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CHANGES IN INVERTEBRATE ASSEMBLAGES OF *POSIDONIA OCEANICA* BEDS FOLLOWING *CAULERPA TAXIFOLIA* INVASION

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MEDITERRANEAN SEA
CAULERPA TAXIFOLIA
INVERTEBRATES
POSIDONIA OCEANICA
INDICATOR SPECIES
INDVAL METHOD
TAXONOMIC SUFFICIENCY

ABSTRACT. – The abundance of the invertebrate fauna inhabiting a phanerogam bed of *Posidonia oceanica* was compared in *Caulerpa taxifolia* invaded and non-invaded patches in the North-Western Mediterranean in order to select the most sensitive taxonomic groups to *C. taxifolia* invasion. A total of 10452 individuals were counted in 36 samples of 0.142 m^2 each, on a sampling period spreading from November 1998 to September 1999. In agreement with the "taxonomic sufficiency" theory, only higher taxonomic groups were analyzed. The Indicator Value Analysis (*IndVal method*) highlighted that Anomura, Peracarida, Decapoda, Echinoidea, Bivalvia and Gastropoda are the groups most sensitive to *C. taxifolia* invasion. On the other hand, Ophiuroidea and, to a lesser extent, Holothuroidea were positively affected by *C. taxifolia* invasion. Our findings are consistent with the hypothesis that *C. taxifolia* negatively affects invertebrate fauna, strengthening the conclusions of previous studies. The increase in the siltation rate within invaded patches and the decrease in micro-habitat availability are likely to be the main factors explaining *C. taxifolia* invasion impacts on invertebrate fauna. Despite the extensive colonization of soft-sediments by *C. taxifolia* worldwide, these impacts have been largely ignored and a large-scale monitoring of the most sensitive groups needs to be carried out in the future.

INTRODUCTION

Biological invasions occur when species that are intentionally or accidentally introduced outside of their native or historical range successfully spread in their new environment (Galil 2008, Levine 2008). They currently represent a major threat to biodiversity world-wide. The introduced alga *Caulerpa taxifolia* (Vahl.) C. Agardh (Chlorophyta) has greatly expanded in the Mediterranean Sea since it was first observed near Monaco in 1984 (Meinesz & Hesse 1991): at the end of 2000, the whole area concerned (not covered) by *C. taxifolia* exceeded 13000 ha from Spain to Croatia and Tunisia (Meinesz *et al*. 2001), and reached 8610 ha in France at the end of 2007 (Cottalorda *et al*. 2008). Strefaris & Zenetos (2006) listed *C. taxifolia* as one of the 100 worst invasive alien species in the Mediterranean.

In the Mediterranean Sea, *C. taxifolia* has several biological characteristics which makes it an invading species likely to interfere with native communities and ecosystem functioning. *Caulerpa taxifolia* outcompetes the Mediterranean native algae and plants with larger and denser fronds (see review by Meinesz 2007). It forms permanent meadows and could therefore induce a long-term impact. *Caulerpa taxifolia* is not water-nutrient limited (Delgado *et al*. 1996) because, as other *Caulerpa* species, it is able to uptake ammonium from the sediments with the rhizoids (Williams 1984, Chisholm *et al*. 1996). Its dense vegetation (covering up to 100 % of the sea bottom; Meinesz *et al*. 1993) induces the sedimentation of mineral and organic particles trapped by the rhizoids, leading to the siltation of the invaded biotopes (Finzer & Poizat 1996). Finally, due to the secretion of toxic secondary metabolites, *C. taxifolia* spreading is hardly limited by native grazers or epiphytes (*e.g*. Guerriero *et al*. 1992, Lemée *et al*. 1993, Amade & Lemée 1998).

It has been shown that invasive plants change the functional composition of plant communities, and thus induce a decrease in the capacity of ecosystems to respond to changes or disturbances (see review by Olden *et al*. 2004). As plants represent most of the primary production and habitat structure, invasive plants can strongly alter the associated animal communities. This has been widely demonstrated in terrestrial ecosystems for birds, rodents, and invertebrates (e.g. Lambrinos 2000, Belnap & Phillips 2001, Toft *et al*. 2001, Banko *et al*. 2002).

Caulerpa taxifolia has a great negative impact on several Mediterranean assemblages: studies reported drastic decreases in the species richness of photophilic algal assemblages (Verlaque & Fritayre 1994), in fish abundance or behaviour (Francour *et al*. 1995, Harmelin-Vivien *et al*. 2001, Arigoni *et al*. 2002, Levi & Francour 2004, Longepierre *et al*. 2005) and in the sea urchin *Paracentrotus lividus* abundance (Ruitton & Boudouresque 1994).

Caulerpa taxifolia also impacts *Posidonia oceanica* (Linnaeus) Delile: when invaded by *C. taxifolia*, *P. oceanica* leaves decrease in length, and show chlorosis and necrosis or loss of their apex (De Villèle & Verlaque 1995, Dumay *et al*. 2002). Surprisingly, few studies have been undertaken to quantify the impact of *C. taxifolia* on invertebrate fauna (Bellan-Santini *et al*. 1996, Gribben & Wright 2006, Wright *et al*. 2007). Only one (Bellan-Santini *et al*. 1996), was performed in the Mediterranean sea, showing that the species richness and abundance of amphipods, polychaetes and molluscs decreased in a photophilic algal biocenosis invaded by *C. taxifolia*, but so far no data are available on the invertebrates inhabiting *C. taxifolia*-invaded *P. oceanica* seagrass beds. Klein and Verlaque (2008) highlighted a similar paucity of studies concerning *C. racemosa* in the Mediterranean sea.

Posidonia oceanica meadows form a complex habitat of primary importance for marine biodiversity due to the high number of species finding food and shelter there (Bianchi & Morri 2000). Consequently, *C. taxifolia* could represent not only a threat for *P. oceanica* habitat but also for the Mediterranean biodiversity. As a first consequence of *P. oceanica* bed invasion by *C. taxifolia*, we hypothesize a decrease in abundance of invertebrates. This study aims also to identify the most sensitive invertebrate taxa to *C. taxifolia* invasion in order to propose a regular monitoring of invertebrate biodiversity in invaded areas.

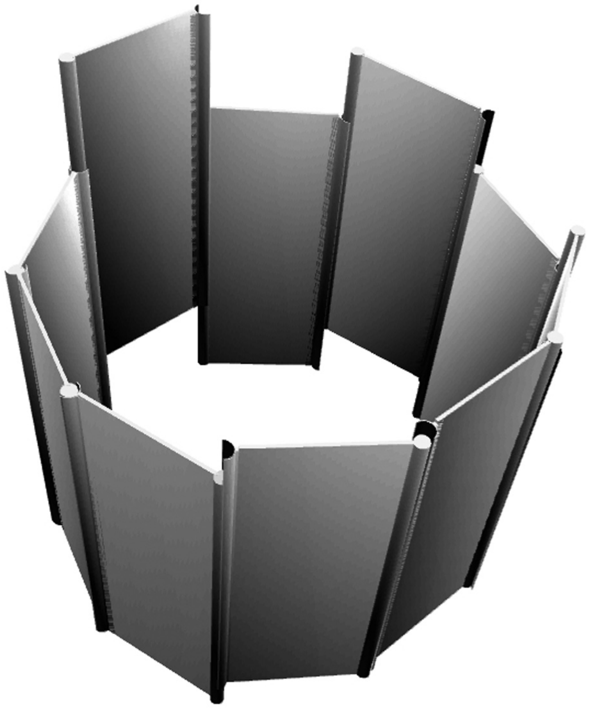

Fig. 1. – The 42.5 cm diameter corer with which samples were taken. The corer was built with twenty-two blades (7 cm wide, 50 cm long and 2 mm thick metallic blades), which were bevelled in order to facilitate their penetration in the seagrass bed matte. Each blade was vertically independent from the others in order to adjust the corer to the irregularly shaped sea bottom.

MATERIALS AND METHODS

Sampling was carried out in the north-western Mediterranean Sea, in a cove near Nice (Anse des Fosses, 43°41.3 N - 07°20.3 E, France) between November 1998 and September 1999. As the growth and toxicity of *C. taxifolia* vary greatly within a year (*e.g.* Amade & Lemée 1998, Thibaut *et al*. 2004), we sampled at two different periods: in spring (January to May, average water temperature 13.3 °C) when *C. taxifolia* fronds measure < 30 cm long and fall (September to December, average water temperature 20.1 °C) when *C. taxifolia* fronds reach their maximum growth, up to 60 cm long.

The study site was characterised by *P. oceanica* beds. *Caulerpa taxifolia* was first observed in this area in 1992 and six years later (1998-1999; sampling period) was patchily distributed, occurring intermingled with uninvaded habitats, in the prior-to-invasion homogeneous, high-density *P. oceanica* beds. No study concerning the spatial distribution of invertebrates was performed in the area prior to *C. taxifolia* invasion, but we assume that no high variability is expected within an homogeneous, high-density *P. oceanica* bed.

Over the study period, a sample/date was randomly collected in eighteen intermingling patches of invaded bed (584 ± 34 *Posidonia* shoots.m^{-2}; 284 ± 23 *Caulerpa* dw g.m^{-2}) and in eighteen uninvaded *P. oceanica* beds (667 ± 39 *Posidonia* shoots.m^{-2}) in an area less than ~100 x 100 m to reduce the potential for confounding spatial effect.

Each sample consisted of a 42.5 cm diameter corer (0.142 m^2, Fig. 1) collected by SCUBA divers, haphazardly positioned between 3.0 and 5.3 m deep (3.7 m on average). After setting the corer, all material contained inside was uprooted by hand and sucked up using a self-contained diver-operated suction dredge with a 3 m long, 10 cm diameter PVC pipe. A 1 mm-mesh nylon net was attached at the other end of the pipe to select the minimal size of the animals sampled. Vagile and substrate-dwelling fauna > 1 mm were thus sampled, together with *C. taxifolia* and *P. oceanica* present in the corer.

Sampling, sorting and identification of all invertebrates is extremely time consuming and is not suitable for regular monitoring: it was therefore decided to sort only the major groups, following recent theories in taxonomic sufficiency highlighting that the species-level analysis is generally not necessary for assessing impacts (Dauvin *et al*. 2003, Dethier and Schoch 2006). All the collected living organisms belonging to crustaceans, molluscs, polychaetes and echinoderms were separated in the laboratory using a stereo microscope.

A PERMANOVA and a Principal Coordinated Ordination (PCO) on Bray-Curtis similarity matrix was conducted using Primer 6 & PERMANOVA+ β17 software (Clark & Gorley 2006), in order to detect significant differences in the invertebrate assemblages as a function of the orthogonal factors Invasion (non-invaded or invaded) and Sampling period (spring or fall); the data matrix was standardized (standardisation by total for each species was used, *i.e.* each abundance value of a spe-

Table I. – Results of the PERMANOVA analysis on Bray-Curtis similarity matrix conducted in order to detect significant differences in the invertebrate assemblages according to the orthogonal factors Invasion (non-invaded *vs*. invaded) and Season (spring or fall).

Source of variation	d.f.	Sum of Squares	Mean Square	Pseudo-F	P(perm)	Number of unique permutations
Season	1	1500.60	1500.60	1.72	0.15	9942
Invasion status	1	6748.70	6748.70	7.72	0.00	9943
Season x Status	1	1109.10	1109.10	1.27	0.26	9942
Residual	32	27966.00	873.92			
Total	35	37324.00				

cies was divided by the total abundance of this species) prior to these analyses, because of large differences in abundance between groups.

In order to determine the sensitivity of sampled invertebrates to the *C. taxifolia* invasion, we applied the *IndVal* method described by Dufrêne and Legendre (1997) as Indicator Species. According to Mouillot *et al*. (2002), this method can be applied to various taxonomical levels, although it was first used at the species level.

IndVal is calculated for each taxonomical level *j* and for each bed *k* according to the formula:

$$IndVal_{kj} = A_{kj} \times B_{kj}$$

where A_{kj} is a measure of specificity, and B_{kj} a measure of fidelity which are calculated as follows :

$$A_{kj} = Nind_{kj} / Nind_{+j}$$

($Nind_{kj}$ is the mean abundance for group *j* in bed *k* and $Nind_{+j}$ is the sum of the mean abundance of species *j* in every bed)

$$B_{kj} = Nsites_{kj} / Nites_{k+}$$

($Nsites_{kj}$ is the number of sites in bed *k* where species *j* is present, and $Nsites_{k+}$ is the total number of sampled sites in bed *k*)

The largest value of *IndVal* observed over the two beds (invaded or not) for a taxonomical level *j* is $IndVal_j$= Max($IndVal_{kj}$). Random permutation tests were carried out, in order to evaluate the significativity of $IndVal_{j.}$ Calculation of *IndVal* values and associated tests were performed using labdsv package for R statistical software (R Development Core Team, 2008; Roberts, 2007); 10 000 iterations were performed.

RESULTS

Abundance

We counted 1824 crustacean individuals among which 633 Peracaridea and 1191 Decapoda, including 134 Brachyura, 626 Natantia, and 420 Anomura; 1451 polychaetes, including 850 sedentary and 601 errant; 6914 mollusc, including 5937 Gastropoda, 845 Bivalvia, and 131 Polyplacophora; and 263 Echinodermata, including 111 Holothuroidea, 125 Ophiuroidea and 27 Echiniodea.

According to PERMANOVA results, the invertebrate assemblages were significantly different in invaded and

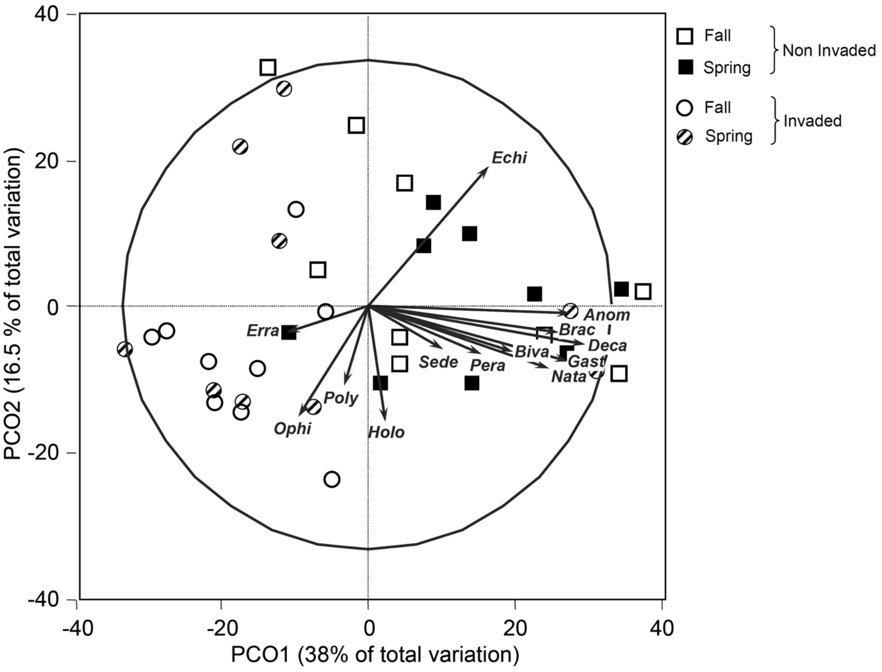

Fig. 2. – Biplot diagram of PCO conducted on abundance data. Taxonomic group codes refer to the first four letters of the considered group.

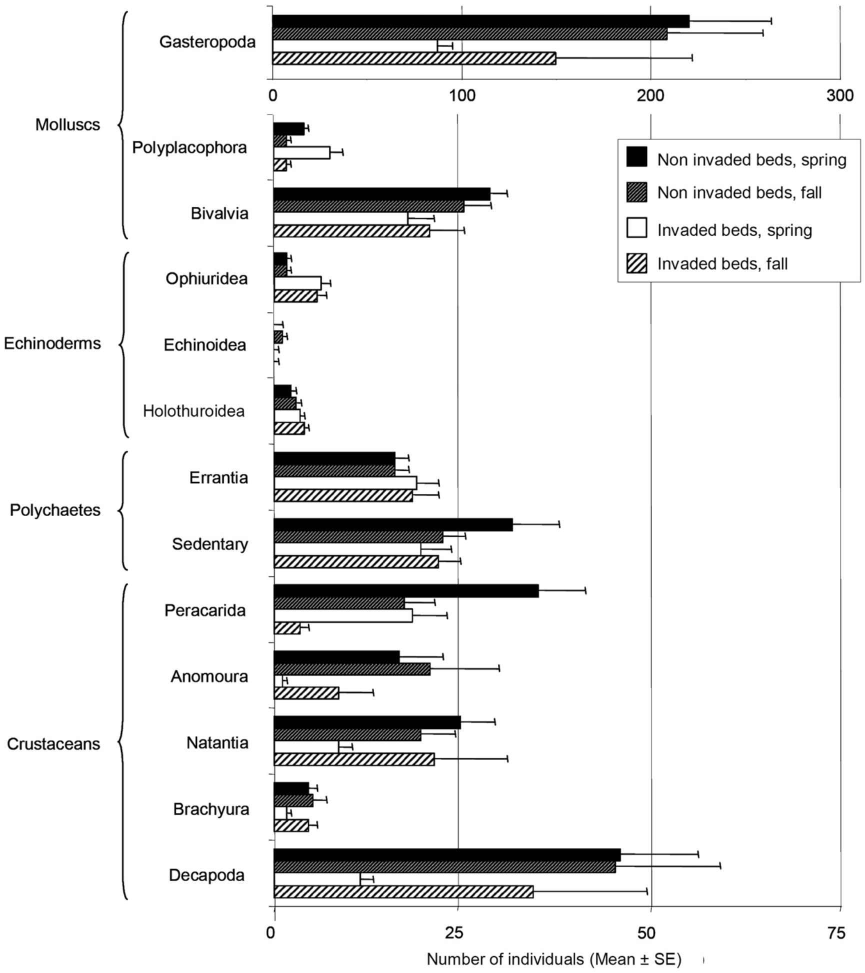

Fig. 3. – Number of individual (average ± S.E.) of the 13 taxonomic groups studied for the surface sampled within the corer (0.142 m^2).

Table II. – Results of indicator species analysis for both invaded or non-invaded beds. Bold denotes significance at $p < 0.05$.

	Taxonomic groups	Bed status	Observed Indicator Value	Associated *p*
Crustaceans	**Anomura**	Non invaded	**0.797**	**0.001**
	Peracarida	Non invaded	**0.707**	**0.004**
	Decapoda	Non invaded	**0.666**	**0.043**
	Natantia	Non invaded	0.598	0.237
	Brachyura	Non invaded	**0.581**	0.085
Echinoderms	**Echinoidea**	Non invaded	**0.453**	**0.049**
	Ophiuroidea	Invaded	**0.785**	**0.000**
	Holothuroidea	Invaded	**0.580**	**0.062**
Mollusks	**Bivalvia**	Non invaded	**0.584**	**0.025**
	Gasteropoda	Non invaded	**0.645**	**0.040**
	Polyplacophora	Invaded	0.429	0.871
Polychaetes	Sedentary	Non invaded	0.569	0.102
	Errantia	Invaded	0.539	0.244

in non-invaded bed (F = 7.72; p = 0.001; Table I). Neither the season (F = 1.72; p = 0.152) nor the interaction between season and invasion status (F = 1.27; p = 0.263) were statistically significant (Table I). The PCO conducted on invertebrate groups abundances allowed us to distinguish between invaded and non invaded *P. oceanica* beds (Fig. 2). Both Axis 1 (38 % of total variation), and to a lesser extent also Axis 2 (16.5 % of total variation), contributed to the separation of these two groups. The non-invaded bed samples were characterised by Anomoura, Brachyura, Deacapoda, and Gasteropoda, whereas the invaded samples were characterised by Errantia and Ophiuroidea. Invaded samples correlated with Axis 2 are different from other samples because characterised by slightly higher abundances of Holothuroidea.

The total abundance of organisms was lower in invaded beds (1742 ± 361 ind.m^{-2}) than in non-invaded beds (2886 ± 331 ind.m^{-2}). The total abundance of crustaceans (especially Decapoda, Anomura, and Peracaridea) was lower in the invaded bed (Fig. 3). Also the total abundance of molluscs (mainly Bivalvia and Gastropoda) was lower in the invaded bed (Fig. 3). Showing an opposite pattern, the total abundance of echinoderms was significantly higher in the invaded bed (Fig. 3), with contrasting patterns for Ophiuroidea (more abundant in the the invaded bed) and Echinoidea (more abundant in the non-invaded bed). Seasonal variation, although not significant in the PERMANOVA (Table I), seems to induce changes in some groups as Peracaridea crustaceans and Polyplacophora molluscs (Fig. 3).

The application of *IndVal* (Indicator Species Analysis) highlighted that a majority of taxonomic groups of invertebrates (Anomoura, Peracarida, and Decapoda for Crustaceans, Echinoidea for Echinoderms, Bivalvia and Gasteropoda for Mollucs) were indicators of non-invaded beds (Table II), whereas only 2 groups of Echinoderms (Ophiuroidea and Holothuroidea at $p = 0.062$) were indicator of invaded beds. Five of the 13 invertebrate groups considered (including Brachyura, Natantia, Polyplacophora and the two Polychaetes groups) cannot be considered as indicators of *C. taxifolia* invasion.

DISCUSSION

As predicted, and in agreement with a previous study (Bellan-Santini *et al.* 1996), invertebrate abundance was lower in the *C. taxifolia* invaded *P. oceanica* bed. Eight out of the 13 groups considered turned out to be indicators of invasion, being more abundant in, alternatively, invaded or non-invaded bed.

Crustaceans

Our results showed a negative impact of *C. taxifolia* invasion on the abundance of crustaceans except for Natantia, that were not significantly affected by *C. taxifolia,* most probably because they are mobile species living in the foliar strata. On the contrary, Anomura mainly include species which move on the substrate and between *P. oceanica* leaves. The presence of inextricable tangle of *C. taxifolia* stolons (Thibaut *et al.* 2004) must hinder their locomotion or, at least, reduce the space available to move as hypothetized by Sanchez-Moyano *et al.* (2001) within a *C. prolifera* meadow.

The results for Brachyura are more contrasted. The PCO analysis showed a correlation with non invaded bed but *IndVal* indicator did not show significant results ($p = 0.085$). The strong seasonal variations in Brachyura assemblages could explain these contrasted results, as much as their different preferred habitats (from substrate level to foliar strata).

Amphipoda and Isopoda, the two main groups of Peracaridea, are small herbivorous crustaceans which are suspension feeders, scavengers and/or grazers of the microflora growing on *P. oceanica* leaves. The decrease in the Peracaridea abundance highlighted is in agreement with the reduced biodiversity of amphipods recorded by Bellan-Santini *et al.* (1996) in invaded macroalgal communities. This general pattern may be due to a combination of factors including i) the reduced abundance of microalgae (Lemée *et al.* 1997), on which they partly feed, ii) the concentration of repellent *C. taxifolia* secondary metabolistes (caulerpenyn) and/or repellent phenolic compounds produced in excess by *P. oceanica* in the neighbourhood of *C. taxifolia* (Dumay *et al.* 2004); iii) siltation of sediments and iv) decrease in *P. oceanica* leaf density and biomass.

Molluscs

The majority of molluscs living in the *Posidonia oceanica* bed seems to be negatively affected by *C. taxifolia* invasion (except for Polyplacophora), as also reported by Bellan-Santini *et al.* (1996) in Mediterranean macroalgal communities and by Wright *et al.* in Australia. In the studied *P. oceanica* beds, both Gasteropoda and Bivalvia were indicator taxa of non-invaded bed. As highlighted by Gribben & Wright (2006) for native bivalves *Anadara trapezia* in Australian estuaries invaded by *C. taxifolia*, the reproduction of this organisms may be involved in the negative impact of *C. taxifolia* invasion.

Polychaetes

A previous study carried out in a photophilic alga biocenosis, found that polychaete abundances decreased after invasion by *C. taxifolia* (Bellan-Santini *et al.* 1996).To the contrary, this study found that the abundance of polychaetes did not significantly differ between invaded and non-invaded *P. oceanica* beds. Most of the polychaetes sampled inhabit the substrate surface between *P. oceanica* scales, in the first centimeters of sediment and into the available spaces between the rhizomes of *P. oceanica*. *Caulerpa taxifolia* induces siltation and may transform the substrate into an anoxic environment in the long-term (Finzer & Poizat 1996). Most polychaetes are sensitive to low oxygen concentration in the sediment, and become rarer in the deep layers of the substrate (e.g. Gambi *et al.* 1998). In our study, errant polychaete abundance was associated with the invaded beds in the PCO but the *IndVal* did not show significant result. These unbalanced results trigger that some polychaete species may be more adapted to the new habitat created by *C. taxifolia* and that a species-level study may be needed in order to assess *C. taxifolia* invasion effect on this group.

Echinodermata

Echinodermata was the only taxonomic group for which abundance was higher in the invaded bed. This was probably linked to the habitat preference of Ophiuroidea and of Holothuroidea, mostly detritivorous organisms preferring the presence of muddy substrate (Coulon & Jangoux 1993). On the contrary, Echinoidea, scarcely represented in our study, is an indicator group of non-invaded beds. In fact, the commonest species of Echinoidea in the studied region, *Paracentrotus lividus*, is known to be a herbivore feeding preferentially on macroalgae, but selectively avoiding *C. taxifolia* (Ganteaume *et al.* 1998).

Invertebrate groups sensitive to C. taxifolia *invasion*

In our study, the results of the multivariate analysis (PCO and PERMANOVA) were coherent with those of *Indicator Values* analysis. Anomoura, Peracarida, Decapoda, Echinoidea, Bivalvia and Gasteropoda, being indicator groups of *P. oceanica* non invaded bed, are likely to be negatively impacted by *C. taxifolia* invasion. On the contrary, Ophiuroidea and Holothuroidea (two of the Echinodermata taxa) as indicators of invaded beds are likely to be positively impacted by invasion. Echinodermata seems to be a particularly informative and sensitive group: relative abundance of Echinoidea and Ophiuroidea vary greatly from non-invaded to invaded bed.

Marine invasive species are considered to be one of the greatest threats to native marine biodiversity and resource values of the world's oceans (see review by Schafflelke *et al.* 2006). They often have strong negative effects on native species (Olden *et al.* 2004). Macroalgae are considered to be especially threatening non-indigenous marine species as they may alter both ecosystem structure and functioning by monopolizing space and changing both the habitat structure and the food webs (Schafflelke *et al.* 2006, Meinesz 2007). However, habitat-forming marine invasive species that form aggregations or dense mats often have positive effects on native biota, facilitating recruitment (see Crooks 2002 for a review). The positive effects of habitat forming invasive species are then related to added habitat complexity favouring recruitment and/or providing refuge from predation (Crooks 2002). Clearly, *C. taxifolia* spreading on an unvegetated substrate will increase complexity and provide shelters for recruits (Harmelin-Vivien *et al.* 2001). However, a similar spreading of *C. taxifolia* within a *P. oceanica* bed will not increase complexity but involve an abiotic homogeneization (Harmelin-Vivien *et al.* 2001). The high specific richness reported within *P. oceanica* beds is related to the diversity of available micro-habitats: leaves, rhizomes, space between them, upper layer of soft sediment trapped between rhizomes (e.g. Francour 1997, Guidetti 2000). The first stage of a seagrass bed invasion by *C. taxifolia* consists of a spreading of stolons within the space available between rhizomes. Then, the vertical growth of *C. taxifolia* will expand to the foliar strata (Molenaar *et al.* 2009). Both stages involve a homogeneisation of micro-habitats and, consequently, a decrease in habitat complexity. As hypothezised by Bartholomew (2002), the inter-structural spaces within the habitat (*i.e.* the space between rhizomes for *P. oceanica*) could limit invertebrates to use such habitats as refuges. At the same time, the development of a thick layer of *C. taxifolia* stolons at the substrate level leads to the siltation of sediment.

In a native *C. taxifolia* meadow (Indian Ocean), Sarma (1974) stated that 'the period of high faunal density coincided with degeneration and decline of algae'. Our findings are consistent with the hypothesis that *C. taxifolia* negatively affects native invertebrate fauna and therefore corroborate the conclusions of the few previous studies (Bellan-Santini 1996, Gribben & Wright 2006, Wright *et al.* 2007). Six years after the *C. taxifolia* invasion, changes in the composition and structure of invertebrate assemblages are recorded in invaded and non-invaded patches of *P. oceanica* beds. Only two groups of Echinodermata, are favoured by *C. taxifolia* invasion of *P. oceanica* beds: Ophiuroidea and, to a lesser extent, Holothuroidea. The increase in siltation and the change in sediment composition are possible explanations for the observed pattern, in agreement with the general ecological traits of these two groups. All the other sensitive groups may be negatively impacted by the decrease in micro-habitat diversity or availability. Even if analyses were done at higher taxonomic levels, the proportion of positively *vs* negatively impacted groups can be related to McKinney and Lockwood (1999) statement: 'Emerging evidence shows that most species are declining as a result of human activies (losers) and are being remplaced by a much smaller number of expanding species (winners)'. Although in our case, the positively impacted groups are not introduced, this statement applies also.

The present study simply describes differences in space with consistent lower abundance for sensitive groups. Sampling has to be carried now on beds invaded by *C. taxifolia* for a longer period of time and at several sites in order to confirm the trends highlighted in this study. However, to avoid time consuming identification of invertebrates at species level, the future studies, with a more complete design, could focus only on some sensitive systematic groups identified in this preliminary study, as, in example, Peracarida, Echinoidea and Anomoura.

The implications of these findings are that the ongoing spreading of *C. taxifolia* within or close to *P. oceanica* beds, as reported by Meinesz *et al*. (2001), will likely result in a change in associated native invertebrate fauna species composition and in a reduction in invertebrate abundance similar to that documented elsewhere (Bellan-Santini *et al*. 1996, Wright *et al*. 2007). The invertebrate fauna of *P. oceanica* beds is diverse and represent a key trophic level on which commercial and recreational fish species depend (Bell & Harmelin-Vivien 1983, Guidetti 2000). Despite the extensive colonisation of soft-sediments and seagrasses beds by *C. taxifolia* worldwide, impacts on fauna have been largely ignored (Wright *et al*. 2007): large-scale and long-term monitoring of invertebrate fauna has to be carried out to assess the consequences of *C.taxifolia* invasion.

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