Human footprints on benthic communities in marine reserves: a study case in the most productive upwelling system worldwide

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ABSTRACT: Fisheries management in marine protected areas (MPAs) aims to preserve the health of ecosystems and the fisheries they support. Fisheries actions in MPAs are selected from a diverse array of management tools and implemented under the assumption that they are not deleterious and do not impede conservation efforts. However, proper evaluations are needed to assess the effectiveness of management strategies. We analyzed 7 yr changes in the structure of benthic communities in the MPA in Bahía Independencia, one of the most productive coastal regions worldwide and part of the Humboldt Current upwelling system off Peru. Owing to the high productivity and the limited resource use allowed, we predicted that environmental variability rather than small-scale fishing activities would drive community changes. We found a significant unidirectional change in benthic community structure of the Bahía Independencia that was strongly associated with the continuous extraction of a few benthic species, with little influence of environmental factors. We suggest that the fishing of filter feeding bivalves and crabs is linked to the disturbances to macroalgae and associated fauna and probably to the release of top-down effects, which led to ~43% reduction in biomass of the whole benthic community. Our findings indicate that establishing MPAs and implementing standard fisheries management strategies in this productive coastal area may not be enough to guarantee the conservation and sustainable use of their resources. Managers should be able to implement site-specific management actions that take into account the full array of interactions between humans, biological communities and particularities of the physical setting.

KEY WORDS: Benthic ecology · Ecosystem-based management · ENSO · El Niño · La Niña · Marine protected areas · Shellfisheries · Upwelling ecosystems

INTRODUCTION

Communities vary in space and time in response to physical and biological factors; determining the extent to which these factors influence ecosystem structure and function is a fundamental question in ecology. In particular, it is considered that the structure of marine benthic communities is largely determined by a complex interplay between physical or physiological disturbance, competition, predation and recruitment (Menge & Sutherland 1987, Jochum et al. 2012). However, human activities impact ecosys-

tems at all levels of complexity of life, including natural communities (Halpern et al. 2008).

Out of a diverse array of human-related disturbances in benthic systems, bottom fishing (i.e. trawling, dredging, raking and suction fishing methods) has the most widespread direct human impact on marine benthic systems (Thrush & Dayton 2002, Hughes et al. 2014). Effects of these perturbations include physical destruction of bedforms, sediment re-suspension, chemical modifications, removal or scattering of non-target benthos, post-fishing mortality and long-term changes in the community structure (Collie et al. 1997, Hughes et al. 2014). Current strategies to reduce these effects and protect biodiversity have been focused on the modification of fishing gears, the reduction of gear interaction with vulnerable habitats and, ultimately, the designation and implementation of Marine Protected Areas (MPAs) (Collie et al. 1997, 2000). Defined as marine units in which fishing and other human activities are either prohibited or restricted (herein referred to as no-take MPAs or r-MPAs, respectively), MPAs frequently represent a precautionary and ecosystem-based approach to ocean management (McCay & Jones 2011). MPAs are assumed to provide protection for critical areas, spatial escape for intensely exploited species and act as buffers to environmental perturbations or unforeseen conditions, hence bridging fisheries management and biodiversity conservation purposes (Allison et al. 1998, Roberts et al. 2001, Gell & Roberts 2003). Fisheries management in r-MPAs is undertaken through a stock of management tools that include licensing, prohibitions on certain fishing gear, regulations on mesh size, establishment of closed seasons or areas, reallocation of benefits among small-scale fishermen and the designation of fishing methods that ensure the continued productivity of the resources (Lauck et al. 1998, FAO 2011). Therefore, the amount of these areas has rapidly increased over the last 2 decades along with advancements in the science and implementation of the so-called Ecosystem-Based Fisheries Management (EBFM) (McCay & Jones 2011, Halpern et al. 2010).

There is worldwide recognition of the benefits of no-take MPAs for conservation and fisheries when they meet certain conditions (Lester et al. 2009, Edgar et al. 2014). However, there is no explicit evaluation of the effects of fishing activities in r-MPAs on the associated benthic communities supporting coastal fisheries. This seems an elusive task, because few r-MPAs have been designed within the context of the EBFM approach, and/or they are not moni-

tored to assess the potential effects on a range of ecological or socioeconomic factors (Halpern et al. 2010). Moreover, there is a lag between EBFM theory and its practice (Möllmann et al. 2014).

The Humboldt Current System (HCS) off Peru is broadly characterized by the upwelling of nutrient-rich cool waters to the surface, dramatically increasing biological productivity. As a result, this system produces more fish per unit area than any other region of the world's oceans (Chavez et al. 2008). Moreover, the system is cooler in comparison with other regions at similar latitudes (sea surface temperature at 5° S off Peru reaches ~16°C, while most other tropical locations are in excess of 25°C) and displays little seasonal variability (Chavez et al. 2008, Carstensen et al. 2010). Located in central Peru, Bahía Independencia can be considered one of the most productive coastal regions worldwide in terms of shellfisheries (Mendo & Wolff 2003, Arntz et al. 2006). The biomasses of valuable benthic invertebrate stocks in this bay are extremely high, with annual productions reaching 2400 g ash-free dry mass m^{-2} (Arntz et al. 2006). While the bay is part of the oldest marine reserve in Peru, the Paracas National Reserve established in 1975, its resources have been exploited by small-scale local fishermen to an unmeasured extent for centuries (e.g. Parsons 1970). Since the creation of the reserve, the Peruvian government has determined suitable fishing methods, fishing quotas and seasons, and regulations for registered small-scale fishermen to protect the strategic value of marine resources. In 1998, the Instituto del Mar del Perú (IMARPE) started a monitoring program which was focused on assessing the biomass of a few exploited resources to assist managers in the implementation of strategies, reflecting the old concept of single-species maximum sustainable yield. It was not until 2004 that IMARPE initiated a rigorous monitoring program that considered not only the exploited species but also the benthic community sustaining them. Fishing methods have not substantially changed since the establishment of the Reserve; instead, efforts have been focused on banning destructive fishing methods that are used elsewhere.

Resource managers in the HCS are challenged by the strong environmental changes that strike this otherwise stable, cool and productive system, caused by the El Niño–Southern Oscillation (ENSO) (Arntz et al. 2006, Thiel et al. 2007). Depending on its intensity and on species biogeographic origins, the El Niño warming phase or the La Niña cooling phase of the ENSO may trigger changes in the distribution

and abundance of ecologically and economically important species (Carstensen et al. 2010). This includes local increases in the abundance of some species (Wolff 1987) or the extinction of some populations, particularly filter-feeding bivalves (Riascos et al. 2009). These perturbations may last for decades and produce long-term changes in the structure of benthic communities (Arntz et al. 1987, Riascos et al. 2011, Pacheco et al. 2012). In contrast, soft bottom communities show rapid (~1 yr) recovery capacity after small-scale disturbance in the HCS (Pacheco et al. 2010).

Our aim was to assess if the community structure of the benthic community in Bahía Independencia reflects the conservation benefits of controlled, non-destructive fishing practices of r-MPAs. We predicted that if small-scale fishing practices are not deleterious, the dynamics of the benthic community would be related mainly to local/regional environmental variability.

MATERIALS AND METHODS

Study area

This study was conducted in Bahia Independencia, located within the Paracas Natural Reserve, Peru (Fig. 1). This bay is one of the most important fishing grounds in the northern region of the Humboldt Current Upwelling System (HCS). Oceanographic conditions within the bay are broadly characterized by low surface temperatures and high nutrient levels due to permanent upwelling. The permanent circulation of water masses modulated by wind patterns determines the presence of an upwelling shadow front, as observed in similar embayments along the HCS (Marín et al. 2003, Quispe et al. 2010). These meso-scale processes may strongly regulate larval movement in this nearshore retention area and hence the recruitment dynamics of benthic organisms (Escribano et al. 2003). Macrobenthic biota in this bay can be broadly characterized into a shallow water zone (to ~30 m depth; sand, rock or algae) with high abundances and strong fishing pressure and a deeper zone of muddy sediment and low abundances (Mendo & Wolff 2003, Taylor et al. 2008).

Field sampling

Macrobenthic communities were sampled in 1 wk surveys during February, corresponding to the austral summer season, between 2004 and 2010 (except for 2008 and 2010 when summer and winter [July] samplings were taken and 2009 when no sampling was performed). Samples were taken as a part of a monitory program for stock assessment of the Peruvian scallop *Argopecten purpuratus* conducted by IMARPE. The program consisted of a grid of 224 cells (400 m × 400 m) covering the typical habitat of *A. purpuratus* (soft bottom and turf algae) located between 5 and 30 m depth (Fig. 1). Below this layer, benthic macrobiota is scarce and the microbial loop is the main functional component (Taylor et al. 2008). At each cell, a 1 m^2 quadrat was placed by Hookah divers and the epifauna and infauna in the upper 5 cm were collected and placed in 5 mm-mesh bags and transported to Isla La Vieja Scientific Station for further analysis. The benthic fauna and macroalgae were weighed (wet mass), sorted into major taxa and identified to species or the lowest possible taxonomic level.

Environmental variability

Oceanographic parameters were registered *in situ* during samplings or derived from secondary sources in order to assess their influence on the biotic structure. Near-bottom water temperature (±0.5°C) was registered using a reversing thermometer (Gen-
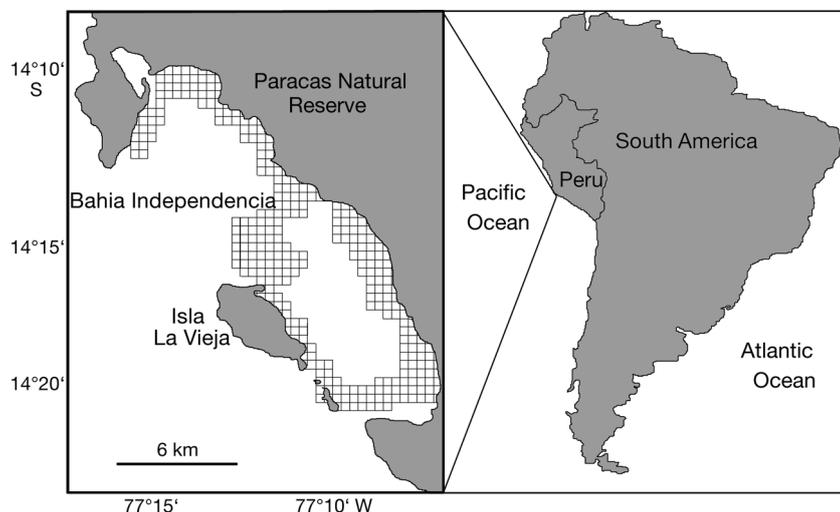

Fig. 1. Map of Bahía Independencia (Peru) and the grid used to locate sampling stations involved in this study

eral Oceanics) and dissolved oxygen (ml l^{-1}) was estimated by the Winkler method (Carritt & Carpenter 1966) from water samples collected with Niskin bottles at each grid cell. Mean near-bottom water temperature and dissolved oxygen were estimated from these data and used for statistical analyses.

According to the National Center of Environmental Prediction, USA (www.cpc.ncep.noaa.gov), there were environmental anomalies associated with episodes of El Niño and La Niña in several regions of the Eastern Pacific Ocean during the study period. Therefore, to assess potential effects of anomalous environmental conditions associated with the ENSO cycle, monthly estimations of the Multivariate El Niño Index (MEI) were obtained from the Earth Systems Research Laboratory–NOAA, USA (available from www.esrl.noaa. gov/psd/enso/mei/table.html). Additionally, monthly data on the Southern Oscillation Index (SOI) were obtained from the Bureau of Meteorology of the Australian Government (available from www.bom.gov. au/climate/current/soihtm1.shtml). To assess effects of this global environmental oscillation in a more regional context, the Peruvian Coastal Thermal Index (PCTI) was provided by IMARPE. Finally, we used the monthly mean upwelling index (offshore Ekman transport; m^3 s^{-1} 100 m^{-1} of coastline) at 15° S, 77° W, provided by the Pacific Fisheries Environmental Laboratory — NOAA, USA. Data for February and July (field surveys) of these secondary sources were used for statistical analyses.

Dynamics of artisanal fisheries

Artisanal fisheries are the main economic activity in the study area. Therefore, monthly landings were obtained from the IMARPE monitoring program for artisanal fisheries and annual or semiannual landings preceding field surveys were estimated to correlate these with changes in the biotic structure. These statistics represent the actual amount of fishing allowed in the bay. From the 21 species included in fisheries statistics we selected 15 macrobenthic species inhabiting soft bottoms and turf algae for further analysis. Only 2 different fishing methods are permitted in this area: (1) Hookah diving fishery (3–4 h d^{-1}) for epifaunal species (e.g. *Argopecten purpuratus*, *Trachycardium procerum*, *Semele solida*, *Gari solida, Transenella pannosa*, *Romaleon polyodon*, *Cancer* spp.) and (2) clam-kicking fishery for infaunal species in shallow areas (i.e. *Ensis macha*, *Tagelus dombeii*). Most of these resources were distributed across a relatively homogeneous zone between 5 and 30 m depth, except for *Tagelus dombeii*, *Transenella pannosa* and *Aulacomya ater*, which display a patchy distribution (R. A. Uribe unpubl.). Because Bahía Independencia is under the regulation of a National Natural Reserve, all fishing activities are permanently monitored by IMARPE and controlled by the Peruvian government. Although illegal, unaccounted fishing activity may still exist, data on fisheries landings generally reflect actual extractions in the study area.

Statistical analyses

A non-metric Multidimensional Scaling (nMDS) was performed to analyze temporal changes in community structure, using a Bray–Curtis similarity matrix calculated from the square root-transformed biomasses (wet weight; g) of all the non-exploited species present in the bay. Square root transformation was applied to down-weight the contributions of quantitatively dominant species to the similarities calculated between species. Exploited species (i.e. 15 species) were not included in the analysis because their abundances would not represent the natural variability of their populations. A permutational multivariate analysis of variance PERMANOVA+ for PRIMER (Anderson et al. 2008) was used to assess significant differences in the assemblage structure and post-hoc comparisons were used to assess between-survey differences. A preliminary analysis of the nMDS ordination plot suggested a unidirectional, chronologically sequential pattern of changes in the community structure in the study area. Therefore, we tested the significance of this temporal pattern of macrofaunal assemblage using the RELATE seriation test in the PRIMER v.6 software (Clarke & Gorley 2001). This analysis uses the Spearman rank correlation coeffiecient (ρ) between the community dissimilarity among surveys and the dissimilarity model matrix that would result from a consecutive pattern of interpoint distances of the same number of surveys. The BIOENV routine implemented in PRIMER was used to assess the explanatory power of environmental factors and fishing activities (annual or semiannual landings per species) on the observed pattern in the community structure by describing the combination of variables that best correlates with the observed changes in community structure. The routine compares biological and explanatory similarity matrices using the Spearman-rank correlation coefficient (ρ). For this analysis all the data of species biomass from the 224 grid cells were collapsed into a

single average for February (and July when available). As environmental and landing data display different measurement scales, data were first normalized to achieve a common scale (Clarke & Gorley 2001). Finally, we used the BVSTEP routine in PRIMER to identify the smaller group of species that would generate a similarly significant ($p < 0.05$) seriation pattern in the nMDS ordination to the primary community set (all the non-exploited species). Spearman rank correlation analyses were used to describe temporal trajectories in the biomass of each species belonging to this small set. These analyses were performed using Statistica v.10 (Statsoft).

RESULTS

A total of 14 phyla comprising 23 classes, 140 genera, 197 species and 70 155 individuals were recorded in the period of the study for all the sampling stations (see the Supplement at www.int-res.com/articles/suppl/m557p065_suppl.xlsx).

In general, the nMDS ordination (Fig. 2) showed an increasing dissimilarity in the structure of the macrobenthic community from 2004 to 2010. The PERMANOVA test showed significant differences in the community structure among surveys (Pseudo-$F_{1,7} = 5.46$, $p < 0.001$) and pairwise comparisons confirmed differences between every pair of surveys (Table 1). The RELATE seriation analysis showed a significant correlation with the model matrix ($\rho = 0.822$, $p < 0.05$), implying that changes in the community structure are related to unidirectional changes in either
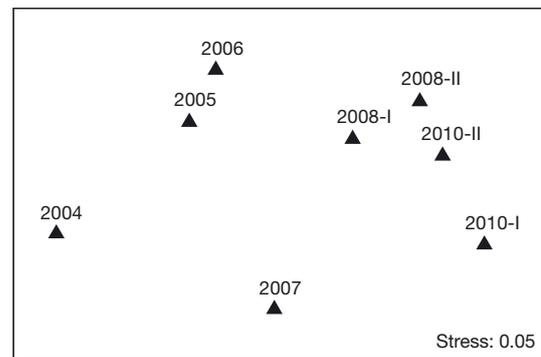

Fig. 2. First 2 dimensions of the non-metric multidimensional scaling (nMDS) ordination analysis showing the temporal variability of the macrobenthic community structure in Bahía Independencia, Peru. Only the survey centroids (center of individual sample points in multivariate space) are shown to highlight the temporal pattern

biotic or abiotic temporal factors. The BIOENV analysis (Table 2) showed that as a single variable, the annual landings of *Cancer porteri* explained ~74% of the observed changes in the community and the best combination of explanatory variables comprised the annual landings of 5 mollusks and one crustacean and the mean annual variability of the upwelling index (UI). Other combinations of variables with less explanatory power comprised only fisheries landings. The best combination of variables accounted for 84% of the observed variability in the community structure. Annual landings for these species (Fig. 3a), mainly represented by the bivalves *Ensis macha* and *Aulacomya ater*, showed a continu-

Table 1. Post hoc between-survey paired comparisons (uncorrected *t*-test among surveys with p-value in parentheses) of differences in community structure in Bahía Independencia. Sampling was in summer for 2004–2007, and summer (I) and winter (II) for 2008 and 2010

	2004	2005	2006	2007	2008-I	2008-II	2010-I	2010-II
2004		1.764 (0.001)	2.360 (0.001)	2.144 (0.001)	2.163 (0.001)	2.908 (0.001)	3.553 (0.001)	3.614 (0.001)
2005			1.802 (0.002)	1.746 (0.001)	1.556 (0.002)	2.266 (0.001)	2.634 (0.001)	2.945 (0.001)
2006				1.469 (0.009)	2.004 (0.001)	2.418 (0.001)	2.573 (0.001)	2.986 (0.001)
2007					1.701 (0.001)	1.740 (0.001)	2.181 (0.001)	2.234 (0.001)
2008-I						1.643 (0.002)	2.302 (0.001)	2.326 (0.001)
2008-II							2.276 (0.001)	1.656 (0.003)
2010-I								2.059 (0.001)

Table 2. Results of BIO-ENV analysis showing the best combinations of potentially explanatory variables (i.e. landings of benthic species and environmental parameters) of changes in community structure. Spearman's rank correlation coefficient (ρ), the corresponding selection of the best 'explanatory' variables and the number (N) of variables included are given

| N	ρ	Best variable combination
1	0.739	*Cancer porteri*
2	0.771	*Thaisella chocolata*, *Ensis macha*
3	0.767	*Thaisella chocolata*, *Cancer porteri*, *Ensis macha*
4	0.784	*Aulacomya ater*, *Cancer porteri*, *Ensis macha*, *Semele solida*
5	0.813	*Thaisella chocolata*, *Aulacomya ater*, *Romaleon polyodon*, *Semele solida*, *Tagellus dombeii*
6	0.814	*Thaisella chocolata*, *Aulacomya ater*, *Romaleon polyodon*, *Ensis macha*, *Semele solida*, *Tagellus dombeii*
7	0.844	*Thaisella chocolata*, *Aulacomya ater*, *Romaleon polyodon*, *Ensis macha*, *Semele solida*, *Tagellus dombeii*, Upwelling index
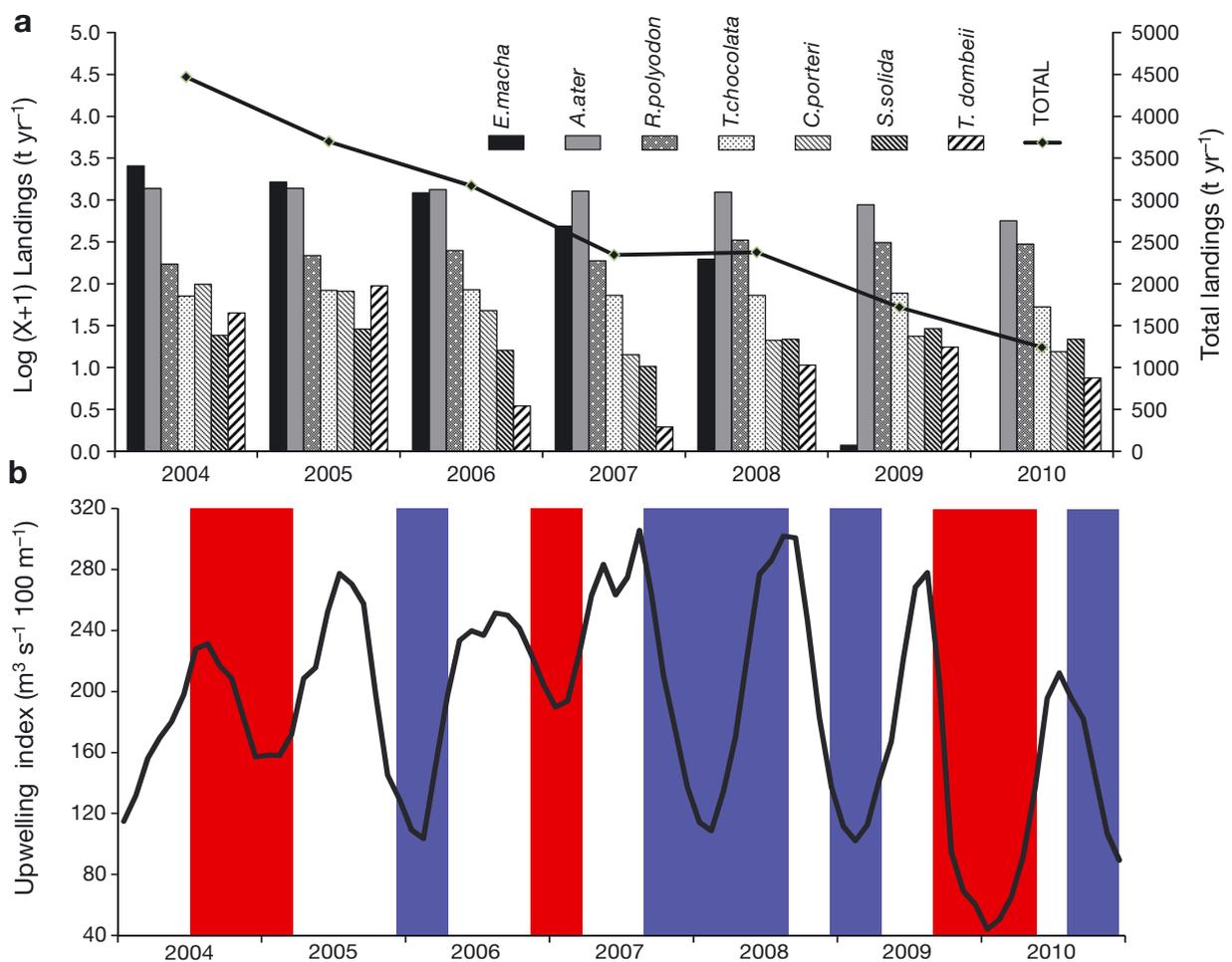
Fig. 3. Annual variability of selected factors explaining changes in the benthic community structure of Bahía Independencia, after BIO-ENV analysis (Table 2). (a) Annual landings of 8 species of mollusks and crustaceans; the black line represents the combined annual landings of those species. (b) Upwelling index at 15°S, 77°W obtained from the Earth Systems Research Laboratory–NOAA, USA; red bars represent warm (El Niño) periods and blue bars represent cold (La Niña) periods according to the National Center of Environmental Prediction, USA

ous drop, from 4469 t yr^{-1} in 2004 to 1241 t yr^{-1} in 2010. UI, the only environmental variable with a limited explanatory potential of the observed biotic pattern, showed a seasonal variability, with increasing

offshore Ekman transport during the first half of the year and decreasing transport during the second half of the year (Fig. 3b). However, strong interannual differences in the UI were observed: the seasonal vari-

ability decreased and the net offshore Ekman transport increased from 2004 to 2007 while the opposite was observed between 2008 and 2010. Moreover, decreased seasonality in UI was often observed during El Niño warming periods, whereas increased seasonality generally occurred during La Niña cooling periods.

The BVSTEP routine allowed the selection of a group of species that generated the temporal seriation pattern in the community structure. However, this pattern persisted after repeating the nMDS ordination excluding those species in the biological data matrix and after testing its significance using the RELATE test. This revealed a high redundancy in the community structure. Therefore, the BVSTEP routine was re-run to select a new group of species that still explained the observed pattern. This process was repeated until the seriation pattern in the community structure was not significant. By doing this, 124 species were finally selected as responsible for the seriation pattern observed in the community structure.

Table 3. Taxa showing a negative or positive significant relationship (p < 0.05) between their biomass and time (survey) (N = 8). Species are ordered according to their contribution to total biomass, following Fig. 4

Taxa	Spearman's ρ	t_{N-2}	p
Negative relationship			
Rhodymenia flabellifolia	−0.833	−3.693	0.010
Macrocystis pyrifera	−0.929	−6.129	0.001
Crossata ventricosa	−0.833	−3.693	0.010
Actinia sp.	−0.833	−3.693	0.010
Oliva peruviana	−0.690	−2.338	0.048
Lessonia trabeculata	−0.850	−3.958	0.007
Ophiactis kroyeri	−0.710	−2.472	0.048
Heliaster helianthus	−0.873	−4.382	0.005
Arbacea spatuligera	−0.738	−2.680	0.036
Ulva costata	−0.736	−2.266	0.037
Taliepus marginatus	−0.928	−6.128	0.001
Metacarcinus edwardsi	−0.736	−2.898	0.027
Chione peruviana	−0.736	−2.898	0.027
Polinices uber	−0.809	−3.377	0.015
Tegula tridentata	−0.874	−4.411	0.004
Caenocentrotus gibbosus	−0.764	−2.898	0.027
Cardita sp.	−0.829	−3.638	0.010
Cycloxanthops sexdecimdentatus	−0.826	−3.594	0.012
Alpheus chilensis	−0.764	−2.898	0.027
Positive relationship			
Diopatra sp.	0.762	2.881	0.028
Phycodrys quercifolia	0.862	4.175	0.006
Cladophora sp.	0.845	3.881	0.008
Patiria chilensis	0.764	2.899	0.027
Brachidontes granulata	0.763	2.989	0.027
Macrobrachium peruvianum	0.791	3.167	0.019

From this subset, 19 species showed a significant temporal trend of decreasing abundance while 6 species increased their abundance through time (Table 3).

The pool of species showing a decreasing abundance represented ~43% of the biomass of the whole macrobenthic community at the beginning of the study and it dropped to only ~14% at the end of the study. Two algae (*Rhodymenia flabellifolia* and *Macrocystis pyrifera*) and a mollusk (*Crossata ventricosa*) were the most important species in terms of biomass (Fig. 4a). In contrast, the 6 species that increased their abundance represented ~10% of the biomass of the whole community at the beginning of the study and ~49% at the end (Fig. 4b). In this case, the most important species in terms of biomass were the polychaete *Diopatra* sp. and 2 species of algae (*Phycodrys quercifolia* and *Agardhiella* sp.). According to Fig. 4, the biomass lost by negatively affected species was not offset by biomass gained in positively affected species; in fact, the biomass of the whole community decreased steeply from 424.5 g m^{-2} in 2004 to 183.9 g m^{-2} in 2010, representing a reduction of 43.3%.

DISCUSSION

Factors influencing change in community structure

The continuous extraction of a few benthic species (mainly mollusks) and the variability in the upwelling index (UI) are the factors that most highly correlated with observed changes in community structure in Bahía Independencia (Fig. 2). The UI, the only environmental parameter selected, entered the BIOENV results as a variable representing only a 3% improvement in ρ. Thus, for the study period, environment did not seem to have an important influence on community changes. This result does not support our prediction that biotic changes would be driven by environmental variability and not by fisheries in this marine reserve. These results are remarkably consistent with those of Pacheco et al. (2012), who analysed the variability in the benthic community structure in a non-protected shallow coastal area in northern Chile between 1991 and 2007. They found that, from a suit of potentially explanatory parameters that included only environmental parameters, upwelling index was the main factor, which however explained only ~17% of the community changes. More importantly, our results raise concerns about the pervasive role of humans as key components of marine ecosystems in the HCS and about the suitability of fisheries
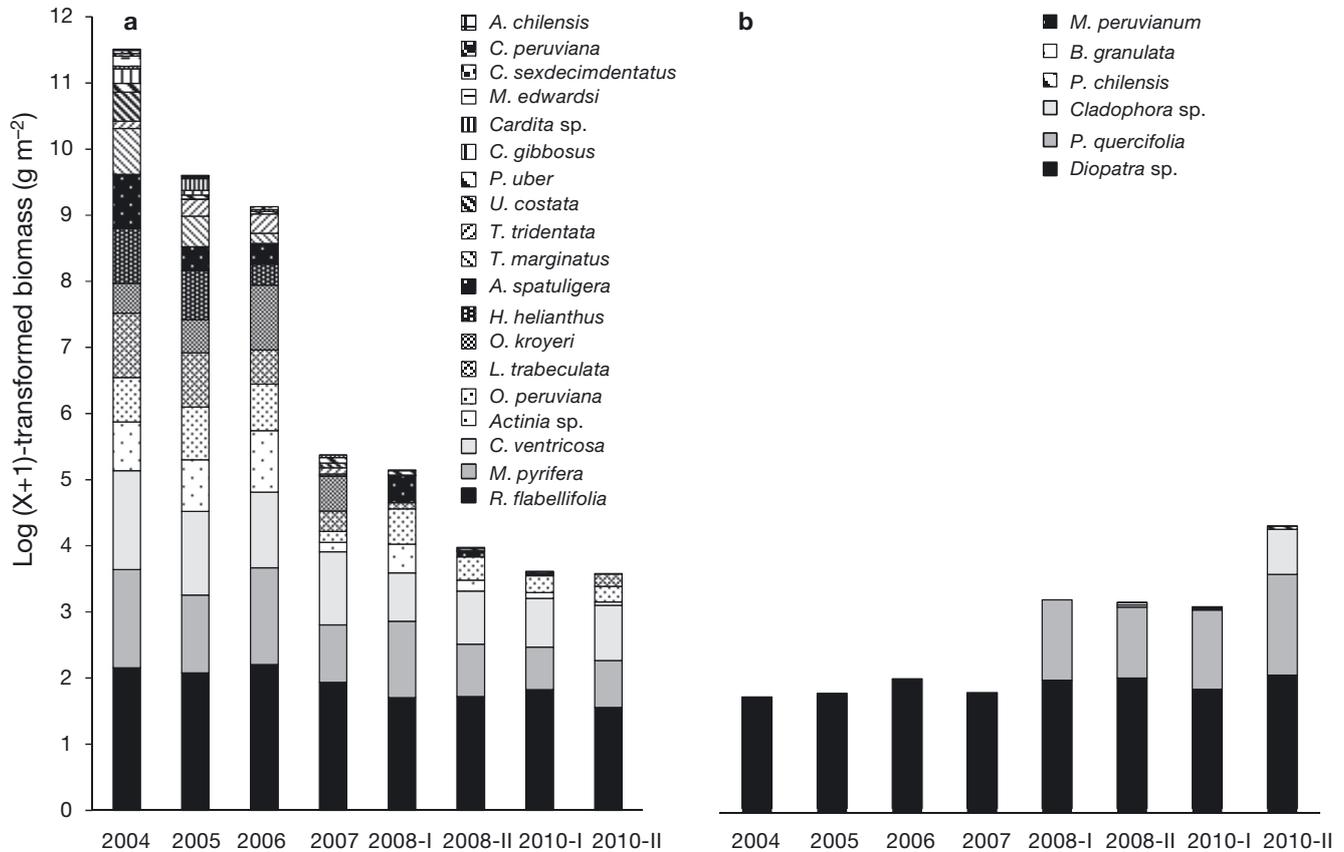
Fig. 4. Changes in the biomass of species that were responsible for the serial temporal pattern of change in community structure and showed (a) decreasing or (b) increasing trends through time (see Table 3). Sampling was in summer for 2004–2007, and summer (I) and winter (II) for 2008 and 2010

management in r-MPAs in this system. Studies in fully protected, 'no-take' areas or reserves in Chile and around the world have demonstrated that humans act as top predators causing trophic-cascade effects in food webs (Castilla 1999) and have shown the multiple benefits of no-take areas for protection and conservation (Lester et al. 2009).

Fisheries landings do not necessarily reflect the abundance of target species, because they are influenced by factors such as differences in fishing effort or changing demand. However, our results show that the continuous extraction of 6 species was associated with the observed community change. Among these species, the suspension feeders *Ensis macha* and *Aulacomya ater* were the most important exploited species in terms of biomass, while *Cancer porteri* was the more important predictor as a single variable. All these species, particularly *E. macha*, showed a continuous drop in fisheries landings, possibly reflecting a decimation of these populations. Suspension feeders, particularly bivalves, play a key role in coastal marine food webs. Because of their filtration capacity,

they capture large amounts of phytoplankton and organic matter, to a point that they may directly regulate primary production and indirectly secondary production of the whole benthic community (Gili & Coma 1998). Owing to the extremely large biomasses (up to 2900 g shell-free dry mass m^{-2}) that suspension feeder bivalves may reach in the HCS (Arntz et al. 2006) the effects of their continuous extraction can be reasonably assumed to be high, although the mechanisms of these changes are yet to be clarified. On the other hand, the strong correlation between the exploitation of the carnivorous *C. porteri* and the community dynamics (~74%) suggest that this species has a disproportionately large effect on the community and its environment (discussed below in the next section).

The strong interannual variability observed in UI, seemingly associated with El Niño–La Niña periods (Fig. 3b), may have influenced some of the observed changes in the community structure. According to Gaymer et al. (2010), increased offshore larval transport associated with stronger upwelling during La

Niña periods has significant effects on recruitment of early ontogenetic stages of major benthic community-structuring species in several locations in the HCS. Under this scenario we could reasonably assume that environmental changes, related with the variations in the upwelling process, translate into important changes in the benthic community structure, but these effects could be (1) partially mitigated by a temporal decoupling of upwelling variability, its effects on larvae and or recruitment and the subsequent changes in adult biomass and (2) eclipsed by the stronger effects of fishing. On the other hand, we cannot rule out additional effects of other environmental factors on the observed changes in community structure because the observed patterns in species biomass can be part of long-term responses to environmental perturbations operating at different temporal scales. Moreover, these responses can be delayed and therefore not easily detected using correlative approaches.

Mechanisms of change in community structure

Most of the observed changes in the community structure can be mechanistically described as the decline in biomass of 19 species, the concomitant increase in biomass of 6 species and the net, strong reduction in the biomass of the whole community (Fig. 4). The macroalgae *Rhodymenia flabellifolia* and *Macrocystis pyrifera*, the most important species in terms of biomass in the first group, are recognized as habitat-forming species (Jones et al. 1994, Almanza & Buschmann 2013, Smale & Wernberg 2013). Therefore, variability in the biomass of macroalgae can be expected to affect their trophic and structural associations. Almanza & Buschmann (2013) showed that seasonal variation in the abundance and size of *M. pyrifera* generates cyclical habitat availability that affects algae and invertebrate abundance and composition under the canopy. However, macroalgal assemblages can be vulnerable to a diverse array of stressors acting at different spatial and temporal scales (Graham 2004, Villegas et al. 2008). The long-term, linear decrease in macroalgal biomass (Fig. 4, Table 3) should promote the simultaneous reduction of the reported algal-associated fauna, which includes carnivores such as *Crossata ventricosa*, *Cancer plebejus*, *Oliva peruviana* (Graham 2004, Villegas et al. 2008); herbivores such as *Tegula atra* and *Tetrapigus niger* (Graham 2004, Almanza & Buschmann 2013); and filter feeders such as sponges and anemones (*Actinia* sp.) (Amsler et al. 1999).

Considering that kelps are not harvested in the study area, the results of the BIOENV analysis suggest that the continuous exploitation of suspension feeders affects the long-term stability of the macroalgae and their associated fauna. *Tagelus dombeii* and *Aulacomya ater*, the most important in terms of biomass of exploited species, are highly efficient suspension feeders; capturing phytoplankton, dissolved organic matter and bacteria at rates that can reach 1787 mg C m^{-2} d^{-1}, one of the highest among suspension feeding organisms (Gili & Coma 1998). The unused food resulting from the removal of these suspension feeders may deeply change the balance of energy and matter, both in the water column and in the substratum. On the other hand, these bivalve species provide physical structure to the community. Therefore, even using the less damaging fishing methods, disturbances to the sediment layer associated with the continuous extraction of benthic species affect macroalgal and benthic assemblages. These conditions may negatively affect perennial algae such as *R. flabellifolia* and favor smaller algae such as *Agardhiella* sp. and small suspension feeders with shorter life-spans (Fig. 4), particularly the polychaete *Diopatra* sp., which is a habitat-forming species that may take advantage of a surplus of detritus. As mentioned before, alternative explanations should also be considered for the observed dynamics of populations. For example, *Diopatra* sp. has been observed to die off following El Niño in Bahía Independencia (Taylor et al. 2008); therefore the observed increase may also represent a long-term response to El Niño conditions.

The strong correlation between the exploitation of *Cancer porteri* and the community dynamics suggest that the exploitation of *C. porteri* may release top-down effects and a perturbation on the environment. Although both, landings of *C. porteri* and its biomass in the benthos, diminished through time, only landings showed a consistent trend (Fig. 5), indicating that a drop in the exploitation rate does not necessarily reflect a drop in the abundance of crabs in the benthos. Therefore, the drop in abundance of *C. porteri* attributable to exploitation may reduce the predation pressure on *Diopatra* sp. and *Phycodris quercifolia* and the competitive interactions with the predator *Macrobrachium peruvianum*, thus explaining their increasing abundance (Fig. 4b). However, an important part of the effect revealed by this strong correlation is seemingly related to the exploitation itself, i.e. the perturbation to the environment associated with the capture of these highly mobile crabs.
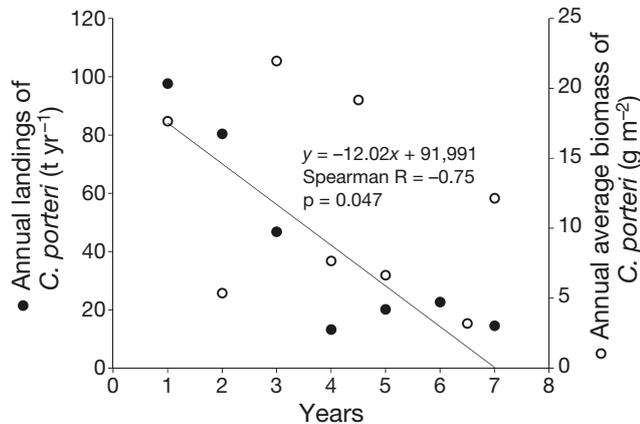
Fig. 5. Variability in annual landings and average abundance of *Cancer porteri* in Bahía Independencia over the study period (2004–2010)

Implications

Preserving healthy marine ecosystems and the fisheries they support is the overall objective of EBFM (Pikitch et al. 2004) and r-MPAs are frequently established as an instrument through which to implement ecosystem-based management actions (McCay & Jones 2011). While this may hold true for no-take MPAs, our results provide correlational evidence suggesting that management actions implemented in a r-MPA may influence community change, including a consistent reduction in biomass as observed over our study period. Fisheries management in r-MPAs should recognize the full array of interactions within an ecosystem. Our analysis of the interactions between human actions and benthic communities showed that not only the communities were affected by this interaction; annual landings of suspension-feeders and carnivores, which influenced community changes, showed a ~72 % decline in biomass, thus highlighting that biological communities and the fishing resources they sustain cannot be seen as separate entities. Therefore, although fisheries regulations in r-MPAs are implemented as precautionary approaches, selecting standard, less damaging methods and small-scale practices, they may not necessarily be enough for meeting the goals of EBFM. Scientists and managers should be able to gather meaningful information from monitory programs and develop site-specific management actions to ensure conservation and long-term use of resources in r-MPAs.

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