zone. Refer to Fig. 1 for localisation and Fig. 2 for key.

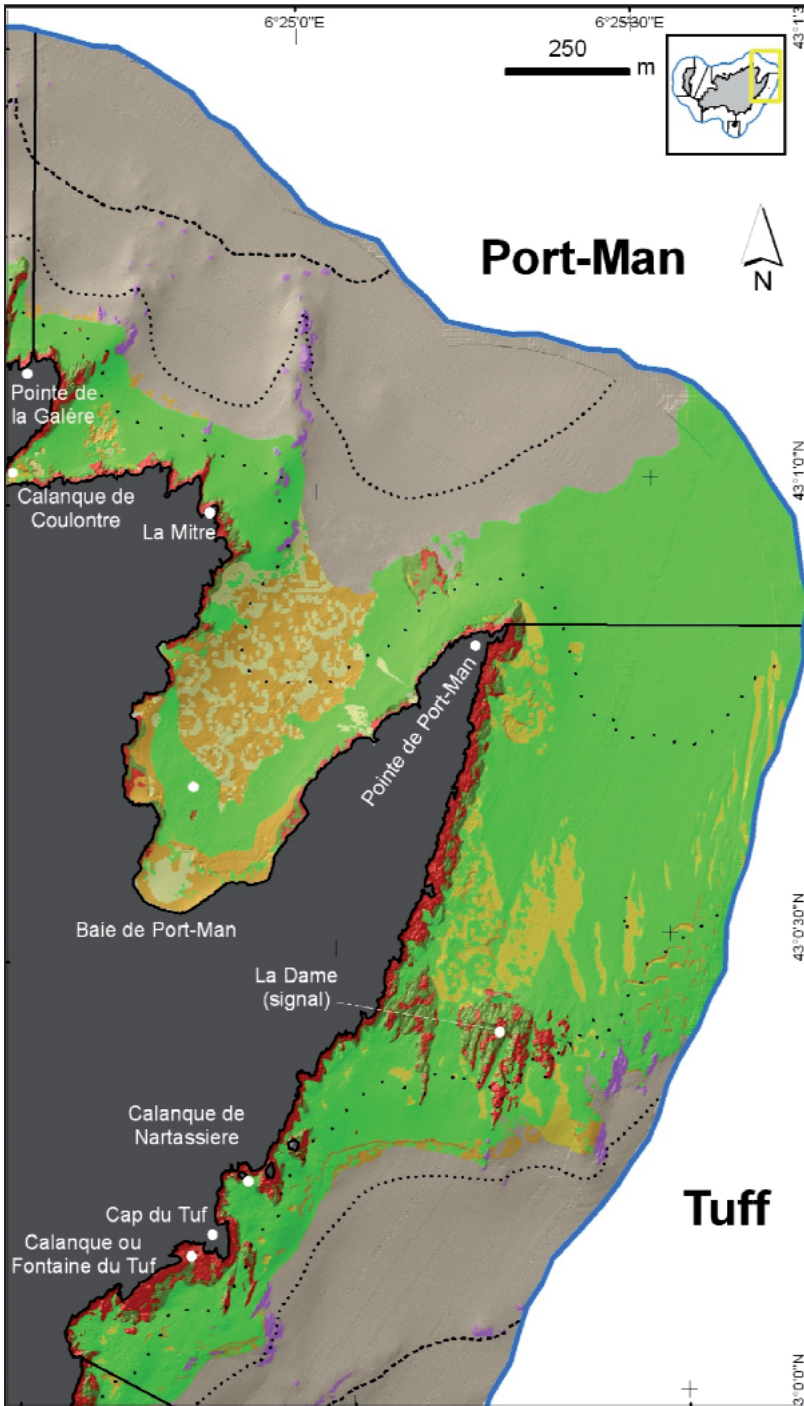


Figure 4. Map of benthic habitats and assemblages: Port-Man and part of Tuff zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

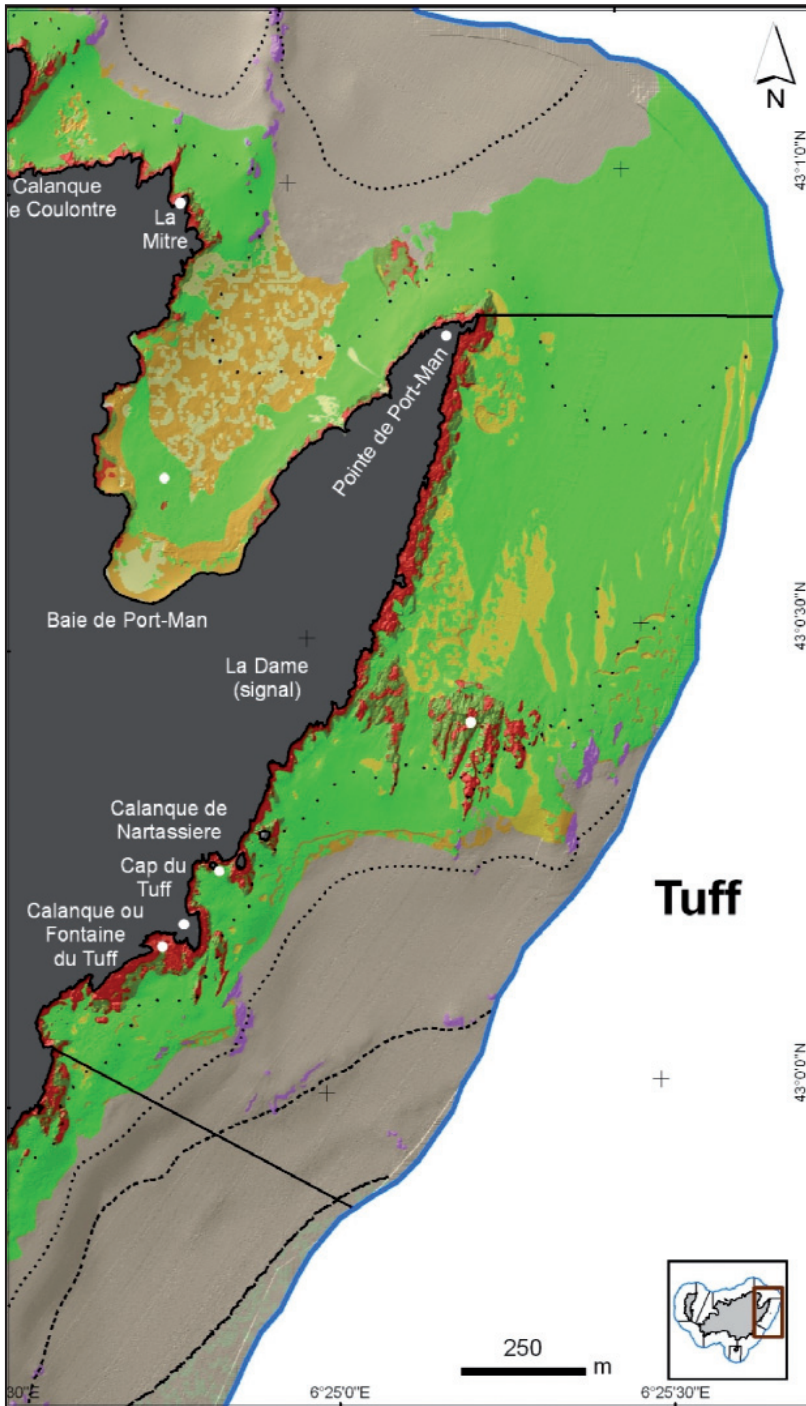


Figure 5. Map of benthic habitats and assemblages: Tuff, part of Port-Man (top) and Vaisseau (bottom) zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

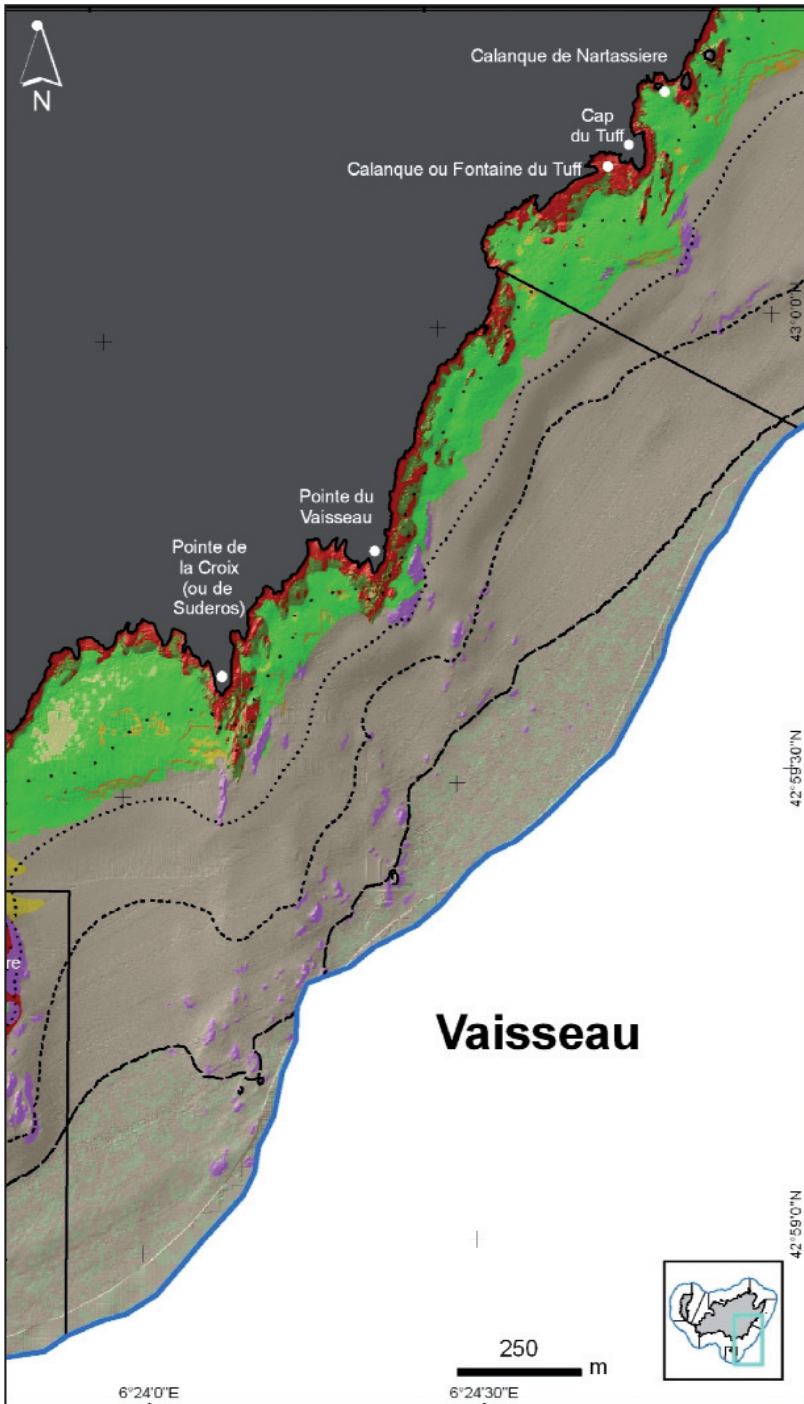


Figure 6. Map of benthic habitats and assemblages: Vaisseau, part of Tuff (top) and Gabinière (bottom left) zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

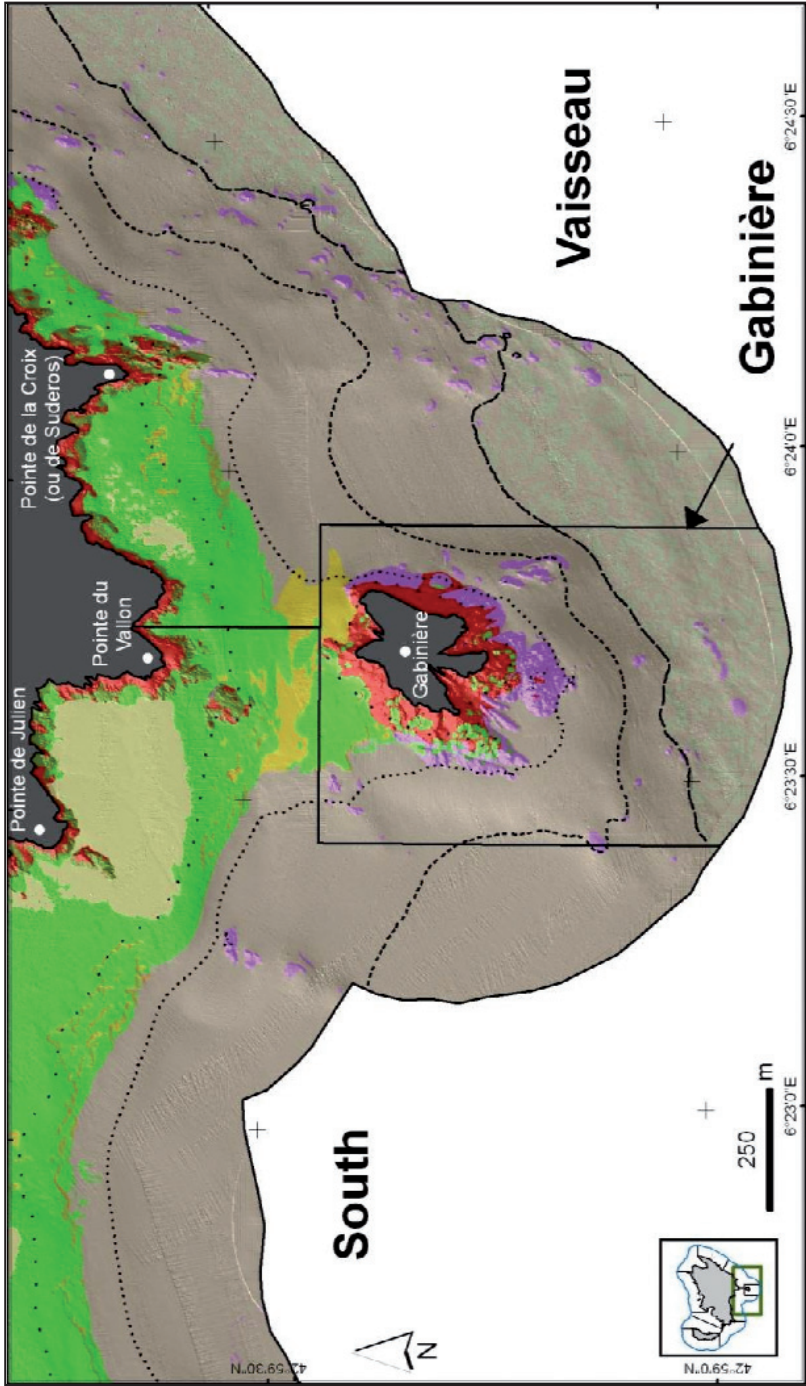


Figure 7. Map of benthic habitats and assemblages: Gabinère, part of Vaisseau (right) and South (left) zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

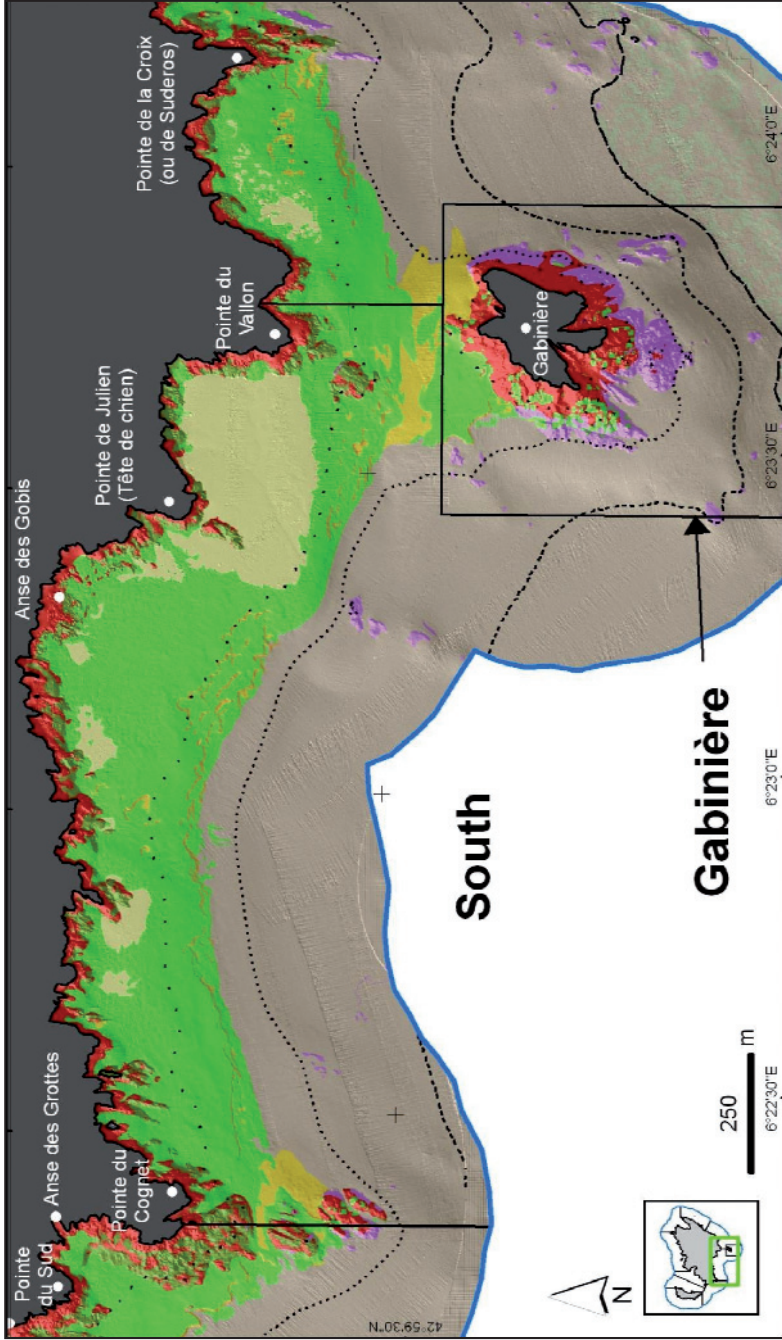


Figure 8. Map of benthic habitats and assemblages: South, part of Gabinière and Vaisseau (right) zones. Refer to Fig. 1 for localisation and Fig. 2 for key

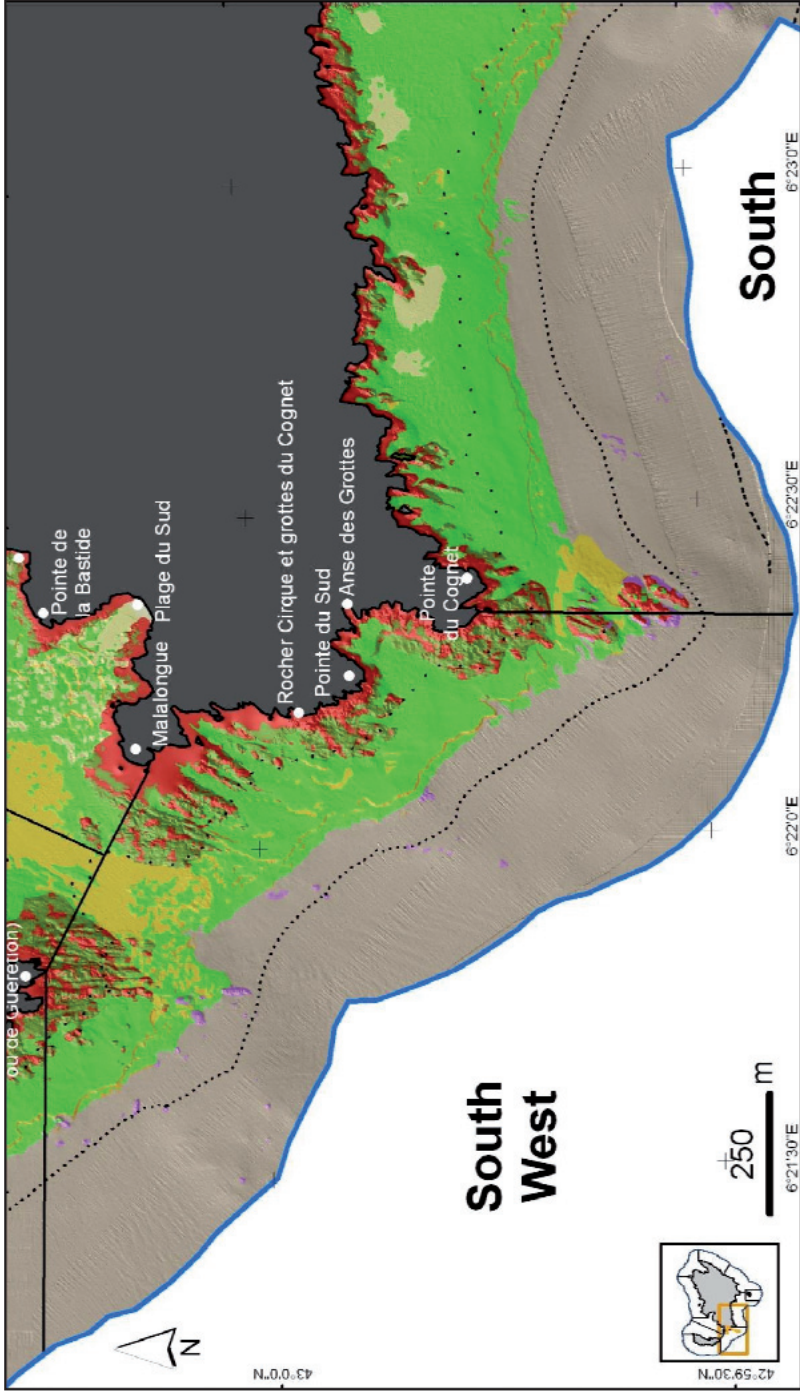


Figure 9. Map of benthic habitats and assemblages: South-West and part of South (right) zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

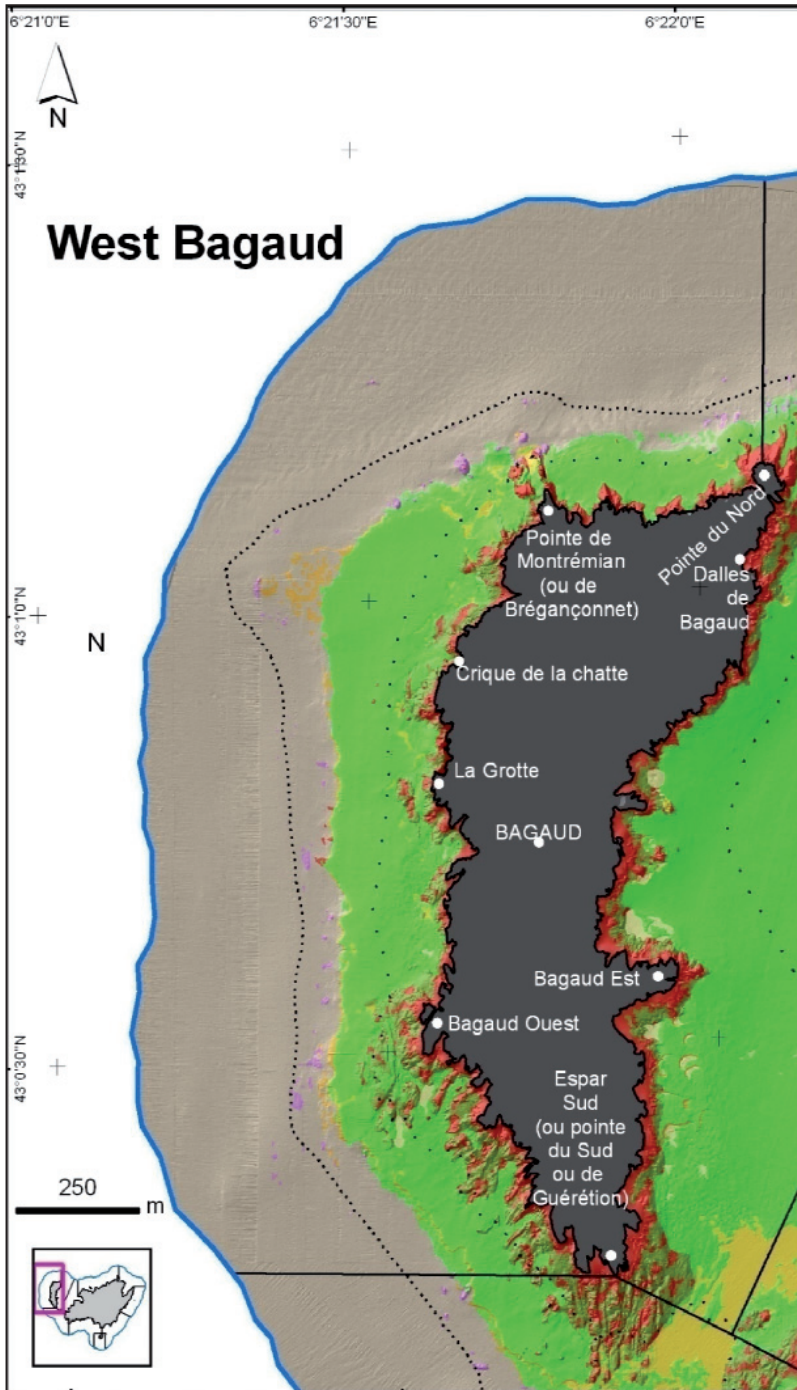


Figure 10. Map of benthic habitats and assemblages: West Bagaud and part of East Bagaud (right) zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

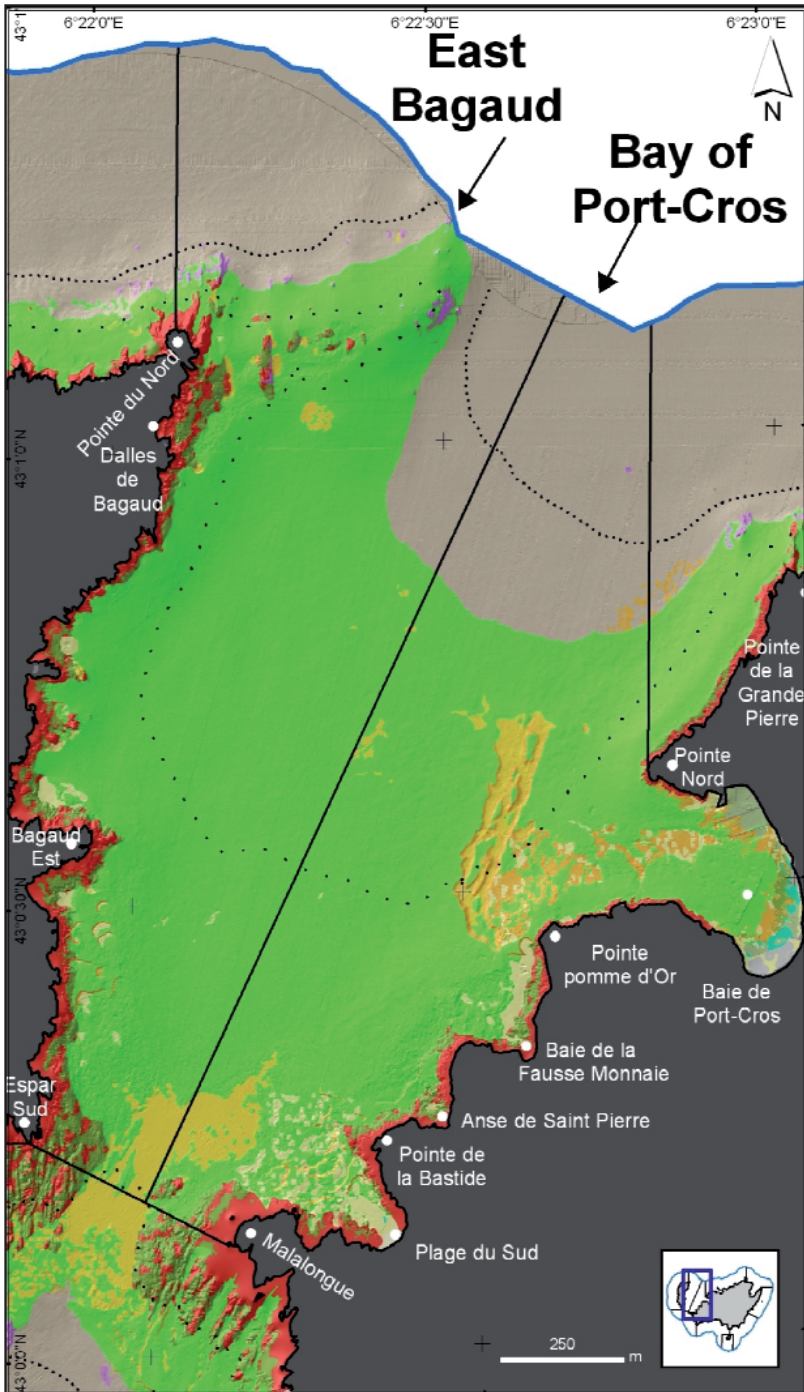


Figure 11. Map of benthic habitats and assemblages: East Bagaud, part of North (right) and Bay of Port-Cros zones. Refer to Fig. 1 for localisation and Fig. 2 for key.

The main difference between the two maps is that Belsher *et al.* (2005) focused on mapping (with the exception of *Posidonia oceanica* seagrass meadows) sediments and hard substrata, whereas the present study focuses on mapping habitats and assemblages. Thus, on loose substrate, the following assemblages are distinguished here: ‘Shallow and sheltered muddy sands’, ‘Very shallow fine sands’, ‘Well-sorted fine sands’, ‘Sublittoral pebbles’, ‘Coastal detritic’ and ‘Shelf-edge detritic’. On hard substrate are distinguished: ‘Sublittoral reef with photophilous macroalgae’, ‘Coralligenous assemblage’, ‘Semi-dark underwater caves’ and ‘Dark underwater caves’.

The Coastal detritic assemblage and *P. oceanica* seagrass meadows are the most abundant habitats by surface area (Table III).

Table III. Surface area of mapped benthic marine habitats and assemblages of PCNP. Gross data were simplified: mosaics of two habitats (Fig. 3 through 11) were incorporated into their corresponding habitats (refer to Materials and methods). Other habitats and assemblages: ‘Very shallow fine sands assemblage’, ‘Shallow and sheltered muddy sands assemblage (with *Cymodocea nodosa*)’, ‘Shallow and sheltered muddy sands assemblage (without *Cymodocea nodosa*)’, ‘Well-sorted fine sands assemblage (with *Cymodocea nodosa*)’, ‘Sublittoral pebbles assemblage’, ‘Semi-dark underwater caves’ and ‘Dark underwater caves’.

Habitats and assemblages	Surface area (ha)
<i>Posidonia oceanica</i> seagrass meadow	438.8
Dead matte of the seagrass <i>Posidonia oceanica</i>	26.3
Sublittoral reef with photophilous ‘macroalgae’	64.2
Coralligenous assemblage	14.2
Well-sorted fine sands assemblage (without <i>Cymodocea nodosa</i>)	25.4
Coarse sands and fine gravels under the influence of bottom currents assemblage	26.0
Coastal detritic assemblage	682.5
Shelf-edge detritic assemblage	17.8
Other habitats and assemblages	2.4

The first estimate of *P. oceanica* meadows surface area was produced by Astier and Tailliez (1984), on the basis of maps drawn up in the 1960s and 1970s by Augier and Boudouresque (1967, 1970a, 1970b, 1976); it was 345 ha. Belsher *et al.* (2005) did not indicate the surface area occupied by *P. oceanica*; on the basis of their map, we estimate it at 418 ha. The newly-produced map presented in this study indicates a surface area of 439 ha (Table III). It is however inappropriate to suggest that the *P. oceanica* surface area has increased since the 1960s-1970s.

The estimates made by Astier and Tailliez (1984) were in fact based on inaccurate maps: Augier and Boudouresque (1967, 1970a, 1970b, 1976) only had uncorrected aerial photographs at their disposal to estimate the location of shallow habitat boundaries; beyond 10-15 m depth, diving positioning remained rather imprecise. The ca. 21 ha increase in *P. oceanica* surface area between 1999 (map by Belsher *et al.*, 2005) and 2000 may be explained by the fact that Belsher *et al.* (2005) labelled 'Sublittoral reef with photophilous macroalgae with *Posidonia oceanica* seagrass meadow' and 'Coralligenous assemblage with patches of *Posidonia oceanica*' habitats as 'rocky substrate', thus underestimating the surface area of *P. oceanica*. This increase may also be explained by positioning inaccuracies; e.g. between Pointe du Nord and Pointe de la Grande Pierre (Fig. 11), the lower *P. oceanica* limit seems to have advanced by ca. 20 m (equivalent to a 1-ha surface area) from 1999 to 2010. Knowing the growth kinetics of deep plagiotropic rhizomes (1.7 to 4.2 cm/a; Mossé, 1984), such a progression is strictly impossible and can only be explained by a positioning error on the Belsher *et al.*'s (2005) map.

The surface area covered by *Posidonia oceanica* dead matte seems to have increased from 6.3 to 26.3 ha (Table III) since 1999 (Belsher *et al.*, 2005). This fact is actually misleading. Indeed, most dead matte is covered by a more or less thin layer of loose sediment. Belsher *et al.* (2005) produced a map that displays sediment types rather than habitats and assemblages and which, therefore, labelled the dead matte found in the centre of the bays of Port-Cros and Port-Man as 'sorted sands and silts' and '*Posidonia oceanica* seagrass meadow detritus (uprooted rhizomes and leaves)'. For the purpose of the present study, when previous maps or field observations reveal what lies below the layer of superficial sediment, the benthos is labelled as 'Dead matte of the seagrass *Posidonia oceanica*' or 'Dead matte partially covered with well-sorted fine sands'. *P. oceanica* matte is home to a unique assemblage (Harmelin, 1964; Pérès, 1967), whether covered by a thin layer of sand or not. It is possible that the surface area covered by dead matte remains underestimated, whether dead matte is of natural (hydrodynamics, construction-erosion cycles, autogenous intermattes; Boudouresque and Jeudy de Grissac, 1983; Boudouresque *et al.*, 2006, 2009) or of anthropogenic origin. As a matter of fact, dead matte is most probably present beneath a certain number of sectors mapped as 'Coarse sands and fine gravels under the influence of bottom currents', in the sublittoral zone. If the layer of sand is thin, 'Dead matte' should have been labelled; if, however, the layer is thick, then 'Coarse sands and fine gravels under the influence of bottom currents' is the correct labelling. Unfortunately, sediment layer thickness, which can only be determined through SCUBA diving operations, remains largely uninvestigated.

Main features of the mapped habitats and assemblages

The Lower midlittoral rock assemblage

The Lower midlittoral rock assemblage was not mapped for the purposes of this study. It makes up a littoral belt that, if projected vertically, has a width ranging from a few centimetres to just over a metre and therefore cannot appear at the scale of the maps produced. Here, we therefore consider maps produced in the 1960s-1970s (Augier and Boudouresque, 1967, 1970a, 1970b, 1976) and in the 1990s-2000s (Meinesz *et al.*, 2000a, 2000b, 2001b, 2001c, 2004; Cottalorda *et al.*, 2004).

In PCNP, the Lower midlittoral rock assemblage, distant from continental coastal sources of pollution, displays a remarkable ecological quality. The Rhodobionta *Lithophyllum byssoides*, is present all around PCNP in areas exposed to strong hydrodynamic conditions. In some places with dim light, it builds up rims usually known as 'trottoirs' which consist of a wide overhanging cornice with a flat upper surface ending in a salient rim with a vertical face (Pérès and Picard, 1964; Laborel, 1987; Relini *et al.*, 2009). The edification of this bioconstruction requires millennia, so that its destruction is irreversible at human scale. It has thus a very high heritage value (Laborel *et al.*, 1983; Boudouresque, 2004). The giant limpet *Patella ferruginea* (Mollusca) was considered extinct in PCNP and the continental coast of France (Laborel-Deguen and Laborel, 1991a). Reintroduction, using Corsican specimens, was attempted in PCNP around the Islet of Rascas (Laborel-Deguen, 1988; Laborel-Deguen and Laborel, 1991b). Systematic exploration of Port-Cros Islands revealed ten or so *P. ferruginea* individuals (Meinesz *et al.*, 2000a, 2000b, 2001b, 2001c, 2004; Cottalorda *et al.*, 2004). These are too sparse to reproduce given their narrow mobility range (Guerra-García *et al.*, 2004). They might be descendants of the small population reintroduced around Rascas Islet at the end of the 1980s. More probably, they come from Corsican larvae transported by currents. The Rhodobionta *Rissoella verruculosa* occurs as a continuous belt under exposed hydrodynamic conditions and is only interrupted in the innermost part of sheltered coves such as the bays of Port-Cros and Port-Man.

Lithophyllum byssoides and *Rissoella verruculosa* are appropriate indicators of good ecological surface water conditions in PCNP. Locally, nitrophilous Chlorobionta (*Ulva* spp., including enteromorpha-like *Ulva*) may indicate some pollution, though they can also characterize natural freshwater runoff; altogether, their very low abundance confirms the good ecological state of this assemblage (Meinesz *et al.*, 2000a, 2000b, 2001b, 2001c, 2004; Cottalorda *et al.*, 2004).

***Posidonia oceanica* seagrass meadows**

The *Posidonia oceanica* seagrass meadow is very extensive, from the sea surface (barrier-reef of the Bay of Port-Cros) down to 29-35 m depth. A 35-m maximum depth was recorded in the north of Bagaud Pass, at Cap du Tuff and at Pointe du Vaisseau. Several types of meadow described by Boudouresque *et al.* (1985a, 2006) were observed: the barrier-reef of the Bay of Port-Cros (Goujard *et al.*, 2010), the 'plain meadow' (West Bagaud, North and South zones), with locally some 'shifting intermattes' (Bagaud Pass and Anse des Gobis), and also the 'staircase meadow' found in Montremian. Another type of meadow, with ripple features, was described at depth in PCNP by Clairefond and Jeudy de Grissac (1979). Finally, *P. oceanica* may occur as a thin layer of rhizomes on a rock substrate and therefore becomes part of a mosaic with 'Sublittoral reef with photophilous macroalgae' or 'Coralligenous assemblage'. Locally, bio-concretions of Corallinales (mainly *Mesophyllum expansum*) are present as an understory on the rhizomes. The noble pen shell *Pinna nobilis* is relatively common in seagrass meadows, with an average density of 1.4 to 3.5 individuals/100 m² (Medioni and Charrier, 2001); this high density is explained by the prohibition of trawling, a fishing method that shatters the organism's shell. Density is however lower than that found in the Gargalu no-take and no-mooring zone of the Scandola Marine Protected Area (MPA) (Corsica; Garcia-March and Vicente, 2011) as anchoring is also responsible for breaking the shells (Vicente and Moreteau, 1991).

The 'Coarse sands and fine gravels under the influence of bottom currents' observed within *Posidonia oceanica* seagrass meadows (e.g. in the Tuff zone and between Espar Sud and Malalongue, Fig. 5 and 11) are probably of natural origin. These passes are indeed subjected to powerful currents. In the pass between Bagaud and Port-Cros, under certain wind conditions, the flow can reach 2 Mm³/h (Jeudy de Grissac, 1982). Numerous erosion channels, which fragment the *P. oceanica* meadow, are also of natural origin (Clairefond and Jeudy de Grissac, 1979). In the innermost part of La Palud (Fig. 3) and Port-Man (Fig. 4, 5) Bays, the presence of dead matte is due to the fact that the matte's ascent towards the sea surface has made it vulnerable to hydrodynamism; these dead mattes are therefore also of natural origin (Molinier and Picard, 1952; Augier and Boudouresque, 1967; Boudouresque *et al.*, 2006).

The vast expanse of dead matte found in the centre of Port-Man Bay is probably relatively ancient; radiocarbon dating of the matte's 'roof' indicates that the meadow's death occurred between 1530 and

1630 CE (CE = Common Era), presuming that no erosion of the dead matte took place (Boudouresque *et al.*, 1980). The cause of death (natural or human-induced) remains undetermined. Between the dead matte that occupies the centre of the Bay of Port-Man and the offshore Coastal detritic assemblage, Augier and Boudouresque (1970a) mapped a strip of live *P. oceanica*; only a few patches of *P. oceanica* are still surviving, the dead matte being now adjacent to the Coastal detritic assemblage (Fig. 5). Within the dead matte that occupies the centre of the Bay of Port-Man, Augier and Boudouresque (1970a) mapped patches of living *P. oceanica*; these patches are no longer present (Fig. 5).

In the Bay of Port-Cros, *P. oceanica* regression is undoubtedly of anthropogenic origin. The *P. oceanica* barrier-reef enabled Moliner and Picard (1952) to understand the construction mechanisms of this type of structure. Barrier-reefs are relatively rare in the Mediterranean, justifying their great heritage value (Boudouresque *et al.*, 1985b, 1990; Boudouresque, 2003; Boudouresque *et al.*, 2006). The surface area of the barrier-reef, at the beginning of the 20th century, was perhaps close to 6 000 m²; subsequently, it steadily declined to 4 500 m² (1968), 3 900 m² (1970-1975), 3 700 m² (1998) and 2 900 m² (2010), i.e. to ca. half of its initial surface area (Augier and Boudouresque, 1970b; Boudouresque *et al.*, 1975; Augier and Nieri, 1988; Goujard *et al.*, 2010); boat-induced erosion in very shallow waters may account for its decline and for the presence of extensive dead matte areas off the barrier-reef (Augier and Boudouresque, 1970b); overgrazing during outbreaks of the sea urchin *Paracentrotus lividus*, due to the overfishing of its predators (Sala *et al.*, 1998) must also have played its part. In the centre of Port-Cros Bay, ancient anchoring (by large warships dating back to the sailing navy era) and recent (recreational boating) explain the dead matte's presence (Fig. 11; Augier and Boudouresque, 1970b; Guérout, 1981; Robert, 1983). The enormous concrete block, in the pass between Port-Cros and Bagaud, used for the anchoring of large ships, is the cause of the presence of an important patch of dead matte (now buried beneath sediment). Outside of the bays of Port-Cros and Port-Man, the relatively rare (except during summer months) anchoring of small recreational boats (<10 m length) may have a lesser impact than traditionally admitted (Ganteaume *et al.*, 2005a; Boudouresque *et al.*, 2009; but see Francour *et al.*, 1999).

In the early 1970s, the lower limit of the *Posidonia oceanica* meadow ranged between (30) 34-36 (38) m depth (Harmelin, 1976; Harmelin and Laborel, 1976). According to Belsher *et al.* (2005), the lower meadow limit was mainly located between 30 and 33 m depth. Current observations show a lower limit located between 29 and 35 m depth, 2/3 of all values being between 31 and 33 m depth. Concrete

markers were laid down by Bonhomme *et al.* (2010a) in 2002 and 2006, at the lower limit of the meadow, 31-34 m depth. Shoot density, number of shoots within patches and cover dramatically declined between 2002 and 2008 (Bonhomme *et al.*, 2010a, 2010b). Therefore, a withdrawal of the lower limit, when compared to the 1970s, cannot be ruled out; the reliability of the 1970s depth gauges was not as poor as is often thought nowadays (Jean-Georges Harmelin *in* Bonhomme *et al.*, 2010a). In the north of the pass between Port-Cros and Bagaud, the lower limit mapped is clearly receding in comparison to Belsher *et al.*'s 2005 map, who described '*individus grêles et très dispersés*' (atrophied and very sparse *Posidonia* shoots), which represents a loss of ca. 1.5 ha.

Taking into account data from other sites in the Northwestern Mediterranean, Bonhomme *et al.* (2010a, 2010b) point to four possible main causes for the withdrawal of the lower limit of the *P. oceanica* meadow: **(i)** direct or indirect effects of the North Atlantic Oscillation (NAO), *via* e.g. rainfall, cloudiness, river discharge and plankton abundance; **(ii)** a rise in relative sea-level, resulting in a decrease of light availability at depth (see also Boudouresque *et al.*, 2009); **(iii)** a negative impact, at least at depth, of Sea Surface Temperature (SST) warming (see also Mayot *et al.*, 2005); and **(iv)** the presence of the introduced and invasive Chlorobionta *Caulerpa cylindracea*.

The invasive Chlorobionta *Caulerpa cylindracea* is abundant around PCNP and can be found in a wide range of habitats and assemblages. Within *P. oceanica* meadows, it is especially abundant around lower limits, in sparse meadows and on dead mattes. Outside of the lower limit, it has not been established that *C. taxifolia* and *C. cylindracea* are successful competitors against *P. oceanica* (Jaubert *et al.*, 1999; Boudouresque *et al.*, 2009; but see Molenaar *et al.*, 2005). On the other hand, it probably inflicts biological stress and oxidation damage upon the emblematic mollusc *Pinna nobilis*, similar to that observed when *P. oceanica* meadows are invaded by the Rhodobionta *Lophocladia lallemandii* (Box *et al.*, 2009).

The Sublittoral reef with photophilous macroalgae

The 'Sublittoral reef with photophilous macroalgae' assemblage is in a very good ecological state in PCNP. At its upper limit, i.e. within immediate proximity to the sea surface, an almost continuous belt of *Cystoseira amentacea* var. *stricta* is present (Meinesz *et al.*, 2000a, 2000b, 2001b, 2001c, 2004; Cottalorda *et al.*, 2004). Its presence and abundance indicate good surface water quality. In lower zones, a high specific diversity of 'macroalgae' can be observed e.g. *Cystoseira*

barbata, *C. brachycarpa* var. *balearica*, *C. compressa*, *C. elegans*, *C. spinosa*, *Sargassum vulgare*, *Dictyopteris polypodioides*, *Spatoglossum solieri*, *Dictyota* spp., *Padina pavonica*, *Chrysomenia ventricosa* and *Acetabularia acetabulum*. This assemblage harbours many Labridae (*Coris julis*, *Symphodus* spp., *Thalassoma pavo*) and Sparidae (*Diplodus* spp.). These are also major habitats for the brown meagre *Sciaena umbra* and the dusky grouper *Epinephelus marginatus* (Harmelin and Robert, 2001; Harmelin and Ruitton, 2007; Harmelin *et al.*, 2010).

In contrast with observations reported from other Mediterranean locations (Thibault *et al.*, 2005b), the Port-Cros populations of *Cystoseira* and *Sargassum* (Phaeophyceae) are still highly diversified and most of them seem stable since the 1970s, although some regression has been observed for *Cystoseira brachycarpa* var. *balearica* (Thibault *et al.*, 2005a, 2007) in many locations where the species was previously reported, forming large and dense populations down to 10 m depth (Augier and Boudouresque, 1967, 1970a; Coppejans and Boudouresque, 1975; Augier and Boudouresque, 1976). Overgrazing by sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) and fish (*Sarpa salpa*) might be involved in this loss.

The invasive Chlorobionta *Caulerpa cylindracea* is abundant at all depths in this assemblage, most particularly in Pointe de la Croix and Gabinière Island (Fig. 7). The Rhodobionta *Womersleyella setacea* and *Acrothamnion preissii*, two other invasive species, are also present though the former is less abundant than in the Coralligenous assemblage. These species probably have an impact on the structure (sedimentation), species diversity and food web of the ecosystem, as already established in other Western Mediterranean areas (Ceccherelli *et al.*, 2001; Piazzì and Cinelli, 2001; Piazzì *et al.*, 2001, 2003; Boudouresque *et al.*, 2005b).

The Coralligenous assemblage

The Coralligenous assemblage is a calcareous formation of biogenic origin produced by bioconstructing Rhodobionta growing in dim-light conditions and relatively calm waters, and resulting from the dynamic equilibrium between bioconstructors and biodestructors (Péres and Picard, 1964; Laborel, 1987; Boudouresque, 2004; Ballesteros, 2006; Relini *et al.*, 2009). In fact, the Coralligenous is not made up of only one assemblage (as, considered here), but of a group of closely related assemblages (Relini *et al.*, 2009). The Coralligenous in PCNP is located between 25 and 75-80 m depth; beyond, a progressive transition to the 'Shelf-edge rock assemblage' is observed. The Coralligenous assemblage found in PCNP is well representative of this habitat, as far as Provence is concerned; it is characterised by dense

and size-diversified populations of *Paramuricea clavata*, *Eunicella cavolini*, *E. singularis* (gorgonians), and by 'macroalgae' (e.g. *Cystoseira zosteroides*, *C. foeniculacea*, *C. funkii*, *C. jabukae*, *Sargassum* spp., *Phyllariopsis brevipes*). This is especially observed at Gabinière Island (west side, east side and Sec de la Gabinière), Pointe du Vaisseau, north and south extremities of Bagaud Island and Pointe de la Galère (Fig. 4, 5, 6). In addition to these coastal spots, the Coralligenous assemblage is present on numerous isolated reef banks within the Coastal detritic assemblage, which are distributed all around the island, especially off Pointe de Julien, Pointe du Cognet (Fig. 9) and the western shore of Bagaud (Fig. 10). On these banks, erect species (gorgonians and *Cystoseira* spp.) are less abundant than in coastal sites, leaving room for *Halimeda tuna*, *Flabellia petiolata*, *Codium effusum*, *Pseudochlorodesmis furcellata* and *Dictyopteris polypodioides*. A spectacular forest of *Cystoseira funkii* and *C. zosteroides* was however discovered at La Roche des Catalans (off the Espar Sud point, Bagaud Island) (Hereu et al., 2003).

To the south-east of Port-Cros Island, from Pointe du Vaisseau to Gabinière Islet, the top of the reef banks isolated within Coastal detritic are home to a spectacular Coralligenous assemblage with very large colonies of the gorgonian *Paramuricea clavata* which are often associated with an under-layer of the sponge *Aplysina cavernicola*. One of these banks, ca. 70 m depth, harbours several large individuals of the sponge *Spongia lamella*, which is rare in PCNP. At the base of these banks (from 75-80 to 90 m), a mosaic of Coralligenous and Shelf-edge rock assemblages is present, the latter progressively replacing the former as depth increases. Light becomes the limiting factor and 'macroalgae' progressively disappear, except the Chlorobionta *Palmophyllum crassum* and a few encrusting Corallinales, replaced by sponges (e.g. *Haliclona poecillastroides*, *H. mediterranea*, *Axinella verrucosa*, *A. damicornis*, *A. polypoides* and *Hexadella racovitzai*; Laborel et al., 1976; Bonhomme et al., 2011).

The invasive Rhodobionta *Womersleyella setacea* (often associated with another invasive Rhodobionta, *Acrothamnion preissii*) forms thick and continuous carpets over large areas of the Coralligenous. As for the Sublittoral reef with photophilous macroalgae, they probably have a high impact on species diversity, sedimentation and the food web (Piazzi et al., 2007). The invasive Chlorobionta *Caulerpa cylindracea* is also present, but to this day, its impact on the Coralligenous remains unproven in PCNP (Ruitton et al., 2009).

Mass mortality affected metazoans (e.g. gorgonians and sponges) in the shallowest PCNP's coralligenous sites during the 1999 and 2003 high temperature episodes along with extensive areas of the

Northwestern Mediterranean (Perez *et al.*, 2000; Garrabou *et al.*, 2001, 2002). The gorgonian *Eunicella singularis* was one of the most severely impacted species and has not recovered since 1999: very dense populations, once observed in 1998 at e.g. Pointe de la Croix (Fig. 8; Bonhomme *et al.*, 2000), have almost entirely disappeared.

The Semi-dark underwater cave assemblage

The assemblage of semi-dark underwater caves makes enclaves within hard substrate habitats, namely the Sublittoral reef with photophilous macroalgae, the Coralligenous assemblage and the Shelf-edge rock assemblage. It thrives under overhangs, in crevices and at the entrance of sea caves. It is characterized by dim-light conditions and by the absence of most suspension-feeders such as gorgonians; in contrast, filter-feeders are usually dominant (Pérès and Picard, 1964; Harmelin *et al.*, 1985; Bellan-Santini *et al.*, 1994).

The Semi-dark underwater cave assemblage of PCNP is mainly constituted by extensive carpets of *Parazoanthus axinellae*. It also harbours a variety of sessile sponges (e.g. *Agelas oroides*, *Aplysina cavernicola*, *Clathrina clathrus*, *Petrosia ficiformis*, *Oscarella* sp.), bryozoans (e.g. *Adeonella calveti*, *Myriapora truncata*, *Reteporella* sp., *Turbicellepora avicularis*) and cnidarians (e.g. *Caryophyllia inornata*, *Leptopsammia pruvoti*). The main vagile organisms are the crustaceans *Palinurus elephas*, *Scyllarides latus* (this species being relatively rare), *Scyllarus arctus* and the teleosts *Apogon imberbis*, *Conger conger*, *Muraena helena*, *Phycis phycis* and *Thorogobius ephippiatus*. A peculiarity of the Port-Cros Semi-dark underwater cave assemblage is the absence of *Corallium rubrum* (Harmelin, 1984); the only sighting of this species is localized 800 m off Pointe du Cagnet (Fig. 9), thus outside the 600-m offshore limit of the PCNP, at more than 60-m depth (Jean-Georges Harmelin, Jacques Laborel and Philippe Robert, unpublished data). Another distinctive feature of this habitat at Port-Cros is the absence or rarity of the sponge *Spongia officinalis* which, in contrast with most Mediterranean localities, inhabits in the Coralligenous assemblage (Vacelet, 1976; Harmelin *et al.*, 2003).

Semi-dark underwater caves constitute seascapes of high aesthetic value. They are therefore frequently visited by amateur SCUBA divers. Divers can severely damage fragile species such as bryozoans; in addition, bubbles can accumulate on the cave roof, resulting in a kind of emersion of the sessile biota. Finally, some species are vulnerable to high temperature episodes (e.g. *Agelas oroides*, *Aplysina cavernicola*, *Parazoanthus axinellae*, *Petrosia ficiformis*), such as the 1999 and 2003 abnormally warm episodes (Garrabou *et al.*, 2001; Cerrano *et al.*, 2006; Pérez, 2008).

The Coastal detritic assemblage

The Coastal detritic assemblage surrounds PCNP at depths of ca. 30 to 75 m. It is unimpacted by trawling, which has been banned since the foundation of the national Park in 1963, as it is highly destructive for fragile and calcified species; in addition, this assemblage is far enough from the mainland not to be impacted by terrigenous sediment deposition; this assemblage therefore displays a remarkable and exceptionally diverse physiognomy. It appears as a mosaic of a variety of patches, due to a spatial variation of dominant species, e.g. rhodolith stands (free living and rounded Corallinales such as *Lithophyllum racemus*, *Lithothamnion valens* and *L. fruticosum*), maerl (free-living and branched Corallinales such as *Lithothamnion corallioides* and *Phymatolithon calcareum*), free-living Peyssonneliaceae such as *Peyssonnelia rosa-marina*, stands of *Osmundaria volubilis*, stands of large bryozoans, etc. Patches of maerl were found south of Gabinière Island, whereas patches of Peyssonneliaceae and of rhodoliths were especially common in the vicinity of Bagaud Island. This variety of stands, which once must have been a dominant feature of Mediterranean Coastal detritic assemblage, can no longer be found in most coastal areas now exposed to intensive trawling. In addition to this variety of stands, the PCNP Coastal detritic assemblage is characterised by a very high specific diversity of non-calcified 'macroalgae', bryozoans, echinoderms and other metazoan taxa (Bourcier 1982, 1985, 1988; Laborel *et al.*, 1976).

The Coastal detritic assemblage, although not listed in the 1992 Habitats Directive, plays an important role in sublittoral and circalittoral ecosystems as it constitutes (i) shelter for numerous species, both residents (e.g. *Cystoseira zosteroides*, *C. foeniculacea*, *Carpomitra costata*, *Chrysomenia ventricosa*, *Osmundaria volubilis*, *Sebdenia dichotoma*, *Ulva olivascens*, large bryozoans such as *Pentapora fascialis*, the cnidarians *Pteroeides spinosum* and *Pennatula rubra*) and migrants (e.g. the spiny lobster *Palinurus elephas*) and (ii) spawning grounds for species that dwell in shallower waters (e.g. the teleosts *Spicara* spp. and *Sarpa salpa*; Harmelin and Harmelin-Vivien, 1976; Charbonnel and Bonhomme, 2002). When compared to observations in the 1970s, it seems that echinoderm abundance has conspicuously decreased.

Off La Gabinière Island, Pointe de la Croix and Pointe du Vaisseau, starting at 75 m depth, a transition zone between the Coastal detritic assemblage and the Shelf-edge detritic assemblage is observed, the latter progressively replacing the former with increasing depth (Fig. 6 and 7).

Ecological diagnosis

Habitat conservation state, which combines three criteria (conservation of spatial structure, conservation of ecological functions and restoration potential), was assessed for *Posidonia oceanica* seagrass meadows (Fig. 12) and Coralligenous assemblages (Fig. 13) in each of the 10 PCNP zones (Fig. 1).

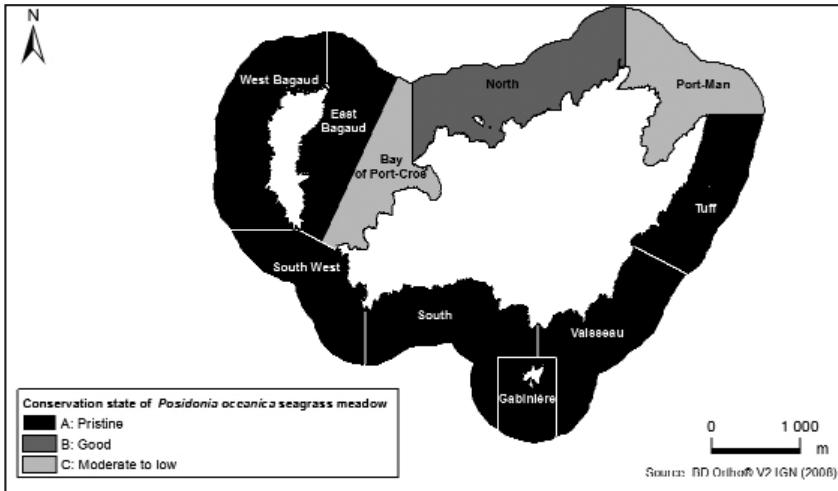


Figure 12. Conservation state of *Posidonia oceanica* seagrass meadows in each of the 10 PCNP zones (see Fig. 1).

Conservation state of *Posidonia oceanica* seagrass meadows is contrasted within the PCNP (Fig. 12). **(1)** It is pristine (A) in most of the area (West Bagaud, East Bagaud, South West, South, La Gabinière, Vaisseau and Tuff zones). **(2)** The conservation state is only good (B) for the North zone. The reasons for this rating are: **(i)** the regression of the lower limit of the meadow (Bonhomme *et al.*, 2010a, 2010b); **(ii)** the abundance of the invasive Chlorobionta *Caulerpa cylindracea* at depth; **(iii)** the presence in La Palud Bay of circular patches of dead matte probably caused by underwater explosions (illegal fishing with dynamite), in the 1940s-1950s; recolonisation has been excessively slow since 60-70 years after the event, it is still inconspicuous (Augier and Boudouresque, 1967; Boudouresque, 2003). In addition, dead matte conspicuously increased in surface area along a central axis in the Bay of La Palud since the first map was drawn up by Augier and Boudouresque (1967). **(3)** Finally the conservation state is moderate to low (C) for the zones that include the bays of Port-Cros and Port-Man. The reasons for this rating are: **(i)** the continuous regression of the barrier-reef of the Port-Cros Bay (Goujard *et al.*, 2010); **(ii)** the presence of a vast zone of dead matte in the central part of the Bay of Port-Man;

(iii) the expansion of this zone in all directions (eastwards, southwards and northwards), when compared to the Augier and Boudouresque (1970a) map; to the north, this zone is now adjacent to the Coastal detritic assemblage, due to the disappearance of a strip of *Posidonia oceanica* meadow. Recreational boating, either directly *via* anchoring or indirectly *via* generated pollution, might account for this regression.

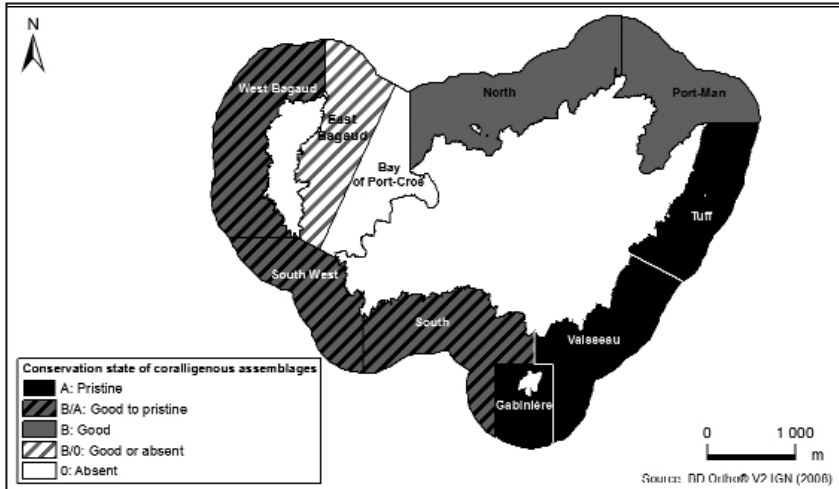


Figure 13. Conservation state of the Coralligenous assemblage in each of the 10 PCNP sectors (see Fig. 1).

Conservation state of the Coralligenous assemblage (Fig. 13) is **(1)** pristine (A) on the south-eastern shoreline of the island from Tuff to Gabinière. **(2)** The conservation state is good to pristine (B/A) in the South, South-West and West Bagaud zones. The teleost abundance and diversity appear to be lessened in comparison to the above mentioned zones. In addition, erect benthic species such as gorgonians and bryozoans are locally less developed. An increased fishing pressure (Bonhomme *et al.*, 2009), added to the impact of lost fishing nets (see Houard *et al.*, 2012) might explain this fact. **(3)** The conservation state is only good (B) in the Port-Man and North zones. These zones were severely impacted by the 1999 positive abnormally warm episode, resulting in mass mortalities of e.g. gorgonians and sponges (Perez *et al.*, 2000; Garrabou *et al.*, 2002; Lejeusne *et al.*, 2010). **(4)** Finally, the coralligenous assemblage is partly or completely absent from East Bagaud and Bay of Port-Cros zones.

Categorisation of conservation priorities

For each monitored main habitat and assemblage, a categorisation of conservation priorities was established (Tables IV through VII). The

strongest conservation priorities concern: **(i)** rhodoliths (free-living Corallinales, Rhodobionta) thriving in the Coastal detritic assemblage surrounding Bagaud; **(ii)** remarkable Coralligenous and Sublittoral reef with photophilous macroalgae assemblages (Gabinière, Pointe de la Croix, Pointe du Vaisseau, La roche des Catalans, Pointe du Cognet, Pointe de la Galère); and **(iii)** the *Posidonia oceanica* seagrass meadow of Port-Cros Bay (barrier-reef), Port-Man Bay, Bagaud Pass and La Palud Bay (population of *Pinna nobilis*).

Table IV. An overview of the conservation issues of *Posidonia oceanica* seagrass meadows.

Ecological interest per zone	Heritage value	Threats	Conservation priorities
Barrier-reef (Bay of Port-Cros)	Very high	High (anthropogenic impacts)	Very high
Meadows of the Bagaud Pass (East Bagaud and Bay of Port Cros)	High	High (anchoring)	High
Meadows and dead matte (Port Man)	High	Moderate (anchoring, contamination from recreational boating)	High
Lower limit (all zones)	High	Moderate (global warming ?)	High
Remarkable population of <i>Pinna nobilis</i> (Anse de La Palud, North)	High	None	Moderate

Table V. An overview of the conservation issues of the Sublittoral reef with photophilous macroalgae assemblage.

Ecological interest per zone	Heritage value	Threats	Conservation priorities
Remarkable habitat (Gabinière)	Very high	Moderate (SCUBA diving, invasive species - <i>Caulerpa cylindracea</i> , global warming)	High
Remarkable habitat (Vaisseau)	High	Moderate (SCUBA diving, invasive species - <i>Caulerpa cylindracea</i> , global warming)	High
Remarkable habitat (Pointe de la Galère, North)	High	Moderate (SCUBA diving, invasive species - <i>Caulerpa cylindracea</i> , global warming)	High
Remarkable habitat (Montremian, West Bagaud)	High	Low (SCUBA diving, global warming)	Moderate
Shallow <i>Cystoseira amentacea</i> var. <i>stricta</i> belt (all zones)	High	Low (surface water pollution, global warming)	Moderate

The overall state of conservation of the PCNP benthic habitats is still high, when compared to their mainland counterparts. However, if the present state of conservation of the PCNP habitats is compared with that described in previous studies, more or less conspicuous degradation is apparent. The most worrying issues are:

(1) The steady and alarming withdrawal of the *Posidonia oceanica* barrier-reef of the Port-Cros Bay, worsened by various past and present anthropogenic causes (Molinier and Picard, 1952; Augier and Boudouresque, 1970b; Boudouresque *et al.*, 1975; Augier and Niéri, 1988; Goujard *et al.*, 2010). The most worrying aspect is that the protective measures that were implemented, e.g. a line of buoys preventing boat access and mooring, and the construction of a sewage treatment plant to reduce pollution, do not seem to have slowed its withdrawal.

Table VI. An overview of the conservation issues of the Coralligenous assemblage.

Ecological interest per zone	Heritage value	Threats	Conservation priorities
Remarkable Coralligenous (Gabinère and Vaisseau)	Very high	Moderate (SCUBA diving, global warming)	High
<i>Cystoseira</i> spp. forest (La roche des Catalans, South West)	High	High (artisanal fishing)	High
Remarkable Coralligenous (Pointe de la Galère, North)	High	Moderate (SCUBA diving, global warming, artisanal fishing)	High
Deep Coralligenous and shelf edge rock assemblages (Vaisseau and Gabinère)	Very high	Low (artisanal fishing)	High
<i>Corallium rubrum</i> (800 m off Pointe du Cognet, South) ^a	Very high	None	High

^a Outside the 600-m PCNP limit.

Table VII. An overview of the conservation issues of the Coastal detritic assemblage.

Ecological interest per zone	Heritage value	Threats	Conservation priorities
Free-living Rhodobionta (South and South-West)	High	Moderate (artisanal fishing)	High
Free-living Rhodobionta (East Bagaud, Bay of Port-Cros)	High	Moderate (artisanal fishing, <i>Caulerpa cylindracea</i>)	High
Free-living Rhodobionta with maerl (Gabinère)	High	Low (artisanal fishing, <i>Caulerpa cylindracea</i>)	Moderate
Free-living <i>Peyssonnelia</i> spp. (West Bagaud)	Moderate	Low (artisanal fishing)	Low
Free-living <i>Peyssonnelia</i> spp. (North)	Moderate	Low (artisanal fishing, <i>Caulerpa cylindracea</i>)	Low

(2) The withdrawal of the lower limit of the *Posidonia oceanica* seagrass meadow (North, Tuff and Vaisseau zones), probably caused by phenomena more widespread than the scale of the park, such as climatic oscillations, global warming and sea-level rise (Boudouresque *et al.*, 2009; Bonhomme *et al.*, 2010).

(3) Anchoring pressure. Boat frequentation is relatively low in most of PCNP, so that the actual impact may be limited (Ganteaume *et al.*,

2005a; Boudouresque *et al.*, 2009). However, the Bays of Port-Cros and Port-Man are over-frequented; boats are an important source of pollution; where sediment deficits leave bare *Posidonia oceanica* rhizomes exposed and/or where the sediment is muddy, which is the case of Port-Cros Bay, the meadow is highly vulnerable to anchors; finally, damage caused by the anchoring of large boats (10-30 m and more) far exceeds that of smaller ones (Ganteaume *et al.*, 2005b). The concrete block in the pass between Port-Cros and Bagaud Islands, used for the mooring of large ships, still continues to impact the *P. oceanica* meadow, either directly by its erosive motion, or indirectly by the increased turbidity caused by sediment re-suspension.

(4) The recurrent mass mortality episodes which significantly affect the Sublittoral reef with photophilous macroalgae and the upper stratum of shallower Coralligenous assemblages (gorgonians, sponges, bryozoans) (Harmelin and Marinopoulos, 1994; Pérez, 2002; Harmelin and Garrabou, 2005). The frequency of these episodes seems to be on the increase in the Mediterranean (Lejeusne *et al.*, 2010).

(5) The omnipresence of *Caulerpa cylindracea* in all hard substrate habitats and assemblages, from the sea surface to depths of over 50 m. The medium and long-term consequences of the presence of this invasive species, added to that of *Womersleyella setacea* (also invasive) in the Sublittoral reef with photophilous macroalgae and the Coralligenous assemblages, could induce a dramatic change in the biodiversity, structure and functioning of these benthic ecosystems (Ruitton *et al.*, 2009).

On the other hand, some very positive features should be emphasised:

(1) The pressure of artisanal fishing is regulated within PCNP by the Fishing Charter that fishers must sign in order to be allowed to fish. The Charter establishes more restrictive limits than those imposed by the *prud'homie des pêcheurs* (fisher's guild) rules for maximum boat length, fishing-net length, mesh-size, soak-time, etc. These restrictions are coupled to the near-prohibition of amateur fishing, of which catches are known to be equivalent or higher than those of artisanal fishing (Combelles, 1991; Boudouresque *et al.*, 2005a; Cadiou *et al.*, 2009). As a result, CPUE (Catch per Unit Effort) is equivalent or higher than in non-protected areas and total catch per fisherman is compatible with cost-effective fishing, whilst also being compatible with teleost stock preservation and natural habitat heritage value preservation (Boudouresque *et al.*, 2004; Cadiou *et al.*, 2009). Nonetheless, it is crucial to bear in mind that this delicate equilibrium requires yearly monitoring and readjustments (Bonhomme *et al.*, 2009).

(2) Absence of trawling. This fishing method is nowadays considered to be one of the greatest causes of benthic habitat degradation. Over decades, trawlers have crushed the fragile species and bioconstructions of Coastal detritic assemblages, ploughed through and destroyed *Posidonia oceanica* seagrass meadows of which they are undoubtedly the greatest impactor and main cause of regression (Ramos-Esplá, 1984; Sanchez-Lizaso *et al.*, 1990; Pasqualini *et al.*, 2000; Ganteaume *et al.*, 2005b). Moreover, when considering the time it takes to return to average ecological state, after the impact has ceased (see Boudouresque and Verlaque, 2010), trawling is one of the worst types of impact and it may take up to 100 years for the ecosystem to recover (González-Correa *et al.*, 2005). It is the strict prohibition of trawling within PCNP that explains, at least partly, the exceptional state of conservation of Coastal detritic and Coralligenous assemblages together with *Posidonia oceanica* seagrass meadows. Although trawling within PCNP is not at all envisageable in the foreseeable future, it is important to emphasise the major contribution of this prohibition to the overall good state of preservation of Port-Cros habitats.

Conclusion

For almost a half century, Port-Cros national Park has truly been a natural laboratory. Hundreds of studies have been conducted in PCNP which have not only unveiled detailed knowledge about its ecology, habitat quality and distribution, but also enabled changes over time to be measured. In comparison to non-protected and/or non-managed areas in the Western Mediterranean which are exposed to high anthropogenic pressure (urbanisation, pollution, trawling, amateur or artisanal overfishing, anchoring of large vessels, etc.), PCNP has become a reference, a place to observe pristine habitats, for the purposes of science or recreation (e.g. SCUBA diving, snorkelling).

Detailed maps of benthic habitats and assemblages coupled to bathymetric data were produced for the purposes of this study. These maps, obtained by means of an Interferometric Multibeam Echo-Sounder and a Side-Scan Sonar, completed by SCUBA and ROV dives, are certainly the most accurate that have ever been made of PCNP. It would however be a mistake to presume that they contain no interpretational errors.

Comparison of the 2010 data with the 1960s-1970s maps and with Belsher *et al.*'s (2005) map, combined with all of the available data (populations, species, higher taxons, habitats or assemblages)

regarding PCNP, does not evidence major environmental degradation. The surface area covered by *Posidonia oceanica* has not diminished; it even seems to have increased, although this might be the result of previous map imprecisions. The meadow's ecological state is, as a whole, 'good' to 'very good', especially if natural phenomena such as hydrodynamic erosion are correctly not regarded as degradation. The large 'macroalgae' found in the Sublittoral reef with photophilous macroalgae and the Coralligenous assemblages are still present and abundant. The Coastal detritic assemblage in PCNP appears as it may once have been in the whole Mediterranean, before its fragile calcified and concreted species were crushed by trawling. Efficient artisanal fishery management has allowed economically-sound fishing and high stocks of teleosts to coexist. Populations of charismatic species, such as the dusky grouper *Epinephelus marginatus* and the brown meagre *Sciaena umbra*, are steadily increasing.

This picture would be untruthfully optimistic if negative issues were not mentioned. The Port-Cros Bay *P. oceanica* barrier-reef inexplicably continues to regress, as does the lower meadow limit. The latter regression may be explained by other than local environmental impact, possibly by climatic phenomena (North Atlantic Oscillation? Global warming?). A higher frequency of positive temperature anomalies linked to global warming has inflicted mass mortality episodes on some charismatic species such as the gorgonians. Several species of introduced 'macroalgae', which originate from the Indo-Pacific, are invading most habitats. Their primary introduction area may be located far from PCNP, but their range has subsequently increased; of course, they do not respect MPA (Marine Protected Area) boundaries. Their impact on ecosystem biodiversity, structure and functioning remains uncertain. The intensity of their impact may increase over time, so this must be monitored as it may be potentially dramatic in the long-run

To conclude, the results of this study reflect on the one hand the long-lasting success of the protection policies of PCNP's natural heritage, but on the other hand its vulnerability to globalised impacts.

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