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H. Jimenez[a,*], P. Dumas[a], L. Bigot[b], J. Ferraris[c]

[a] Institut de Recherche pour le Développement, IRD, UMR ENTROPIE, Laboratoire d'Excellence LabEx CORAIL, 101 Promenade Roger Laroque, BP A5, 98848 Nouméa, New Caledonia
[b] Université de La Réunion, UMR ENTROPIE, Laboratoire d'Excellence LabEx CORAIL, Avenue René Cassin, BP 7151, 97715 Saint Denis Cedex, France
[c] Institut de Recherche pour le Développement, IRD, UMR ENTROPIE, Laboratoire d'Excellence LabEx CORAIL, Observatoire Océanologique de Banyuls, 66650 Banyuls-sur-Mer, France

ABSTRACT

Despite the importance of invertebrate resources for Pacific coral reef islands, few studies have specifically addressed the effects of harvesting on invertebrate assemblages including targeted and non-targeted species. The impacts of recreational harvesting on reef and seagrass invertebrate assemblages in New Caledonia (South Pacific) are investigated by comparing communities in non-MPA and MPA areas. Sampling was done using a standard core method on seagrasses and by visual survey along belt transects on reefs. A total of 371 species were recorded, 174 on seagrasses and 254 on reefs, with 57 common species. Reef and seagrass invertebrate communities were very different in MPA and non-MPA areas. On both habitats, MPAs were identified as undisturbed areas while non-MPAs were defined as moderately disturbed with a predominance of small-sized and opportunistic species. Fishing not only affects target species but also non-target species through secondary effects. These results highlight the necessity of a community based approach for the conservation of resources in tropical poorly known environments.

1. Introduction

Marine ecosystems are subjected to increasing anthropogenic activities which disrupt their functioning, particularly in coastal areas (Suchanek, 1994; Fraschetti et al., 2001; Jackson et al., 2001). Among these activities, invertebrate harvesting during low tides is considered as an important cause of disturbance to intertidal communities (Moreno et al., 1984; Castilla and Duran, 1985; Duran and Castilla, 1989; Keough et al., 1993; Rius et al., 2006). This activity has been practiced by coastal inhabitants for centuries (e.g., Swadling, 1976; Hockey, 1988; Siegfried et al., 1994; Griffiths and Branch, 1997; Castilla, 1999) and still remain common today. In most Pacific islands for example, invertebrate resources represent a large part of local consumption and/or cash income (e.g., Dalzell et al., 1996; Kinch, 2003).

The effects of collecting intertidal resources have been described in several studies, from South America (e.g., Moreno et al., 1984; Castilla and Duran, 1985; Ortega, 1987; Defeo and Alava, 1995; Pombo and Escofet, 1996; Brazeiro and Defeo, 1999), to South Africa (e.g., Hockey and Bosman, 1986; Lasiak and Field, 1995; Griffiths and Branch, 1997), and Australia (e.g., Catterall and Poiner, 1987; Underwood and Kennelly, 1990; Kingsford et al., 1991; Sharpe et al., 1998). Generally reported effects include a decrease in targeted species density, generally up to 90% (e.g., Castilla and Duran, 1985; Siegfried et al., 1994; Roy et al., 2003), a decrease in total density and biomass (e.g., Wynberg and Branch, 1994; Lasiak and Field, 1995; Griffiths and Branch, 1997; deBoer and Prins, 2002), and a 10–20% decrease in mean size (e.g., Moreno et al., 1984; Hockey and Bosman, 1986; Ortega, 1987) due to the preference for collecting larger individuals. In terms of community composition, studies have reported a predominance of rapidly growing, low biomass, opportunistic species in exploited areas compared to non-exploited areas (e.g., Marine Protected Areas, MPAs thereafter), which are preferentially dominated by slow-growing, large-biomass, 'conservative' species present in low density (Lasiak and Field, 1995; deBoer and Prins, 2002). Harvesting can also alter the variability of invertebrate assemblages, through changes in the population structure of individual species or changes in the succession of species (Chapman et al., 1995). This consequently increases the dissimilarity among samples in exploited areas (Warwick and Clarke, 1993).

Coral reefs are highly diversified environments where few studies have addressed harvesting activity effects (Newton et al., 1993; deBoer and Prins, 2002; Rius et al., 2006). However, the poor

* Corresponding author. Present address: Smithsonian Environmental Research Center, 3150 Paradise Drive, Tiburon, CA 94920, United States. Tel.: +1 415 435 7128.
E-mail address: haizea.jimenez@gmail.com (H. Jimenez).

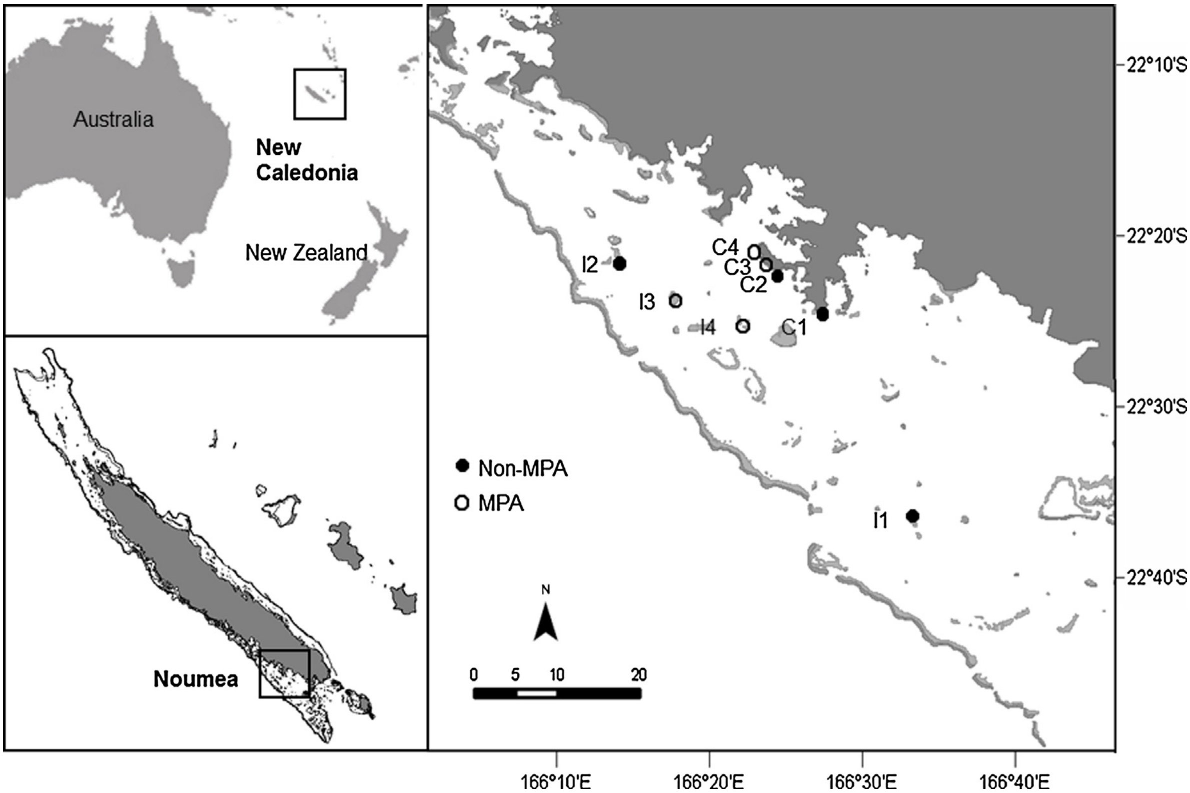

Fig. 1. Map showing the position of eight sampling stations located around Nouméa, New Caledonia, South Pacific. Coastal (C1, C2, C3, C4) and islet (I1, I2, I3, I4) flats are shown with MPAs (●) and non-MPAs (○) indicated.

knowledge of these activities (Dalzell et al., 1996), and the lack of invertebrate assemblage descriptions in tropical areas (e.g. Stella et al., 2011), represent a challenge, particularly when the effects of fishing are studied for the whole community, including both targeted and non-targeted species. Like most Pacific islands, New Caledonia is facing rising fishing pressure; intertidal shores close to the urban areas are increasingly subjected to recreational and subsistence harvesting (Jimenez et al., 2010, 2011).

This study aims to understand how harvesting activities affect reef and seagrass assemblages in New Caledonia by comparing community composition between MPA and non-MPA areas.

2. Materials and methods

2.1. Study site and sampling design

This study was carried out in New Caledonia, a large island located in the southwest Pacific (166° E, 22° S). New Caledonia is characterized by a large lagoon covering an area of 19 000 km^2, with numerous patches, islets and fringing reefs. Climate is defined as subtropical to temperate with a warm and wet season from mid-November to mid-April (called "summer"), and a cool and dry season from mid-May to mid-September (called "winter") (Météo France, 2007). Coastal and islet reef flats have been subjected to human exploitation for centuries and fishing pressure increased in the recent decades due to the growing urbanization around Nouméa city (Fig. 1). In 2009, human frequentation on reef flats was estimated to about 10 000 visitors, with an annual harvesting pressure of 8.4 ± 0.7 tons of invertebrates for an area of 324 Ha (see Jimenez et al., 2011). Collecting activity is essentially recreational and non-commercial (Baron and Clavier, 1992). Several protected areas (hereafter MPAs) were implemented in the 1990s to conserve local biodiversity and to sustainably manage marine resources. All fishing or harvesting activity is prohibited in these areas. The MPAs are mainly located in the southwest lagoon around Nouméa (cf. Fig. 1). These protected areas were initially chosen without a priori high diversity criteria. Collecting activities are strictly prohibited, regulated by local authorities and stakeholders.

Eight coastal (C_1, C_2, C_3, C_4) and islet (I_1, I_2, I_3, I_4) intertidal stations were selected in the southwest lagoon around Nouméa (Fig. 1, Table 1). Four stations were areas visited by invertebrate harvesters (non-MPAs) while the other four stations were closed to fishing (MPAs). For non-MPAs, the annual harvesting pressure was estimated by visual censuses of harvesters and interviews (see Jimenez et al., 2011) (Table 1). All stations are subject to semi-diurnal tides with a maximum amplitude of 1.8 m and oriented in front of a general hydrodynamic flow (from southwest to northeast). Two habitats were considered i.e., soft (sand/seagrass dominated) and hard (reef) bottom. Harvested species differed among habitats (see Jimenez et al., 2011). Both habitats were characterized using a photographic-based method to estimate benthic category percentage coverage (see Dumas et al., 2009). Soft-bottom habitat was dominated by seagrasses species *Cymodocea serrulata* and *Halodule uninervis* (~62%), green algae (*Halimeda spp.*, *Ulva spp.*, *Codium spp.*) and brown algae (*Padina sp.*, *Sargassum spp.*, *Turbinaria ornata*). Algae represented ~22% of community composition and sand ~16%. Hard-bottom habitat was mainly composed of dead corals, boulders or rubbles (~82%) (due to the high exposition of crests) with encrusting algae (~13%), living corals (~4%) and sponges (~1%) (from Jimenez et al., 2010). Seagrass habitats were found only on coastal stations while reef habitats were present on both (coastal and islets) stations (Table 1).

2.2. Invertebrate sampling

Field studies were conducted over two years (2008–2010) and two seasons (winter and summer), accounting for a total of four field surveys of 12 consecutive days. Intertidal macrofauna and

Table 1
Characteristics of sampling stations in the south-west lagoon of New Caledonia. Type of flat, habitat, status and implementation year for MPAs and harvesting pressure (from Jimenez et al., 2011) are given per station.

Station	Type of flat	Habitat	Status (implementation year)	Harvesting pressure (number of harversters Ha^{-1} $year^{-1}$)
C_1	Coastal	Hard-bottom + Soft-bottom	Non-MPA	29
C_2	Coastal	Hard-bottom + Soft-bottom	Non-MPA	29
C_3	Coastal	Hard-bottom + Soft-bottom	MPA (1998)	0
C_4	Coastal	Hard-bottom + Soft-bottom	MPA (1998)	0
I_1	Islet	Hard-bottom	Non-MPA	2.4
I_2	Islet	Hard-bottom	Non-MPA	2.4
I_3	Islet	Hard-bottom	MPA (1989)	0
I_4	Islet	Hard-bottom	MPA (1994)	0

Non-MPA: harvested, MPA: non-harvested.

megafauna assemblages (excluding nematodes, bryozoans, flatworms and nemerteans) were sampled during low tide when invertebrates were the most accessible. Soft-bottom communities were sampled on coastal stations (4) while hard-bottoms were sampled in coastal and islet stations (8). According to studied habitat, different sampling techniques were used (for details see Jimenez et al., 2010):

(1) Seagrass macrofauna were sampled by removing sand from $0.1 m^2$ circular grabs pushed 30 cm deep and by sieving on a 1 mm round mesh, immediately fixed in 5% formalin and conserved in plastic bags. Five replicates (grabs) randomly selected were sampled per station and per period (year-season) leading to a total of 80 samples (2 years*2 seasons*4 stations*5 replicates).
(2) Reef fauna were sampled by visual survey along belt transects of 20*2 m in parallel to the shoreline. All mobile and sessile epibenthic invertebrates (megafauna >1 cm) were collected and later conserved frozen in plastic bags. Five replicates (transects) randomly selected were sampled per station and period (year-season) leading to a total of 160 samples (2 years*2 seasons*8 stations*5 replicates).

Sorting and identifications were performed at the laboratory under a binocular microscope. All specimens were identified to the lowest possible taxonomic level, which in 80% of cases was the species level. Individuals were then conserved in 70% ethanol for a long-term preservation.

2.3. Data analysis

First, the species abundance by sample per habitat was double-root transformed to emphasize rare species and de-emphasize the importance of common species in the analysis (adapted from Legendre and Legendre, 1998). Then, benthic invertebrate communities were described using multivariate analyses. Differences in species composition between MPA and non-MPA areas were investigated using non-metric multidimensional scaling (nMDS) for each habitat. This 2D spatial representation is a description of similarities between samples in terms of their species composition based on Bray–Curtis similarity. Observed differences between MPA and non-MPA assemblages were further tested with one-way analysis of similarities (ANOSIM). The associated R-statistic value provided the degree of difference and the p-value the significance of that difference. Subsequently, the contribution of species to between-group similarity was assessed using a SIMPER (similarity percentages) analysis (Clarke and Warwick, 1994). Dispersion values within MPA and non-MPA stations were also calculated with PERMDISP (PERmutational Multivariate analysis of DISPersion) procedure, a distance-based test for homogeneity of multivariate dispersion. This analysis tests the heterogeneity of stations within MPA vs. non-MPA areas. Finally, changes in community structure between MPA and non MPAs were compared using abundance/biomass (ABC) plots and the associated W statistic (Dauer et al., 1993; Warwick and Clarke, 1993) was calculated.

All data analyses were performed using PRIMER v.6.1.12 packages (Clarke and Gorley, 2006).

3. Results

3.1. Benthic survey

Overall, almost 25 000 individuals belonging to 371 taxa were recorded during the study: 4707 individuals belonging to 174 taxa on seagrasses and 20 253 individuals belonging to 254 taxa on reefs. 57 species were common to both habitats (see Supplemental Material, Appendix A). On reefs, molluscs were dominant both in terms of number of taxa (150) and relative importance (50% of total abundance and 55% of total biomass) (Fig. 2). The other dominant phyla were crustaceans (68 taxa, 6.1% and 26%), echinoderms (42 taxa, 12.2% and 18%), and annelids plus cnidarians (17 taxa, 1.6% and 1%). On seagrasses, three phyla were dominant; molluscs (72 taxa, 31.7% of abundances and 70.3% of biomasses), followed by polychaetes (45 taxa, 23.9% and 13.3%) and echinoderms (25 taxa, 23.6% and 7.6%), then crustaceans (34 taxa, 8.6% and 5.6%) and other taxa including cnidarians, sponges and sipunculids (1 taxa, 8.6% and 3.2%). 32 reef species and 30 seagrass species were targeted by harvesters (cf. Supplemental Material, Appendix A). These species constituted a minor part of the total community in terms of abundance: 16% and 9% on reefs and seagrasses, respectively. In contrast, they accounted for a high fraction of the biomass: 52 and 64% of total dry weights respectively.

3.2. Invertebrate community structure and composition

On reefs, invertebrate assemblage samples showed a clear separation between MPA and non-MPA stations (Fig. 3a). This difference was more marked for coastal flats than for islets flats. Statistical tests revealed a significant effect of status (ANOSIM, $R = 0.515$, p-value < 0.001). On seagrasses, MPA and non-MPA assemblages appeared also highly different (Fig. 3b, ANOSIM, $R = 0.33$, $p < 0.001$). Species composition was approximately 80 and 75% dissimilar between MPA and non-MPAs for reefs and seagrasses respectively. Targeted species contributed to one fifth of this dissimilarity in both habitats (Table 2). Additionally, dispersion values within MPA stations were always smaller (54.92 ± 0.82 on reefs and 47.58 ± 0.81 on seagrass) than within non-MPA stations (58.51 ± 0.58 on reefs and 50.80 ± 1.07 on seagrass) as tested by PERMDISP analyses ($F = 12.89$, p-perm = 0.003 for reefs; $F = 4.81$, p-perm = 0.033 for seagrass).

The ABC plots revealed similar results for both habitats (Fig. 4). In MPA locations, abundance curves (circles) remained below the biomass curve (crosses). This pattern is usually characteristic of the dominance of large-sized but not very abundant taxa. In non-MPA

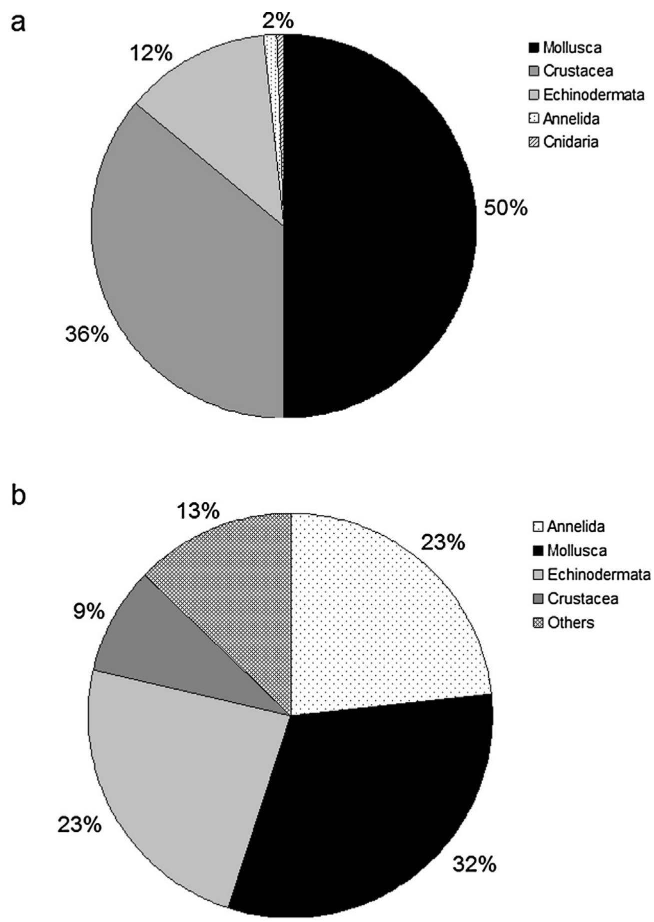

Fig. 2. Community composition on (a) reef and (b) seagrass invertebrate assemblages. Abundance percentages per phyla are given.

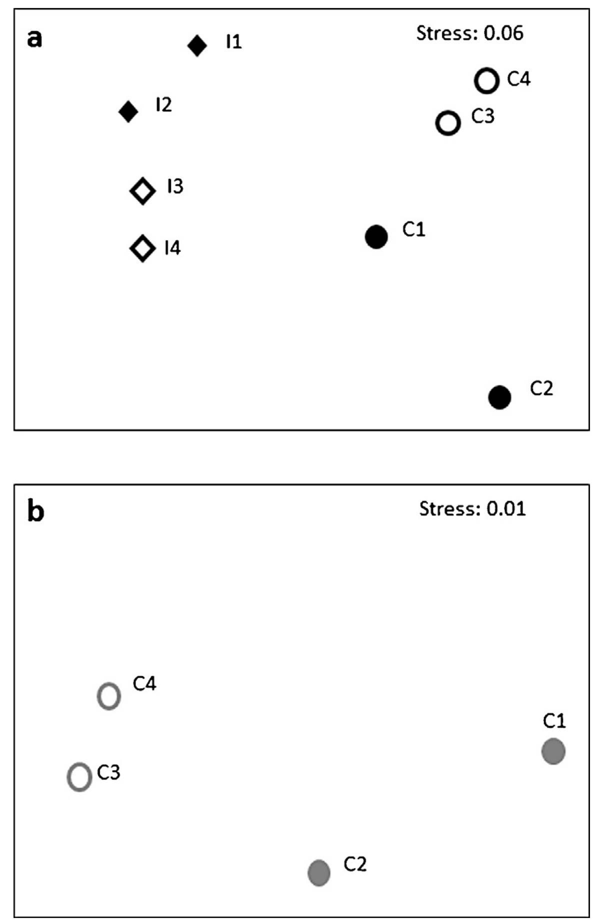

Fig. 3. Non-metric multidimensional scaling (nMDS) results for (a) reefs and (b) seagrass invertebrate assemblages. Blank circles represent MPA stations and full circles non-MPA stations. The stress value represents the spatial dispersion based on resemblances among stations.

locations however, the abundance curve surpassed the biomass curve, reflecting the dominance of small-sized, very abundant taxa. Moreover, the W index was positive in MPA areas and slightly negative in non-MPAs which - according to the designations of Warwick (1986) – would categorize MPA communities as "undisturbed" while non-MPA communities may be "moderately disturbed".

4. Discussion

In tropical environments, little is known about the effects of harvesting on invertebrate assemblages, especially in terms of community-wide effects.

Table 2
Species contribution to more than 30% of the dissimilarities between MPA and non-MPA areas. Results of SIMPER analysis. Target species are indicated in bold.

Species reefs	Dissimilarity contribution %	Species seagrass	Dissimilarity contribution %
Barbatia amygdalumtostum	2.59	***Gafrarium tumidum***	**3.99**
Trochus niloticus	**2.4**	*Bhawania cryptocephala*	2.96
Clibanarius virescens	2.36	*Pyrene versicolor*	2.93
Parasalenia gratiosa	2.18	***Codakia tigerina***	**2.72**
Arca avellana	1.94	*Ircinia sp*	2.48
Drupella cornus	1.81	*Phasianella variegata*	2.32
Nardoa sp	1.8	*Ophiactis savigny*	2.26
Echinometra mathaei	1.72	*Amphiura sp2*	2.25
Monetaria annulus	**1.49**	*Eunice sp2*	1.91
Astraea stellare	1.4	*Pectinaria antipoda*	1.76
Turbo chrysostomus	**1.38**	*Marphysa mossambica*	1.68
Pollia undosa	1.29	*Anodontia ommisa*	1.58
Ophioarthrum elegans	1.26	***Pinctada maculata***	**1.58**
Spondylus varians	**1.26**		
Morula granulata	1.12		
Morula uva	1.09		
Cardita variegata	1.07		
Ophiomastix annulosa	1.06		
Thalamita spp	1.06		
Total	30.29%	**Total**	30.42%

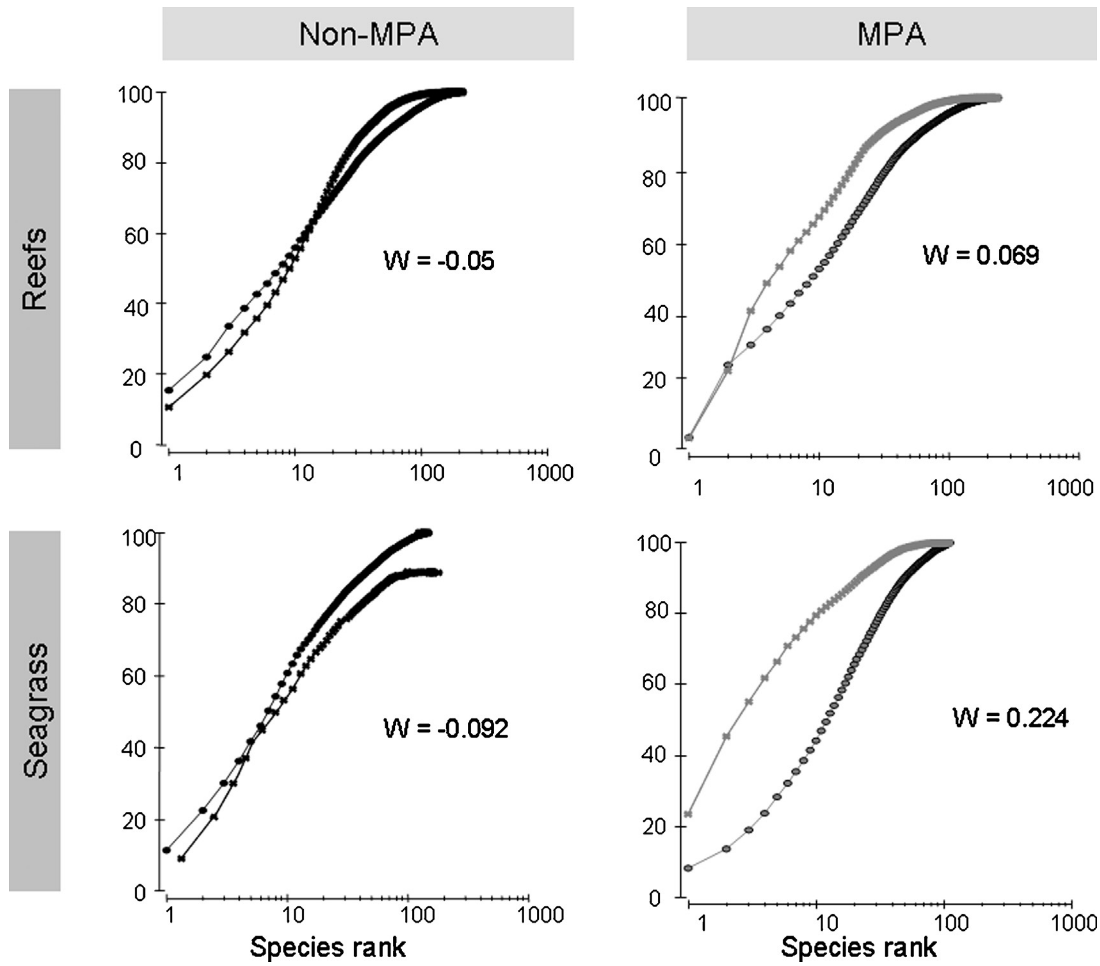

Fig. 4. Abundance biomass curves (ABC) for reefs and seagrass invertebrate assemblages comparing MPA and non-MPA areas. Circles represent abundance data and crosses biomass data. The W statistic is positive when abundance curve remains below biomass curve and is negative when the two curves cross.

4.1. Description of benthic communities and comparisons

The distribution of benthic communities on tidal flats is well known for temperate areas, especially for the northern hemisphere where quantitative studies started in the 1960s (e.g., Sanders et al., 1962; Kay and Knights, 1975; Whitlatch, 1977; Jaramillo et al., 1985; Reise, 1991; Beukema, 1995). Tropical environments have been explored more recently (Stella et al., 2011), despite some early studies in Asia (Broom, 1982; Lui et al., 2002; Purwoko and Wolff, 2008), America (Vargas, 1988; Fernandes and Soares-Gomes, 2006), the Pacific islands (Dittmann, 1996, 2000; Frouin and Hutchings, 2001) and the Indian Ocean (deBoer and Prins, 2002; Mackie et al., 2005). So far, inventories and quantitative descriptions of invertebrate assemblages in New Caledonia have been limited to very few studies devoted to subtidal communities (Chardy and Clavier, 1988; Garrigue et al., 1998) or to the description of some intertidal populations (Baron and Clavier, 1992; Dumas et al., 2013). Jimenez et al. (2010, 2012) started describing intertidal reef and seagrass invertebrate assemblages. The present study identified 371 taxa, constituting the first comprehensive record of intertidal invertebrate biodiversity for the studied area.

Comparisons of our records with similar studies on tropical benthos highlighted similar patterns in terms of taxonomic composition. Seagrass assemblages were dominated by polychaetes, as already reported for tropical sedimentary fauna (Alongi, 1990; Frouin and Hutchings, 2001; McCarthy et al., 2000; Paiva, 2001; Lancellotti and Stotz, 2004; Shin and Ellingsen, 2004; Bigot et al., 2006). Similarly, mollusc taxa were dominant in reef flats, as originally mentioned by McClanahan and Muthiga (1992), Zuschin et al. (2001), Bouchet et al. (2002) and Stella et al. (2011).

4.2. Harvesting effects on invertebrate assemblages

The major result of this study is that "traditional" gathering of some invertebrate species on tropical flats clearly affects community-wide structure and composition through secondary effects.

Species composition was different in MPA and non-MPA areas for both communities (reef and seagrass) as shown by nMDS and ANOSIM analyses. On reefs that difference was more marked for coastal flats comparing to islet flats, suggesting a correlation with fishing effort and the frequency of human impacts. In fact, marked differences in trends of frequentation and harvesting activities between islet and coastal reef flats were shown, due to the accessibility of different sites (Jimenez et al., 2011). Similarly, MPA areas were categorized as "undisturbed" areas dominated by high biomass species which present a relatively low abundance (cf. abundance/biomass curves and dispersion values) while non-MPAs were characterized as "moderately disturbed" dominated by small size and abundant species as already reported in harvesting-related impacts (Lasiak and Field, 1995; deBoer and Prins, 2002). Species responsible for the main dissemblances between MPA and non-MPA communities were *not* harvested species as initially expected. We hypothesize that harvesting activities have cascading effects on community structure and would likely affect ecosystem functioning. Harvesting activities thus seem to influence the dominance of many common species, rather than only affecting a restricted number of target species through direct removal. Similar results were reported by Lasiak and Field (1995) in rocky infratidal macrofauna assemblages of the Transkei coast, South Africa.

Modification of the structure and species composition observed can be acceptable as long as the functioning of the ecosystem is not altered. This can be measured by the ecological redundancy in functional diversity; some species have similar functions in the ecosystem so even though one of the species is disappearing (example of the disappearance of *Turbo marmoratus* in Vanuatu, see Dumas et al., 2010), the function can be maintained. In contrast, the transition of a coral-dominated system to algal-dominated system along with a reduction of the number of herbivorous is known to involve severe changes in species composition and to be associated with an alternate state of the ecosystem (Norström et al., 2009). Systems with high species richness and high functional diversity should be relatively stable and insensitive to perturbations (McCann, 2000; Bellwood et al., 2003).

In New Caledonia, and specifically in the South province, the merchant marine published some management strategies based upon size and number limitations for commercial species in 2004. Top shell collecting is restricted to individuals with a diameter larger than 9 cm and smaller than 12 cm. Collection of giant clams is limited to five individuals per boat. There are also size limitations for holothurids but they concern other species that those found in this study. All of these management tools are for boats, and harvesting during low tides on coastal flats is not impacted by these prohibitions. These limitations could be extended to costal reef flats and to non-commercial species. Given our observations, i.e. the modification of community-wide species composition, one of the other measures could be to implement participative management with regulation of catch and effort for commercial and non-commercial species including closed seasons and MPAs. This kind of management strategy is already working in North New Caledonia for the *Holothuria scabra* fisheries and it is showing good results (Léopold et al., 2013). Stock estimation is easy for non-mobile invertebrates and participative co-management involving local people in management decisions is currently used in other islands in the South Pacific such as Vanuatu (Dumas et al., 2010). The extension of participative management to other regions in New Caledonia will help in preserving invertebrate resources.

5. Conclusions

Harvesting activities have community-wide effects in highly diversified ecosystems such as coral reef flats, changing the structure and species composition including both targeted and non-targeted species. Studies addressing harvesting effects in tropical invertebrate communities would ideally encompass the whole assemblage, rather than focusing on a set of few, pre-selected species. Participative management and invertebrate catch limitations could help sustainably protecting marine invertebrate resources. However, more research effort is still required in a wider array of environmental contexts and habitats, including the quantification of changes in functional diversity before more generalized and/or operational management recommendations can be made.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2015.02.001.

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