



A framework to assess the health of rocky reefs linking geomorphology, community assemblage, and fish biomass



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ABSTRACT

The recovery of historic community assemblages on reefs is a primary objective for the management of marine ecosystems. Working under the overall hypothesis that, as fishing pressure increases, the abundance in upper trophic levels decreases followed by intermediate levels, we develop an index that characterizes the comparative health of rocky reefs. Using underwater visual transects to sample rocky reefs in the Gulf of California, Mexico, we sampled 147 reefs across 1200 km to test this reef health index (IRH). Five-indicators described 88% of the variation among the reefs along this fishing-intensity gradient: the biomass of piscivores and carnivores were positively associated with reef health; while the relative abundances of zooplanktivores, sea stars, and sea urchins, were negatively correlated with degraded reefs health. The average size of commercial macro-invertebrates and the absolute fish biomass increased significantly with increasing values of the IRH. Higher total fish biomass was found on reefs with complex geomorphology compared to reefs with simple geomorphology ($r^2 = 0.14$, $F = 44.05$, $P < 0.0001$) and the trophic biomass pyramid also changed, which supports the evidence of the inversion of biomass pyramids along the gradient of reefs' health. Our findings introduce a novel approach to classify the health of rocky reefs under different fishing regimes and therefore resultant community structures. Additionally, our IRH provides insight regarding the potential gains in total fish biomass that may result from the conservation and protection of reefs with more complex geomorphology.

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1. Introduction

Humans have impacted ecosystems to such an extent that few places on Earth have escaped anthropogenic influence. Just considering marine ecosystems alone, most oceans are trawled and fished repeatedly (Halpern et al., 2008), new areas are impacted through

ever-expanding fisheries (Zeller and Pauly, 2005), marine species abundance is being driven to unprecedented low levels through overfishing (Worm et al., 2006), and community assemblages are altered in diverse ways (Tegner and Dayton, 2000; Turner et al., 1999). The recovery of historic community assemblages on reefs is a primary objective for the management of marine ecosystems worldwide; both for the health of marine resources, and for the heightened economic benefits and food security of coastal communities that depend on them (Beaumont et al., 2008; Cinner et al., 2012; Newton et al., 2007).

To date, most studies of reef community recovery have focused on the monitoring of reef fish biomass and abundance of associated invertebrate populations as a proxy of the health of the reef systems. These studies have used the effect of no-take marine reserves (NTMRs) or gradients in fishing pressure (Lotze et al., 2011)

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to attempt to understand changes in fish biomass after the implementation of such reserves or along gradients of exploitation pressure (Browman, 2011; Hawkins et al., 2006; McClanahan et al., 2007; Roberts, 1995; Russ et al., 2005; Wantiez and Thollot, 1997). These studies or natural experiments demonstrate an ecological succession to the recovery of species richness: the quick, initial return of herbivorous fishes followed more slowly by the rebuilding of carnivores and piscivores. Additionally, they have shown that macro-invertebrates such as sea urchins decline concomitantly and, in many cases, calcareous algae increase to become a dominant group in the benthos. Other studies have used paired comparisons to demonstrate differences in community and food-web structures between NTMR (or areas of low fishing pressure) and open-access areas by analyzing the re-establishment of predatory interactions within the communities (Edgar et al., 2011; Edgar and Stuart-Smith, 2009; Floeter et al., 2006; Guidetti et al., 2008; Halpern, 2003; Lester and Halpern, 2008; Lester et al., 2009; McClanahan, 2011; Micheli et al., 2004; Mumby et al., 2006; Pollnac et al., 2010; Tyler et al., 2011). Some studies have correlated gradients of fishing pressure or human population size to fish biomass (Dulvy et al., 2004; Friedlander and DeMartini, 2002; Pinca et al., 2011; Sandin et al., 2008). These reveal that with a move towards healthier systems there are concurrent, significant increases in secondary productivity and ecosystem stability, and generally elevated rates of population recruitment and resilience. Finally, a last group of studies correlate gradients in fish biomass with reef community attributes, such as algal cover or sea urchin densities, using degree of fishing pressure as an explanatory variable (McClanahan et al., 2011; Mora et al., 2011; Newman et al., 2006) and show that thresholds in the community assemblage can be seen along a gradient of fish biomass in ways that can inform fisheries management (Honey et al., 2010).

All of the aforementioned studies illustrate differences in reef community assemblages and the fish biomass along a gradient of anthropogenic/fishing pressure, but due to the enormous variation in type and quality of the observations in many of these studies, direct comparison is difficult and predictive capacity for non-surveyed areas is limited (Hughes et al., 2010). For instance, a meta-analysis must account for (1) distinctions between the absolute and relative effects of a NTMR, (2) inconsistencies in protection level among NTMRs, and (3) the different ecological characteristics of NTMR and control sites (e.g., substrate rugosity, depth, current regime, etc.) (Halpern, 2003). Furthermore, most methodologies do not account for differences in fishing practices across study reefs. The common lack of baseline data in many of the studies also complicates the extrapolation of results (Sandin et al., 2008).

Here we present a general framework to describe and compare changes in the community assemblages of macro-invertebrates and fishes on rocky reefs that occur along a gradient of fishing pressure, and develop an index that characterizes the level of health of these rocky reefs, which can be compared across the gradient to understand the stages of reef community assemblages. In order to develop an approach that could be applied to rocky reefs outside our study area, we emphasized a priori five critical design considerations: (1) sampling scale must be large enough to capture biogeographic variation; (2) within different regions inside our sampling study area, reefs in protected/low fishing pressure areas that have low or zero extractive activities must exist to ensure a reliable baseline for “unimpacted”/“healthy”; (3) all reefs sampled must share similar rocky habitat characteristics in order to avoid habitat-related differences in reef community species (Sala et al., 2002); (4) two levels of geomorphologic reef structure – complex and simple – can be recognized; and (5) fishing practices are similar and typical of artisanal fishing along the region (Aburto-Oropeza et al., 2008; Sala et al., 2004).

Working under the overall hypothesis that, as fishing pressure increases, the biomass in upper trophic levels decreases followed by intermediate levels, whilst herbivores increases in relative abundance, we focused on answering five primary research questions: (1) How does the reef community as a whole vary as a function of increasing fishing pressure?; (2) what species are good indicators of reef conservation status?; (3) of these potential indicator species, what is the minimum number that can be used to assess reef health?; (4) how do these species agree with other indicators used in the literature?; and (5) how do changes of these indicators explain the absolute and relative changes of different components of these assemblages?

2. Material and methods

2.1. Reefs studied

In order to account for biogeographic patterns in species richness, we distributed the sampling effort across approximately 1200 km of latitude (10.62 degrees from the southernmost reef to the northernmost reef), covering seven regions of reefs along the Gulf of California from the southern Islas Marias archipelago to the Midriff Islands in the north (Fig. 1). The importance of properly setting historical baselines, which are defined as the condition of a given area or ecosystem prior to or in the initial stage of a human stressor (i.e. fishing pressure), is recognized as fundamental in research concerning reef community health (Edgar et al., 2004). The lack of a historical baseline makes it difficult to assess the health of a particular reef and, in many cases, compromises many of the models that test community change and reef health (Edgar et al., 2009; Jennings and Blanchard, 2004). We sampled reefs in “protected/low fishing pressure” marine areas in the region, in order to set them as baselines for this study:

Cabo Pulmo National Park is a high biodiversity area and has a large cover of coral populations settled on long basaltic dykes that run parallel to the coast. The Mexican government declared the area a Marine National Park in 1995, covering 71 km² of coastal and offshore reefs. After the designation, people from Cabo Pulmo town self-organized and acted collectively to pass a resolution that prohibits all commercial extractive activities throughout the park. Fish biomass inside the park has increased significantly in all trophic levels at annual rates varying between 12 and 25% and total biomass has increased by 3.49 t ha⁻¹ in one decade (Aburto-Oropeza et al., 2011).

Islas Marias Archipelago is a group of four volcanic islands approximately 150 km northwest of Nayarit, Mexico. The archipelago was officially declared a biosphere reserve in 2000, however, a federal penal colony established on the largest island (Maria Madre) has been functioning since 1905 and serving as a *de facto* reserve. The island complex has therefore been consistently patrolled by the Mexican Navy, limiting access to vessels unrelated to the operation of the facility to 15 nautical miles offshore. Although precise catch data is not available, the surrounding waters of the islands are lightly exposed to anthropogenic pressures from hook and line fishing by the prison inmates. Nevertheless, this fishing pressure on nearshore reefs is considered low by comparison to the rest of the Gulf of California (Erisman et al., 2011).

With the exception of reefs in Cabo Pulmo and Islas Marias regions, all the other surveyed reefs allow fishing activities and thus were placed in one of two categories: (1) MPAs, reefs that are inside one of the other five Marine Protected Areas in the region but are under unregulated fishing pressure or those lacking enforcement (Rife et al., 2012); and (2) open access, reefs that do not have any protection and receive consistent fishing pressure throughout the year.

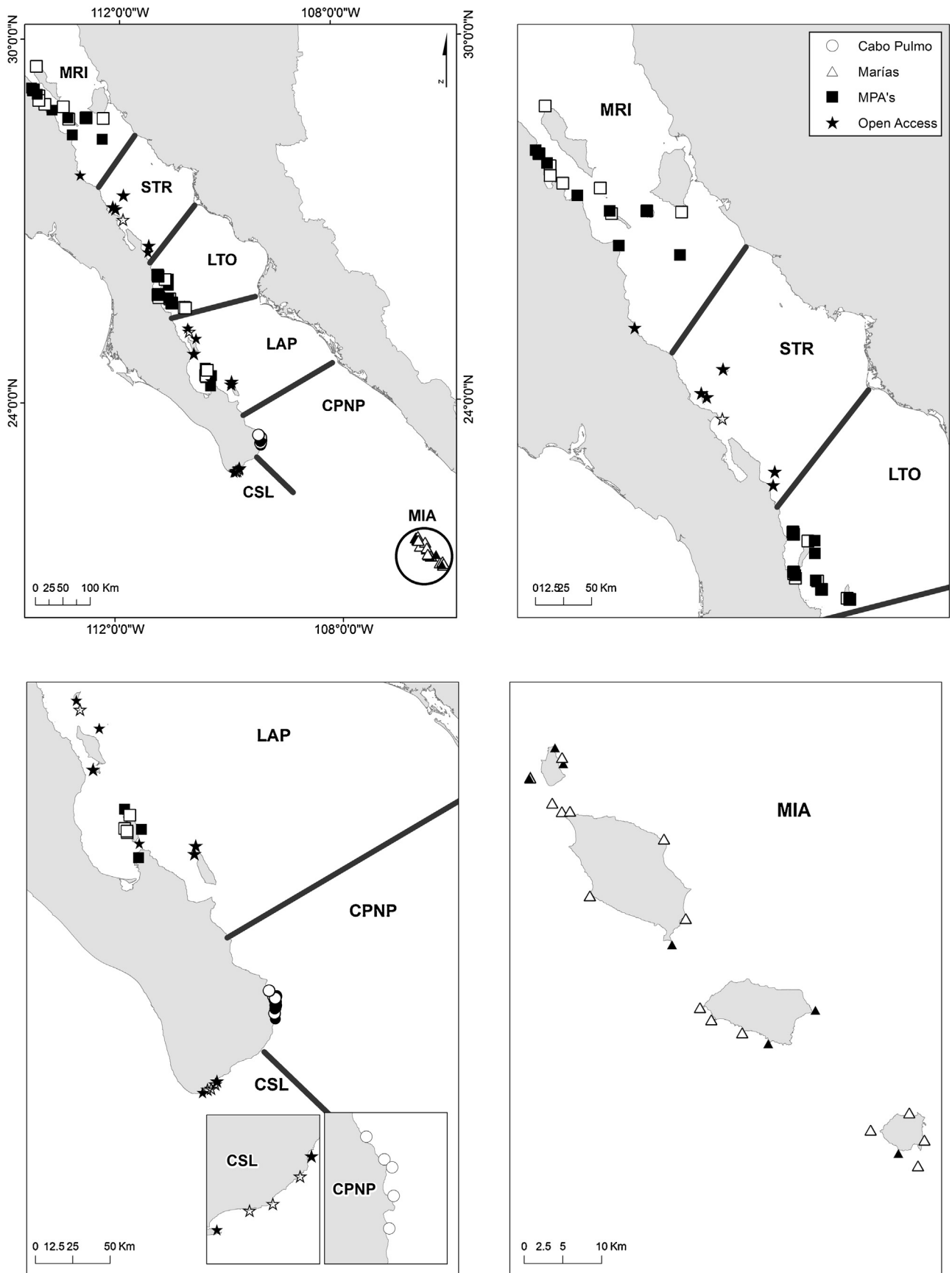


Fig. 1. Map of the study area in the Gulf of California, Mexico. Geomorphologically complex reefs are indicated with black symbols, whereas simple reefs are indicated with open symbols. CPU: Cabo Pulmo National Park; MIA: Marias Islands Archipelago; CSL: Cabo San Lucas; LTO: Loreto; LAP: La Paz; MRI: Midriff Islands; STR: Santa Rosalia.

We sampled reefs in the regions of La Paz (LAP), Loreto (LTO), Sta. Rosalía (STR), and Midriff Islands (MRI) in July 2009. We sampled Cabo Pulmo (CPU) and Cabo San Lucas (CSL) reefs in September 2009. Surveys of the Islas Marías (MIA) reefs were delayed to November 2010 due to security regulations and issues regarding permit granting. While the timing was different, the water temperatures were similar ($\sim 22^\circ\text{C}$) to those during the time that other surveys were undertaken.

2.2. Geomorphology of survey reefs

We surveyed rocky habitats, mainly boulders and walls, known to share statistically-similar reef community components (Aburto-Oropeza and Balart, 2001; Sala et al., 2002). Based on previously recorded geomorphological characteristics of rocky habitats (Aburto-Oropeza and Balart, 2001; Sala et al., 2002), we sampled reefs of two types: (1) *complex reefs* were characterized as offshore or rocky points with a steep slope ($>60\%$), a high rugosity rock cover of more than 90% with boulders ≥ 3 m in diameter, at least 3% cover of gorgonians, and in areas of strong currents or intense hydrodynamic dynamics; (2) *simple reefs* characterized as near-shore reefs, or reefs within bays with a low bathymetric profile had low rugosity, greater than 50% rock cover by rocks < 1 m in diameter, greater than 15% sand cover, a hard coral cover of more than 3%, and comparatively weak currents or less variable hydrodynamic conditions. We sampled each reef type with 3–6 transects per reef and at shallow (< 10 m) and deep depths (> 15 m, when available). In total, we sampled 147 reefs: 78 complex reefs and 69 simple reefs.

2.3. Field survey protocols

We conducted SCUBA-assisted underwater surveys using standard methods for visual belt transects (Harmelin-Vivien et al., 1985). A total of six divers counted and identified all fishes observed to species level at each reef site. The entire dive team has been working together to survey reefs in the Gulf of California for more than a decade (Aburto-Oropeza et al., 2011; Erisman et al., 2011; Mascareñas-Osorio et al., 2011). Each diver has undergone training prior to the surveys consisting of in situ species identification and size and distance estimation at training sites throughout the region. At each site, two-person diving teams swam along 50-m transects one observer recording fishes and the other macro-invertebrates. Fish divers counted and estimated the size of all fishes within a five-meter wide belt along each transect during two passes (250 m² total area). Different behavioral groups (mobile species versus territorial species) were surveyed in separate passes, to ensure that individuals were only counted once. All macro-invertebrates were counted and identified along each transect. Invertebrate transects were 30 m long by one meter wide (30 m²). Using this method, we completed 599 total transects, surveying 149,750 m² of fish habitat and 17,970 m² of invertebrate habitat.

2.4. Data analyses

At each reef, we counted the number of individuals of both fish species and marine macro-invertebrates, and estimated the length-class of each fish and invertebrate counted. We calculated the species richness of each survey reef, as well as the size structure and biomass of the fish community. To estimate fish biomass, we first estimated the biomass of individual fish using the allometric length-weight conversion ($W = a \times TL^b$), where parameters a and b are species-specific constants obtained from FishBase, TL is total length in mm recorded from the survey, and W is weight in grams. In accordance with existing studies, we converted all biomass values to tonnes per hectare (t ha^{-1}). We assigned all fishes to four major trophic groups based on

life history (Supplementary Table S1): piscivores, carnivores, zooplanktivores, and herbivores. Macro-invertebrates were assigned to seven major taxonomic groups and one miscellaneous group: sea stars (Asteroidea), bivalves (Bivalvia), sea urchins (Echinoidea), snails (Gastropoda), hard corals (Hexacoralia), sea fans (Octocorallia), sea cucumbers (Holothuroidea), and others (Misc.). Using this data, we calculated a suite of synthetic community variables (e.g., diversity indices, trophic structure indices, etc.) to further describe the community assemblage at each survey reef. We used 26 variables for fish and 25 variables for macro-invertebrates grouped into 4 main categories – species richness, individual size, abundance, and biomass – as indicators of community assemblage change (Supplementary Table S2). For abundance and biomass, we used both absolute and relative variables.

In a matrix of field data with many variables, it is likely that some of the variables may be correlated, i.e., are different expressions of the same trend. To determine correlative trends in the indicators of the reef assemblages, we applied a Principal Component Analysis (PCA) using the descriptors measured in the field. PCA is a statistical procedure that uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of linearly uncorrelated principal components. The first principal component has the largest possible variance (that is, accounts for as much of the variability in the data as possible), and each succeeding component in turn has the highest variance possible under the constraint that it is orthogonal to (i.e., uncorrelated with) the preceding axes. Because, statistically, only the first and significant axes need to be kept (Jackson, 1993), the method serves as an efficient procedure to reduce the dimension of large, but internally correlated, data sets (Pielou, 1984).

The matrix we used contained 147 reefs and 51 raw-data variables. The matrix rows were centered and standardized, as the variables were measured in different units and scales, and principal axes were extracted using the resulting correlation matrix (Gower, 1966). In order to select axes suitable for interpretation, the axes were tested against the broken stick distribution as a null random model (Jackson, 1993). We accepted only those axes whose explained variation was higher than the maximum proportion of the variance that could be expected by chance alone. We then tested each significant axis against two external variables: (a) fishing pressure and (b) depth of the site survey, using the Linear Model (LM) procedure in the R program (R Core Team, 2014).

Finally, the results of the PCA informed our selection of variables that best illustrated the variation captured by each axis (King and Jackson, 1999). In a standardized PCA the coefficients or “loadings” of each variable can be interpreted as correlation coefficients between the variable and the PCA axis, we therefore selected those variables whose loadings were higher than 0.5 (a critical r value for a Bonferroni-corrected threshold of $P = 0.01$ and $n = 51$). Based on these loadings, we selected a group of ten variables highly correlated with fishing pressure.

We then tested whether these 10 variables, which summarize the status and health of the whole reef community, could be simplified even further without significant loss of precision in the monitoring process. For this purpose, we then selected five variables within these ten significant contributors to the main axis, choosing from those that have been identified in the literature as having both an important ecological function and have been used in previous rocky reef studies (e.g. Dulvy et al., 2000; Sandin et al., 2008; Edgar et al., 2009; Lester et al., 2009; McClanahan et al., 2011). With this selection, we expected to (a) make sure that monitoring is based on ecologically meaningful indicators and (b) make our results comparable with other monitoring efforts. For our variable selection, we chose two variables positively and strongly correlated with axis 1: the biomass of carnivorous fish (BC), and the biomass of piscivores (BP), as well as three variables that were negatively

associated with axis 1: the relative abundances of zooplanktivores (*RZ*), of sea stars (*RS*), and of sea urchins (*RU*). We then tested the robustness of our five chosen indicator variables by doing a second PCA for all 147 reefs, using only these five variables as reef indicators, and confirmed that the first axis of the simplified 5-indicators data matrix was highly correlated to the first multivariate axis of the whole 51-variables matrix (Supplementary Fig. 1).

Having confirmed that the five chosen indicators were (a) highly correlated among themselves and (b) highly correlated with the main variation in the overall dataset, we then developed a simple index of reef health (*IRH*), simply using the average of the normalized values of these five variables with their PCA scoring sign: $IRH = (bp + bc - rz - rs - ru)/5$, where each lowercase variable represents the normalized transformed value of the original variable, such that biomass of piscivorous fish: $bp_i = (BP_i - \overline{BP})/sd(BP)$. By subsequently de-standardizing the equation to use the variables in their original units, we got the final equation for reef-health scoring: $IRH = (a \times BP + b \times BC - c \times RZ - d \times RS - e \times RU - const)/5$, where *BP* and *BC* are biomass values in ton/hectare; *RZ*, *RS*, and *RU* are relative abundances in percentage values; the coefficients *a*, *b*, *c*, *d*, *e* are the inverse of the standard deviations of each variable ($a = sd(BP)^{-1}$, $b = sd(BC)^{-1}$, etc.); and the constant is the algebraic sum of the normalized means [$const = \overline{BP}/sd(BP) + \overline{BC}/sd(BC) - \overline{RZ}/sd(RZ) - \overline{RS}/sd(RS) - \overline{RU}/sd(RU)$].

3. Results

3.1. Health index

We obtained three significant PCA axes, according to the broken-stick criterion. For both complex and simple reefs, the first multivariate axis clearly ordered reefs from those protected from fishing set as our baselines, to reefs within MPAs, and those under open access fishing regimes (Supplementary Fig. 2). A one-way ANOVA with four factor levels [(a) Cabo Pulmo, (b) Islas Marias, (c) MPAs, and (d) open access reefs] showed significant differences along axis 1 ($F = 41.8$, $P < 0.00001$), with Cabo Pulmo and Islas Marias to the right of the axis (mean axis scores 1.30 ± 0.14 , and 1.54 ± 0.12 , respectively), and other MPAs and open access reefs to the left (-1.10 ± 0.17 , and -0.65 ± 0.29 , respectively). Axes 2 and 3 were significantly related to the site's total biomass and the depth of the survey transect, but showed no significant relationship with the reefs' conservation and health status. For this reason, we concentrated our analysis on the survey variables that had high bearing on the values of axis 1, the best indicator of the reefs' conservation status.

Of the 51 variables used for the analysis, the ten that most significantly correlated with the multivariate axis were selected. Half of these selected variables were chosen as indicators of reef health as they drove the reef scores towards the right side of axis (i.e., the protected/low fishing pressure). These five indicator variables were the relative and absolute abundance of carnivores, the absolute biomass of carnivores, the relative abundance of octocorals' (sea fans), and the absolute abundance of piscivores. The remaining five variables of the primary ten selected were indicators of reef degradation, i.e., they pulled the reef scores towards the unprotected/high fishing pressure MPAs or open access reefs. These were: the relative and absolute abundance of Asteroidea (seastars), the relative abundance of zooplanktivores, and the trophic diversity and species richness of macro-invertebrates.

From these ten variables we then selected five variables that are used in the literature as indicators of reef health. The final five indicators selected were: the biomass of piscivores and carnivores which were positively associated with reef health; as well

as the relative abundances of zooplanktivores, sea stars, and sea urchins, all of which were negatively correlated/associated with degraded reefs health. These five indicators were combined into a new PCA multivariate axis, and correlated significantly with the first multivariate axis of the 51-variables matrix ($r^2 = 0.84$, $F = 738.3$, $P < 0.0001$, Appendix S4). This indicated that most of the correlative variation in the original matrix was recovered moving from 51 to 5 variables. As with the full dataset, the first eigenvector scores for this 5 indicators analysis showed significant differences with in historic fishing pressure, with negative scores for open access reefs and other MPAs, and positive scores for the reefs at Cabo Pulmo and Islas Marias ($P < 0.00001$; Fig. 2a).

De-normalizing the 5 selected indicator variables, the final equation for reef-health scoring was: $IRH = 0.186 BP + 0.317 BC - 0.0084 RZ - 0.0184 RS - 0.0093 RU - 0.26$; where biomass values were measured in tons per hectare, and relative abundances were represented as percentage values. This index represents an average of normalized deviates that are correlated among themselves, therefore, the result is interpretable in terms of normalized deviations from the mean condition of the Gulf's rocky reefs. Ninety-nine percentage of the values within our study area (Fig. 2b) ranged from -2 (for highly degraded reefs) and 2 (for highly preserved reefs). Ninety-five percentage of the Cabo Pulmo reefs and 93% of Marias reefs had positive *IRH* values; while only 29% of reefs in MPAs and 36% of open access reefs had positive *IRH* values. The *IRH* values were almost identical to the 5-indicators multivariate score differing only in scale ($r^2 = 0.99$, $F = 18214$, $P < 0.0001$), and were also very highly correlated with the main multivariate axis of variation in the complete 51-indicator matrix ($r^2 = 0.88$, $F = 1024.7$, $P < 0.0001$).

3.2. Absolute and relative changes of assemblage composition

Grouping the reefs every 0.5 points along the *IRH* values, we were able to explore patterns for all variables along the gradient. We found significant differences in the average size of holothurians ($r^2 = 0.95$, $F = 119.34$, $P < 0.0001$), sea stars ($r^2 = 0.84$, $F = 30.62$, $P < 0.01$), and sea urchins ($r^2 = 0.80$, $F = 28.35$, $P < 0.01$); the average size of these groups increased significantly with decreasing values of the *IRH* (Fig. 3a). In contrast, we found an opposite pattern for three other macro-invertebrates groups, such that the average size of sea fans ($r^2 = 0.93$, $F = 87.38$, $P < 0.0001$), bivalves ($r^2 = 0.72$, $F = 18.3$, $P < 0.01$), and gastropods ($r^2 = 0.76$, $F = 22.04$, $P < 0.01$) increased significantly with increasing values of the *IRH* (Fig. 3b).

For both simple and complex reefs, total fish biomass increased significantly with increasing values of the *IRH* ($r^2 = 0.44$, $F = 143.0$, $P < 0.0001$) (Fig. 4a); i.e., increased towards the protected reefs, and decreased away from them. Furthermore, significantly higher total fish biomass was found on complex reefs compared to simple reefs ($r^2 = 0.14$, $F = 44.05$, $P < 0.0001$; for the whole model, $r^2 = 0.58$, $F = 87.2$, $P < 0.0001$), with a log-linear slope of 1.4 times higher on complex reefs. The trophic biomass pyramid also changed along the gradient *IRH* values (Fig. 4a). Reefs at the left/degraded reefs side of the gradient depict a standard biomass pyramid typical of certain terrestrial ecosystems, such as grasslands or forests, where a comparatively small biomass of consumers is supported by the large biomass of producers. In contrast, the right/healthier reefs side of the axis showed an inverted biomass pyramid where the biomass of primary producers is low in comparison to the biomass of piscivores.

Similarly, the relative biomass of the three trophic groups (herbivores and zooplanktivores combined) had a clear pattern along the gradient of *IRH* values (Fig. 4b). The relative biomass of low-trophic level fishes, increased significantly on degraded reefs ($r^2 = 0.26$, $F = 25.2$, $P < 0.0001$); in contrast, the relative biomass of

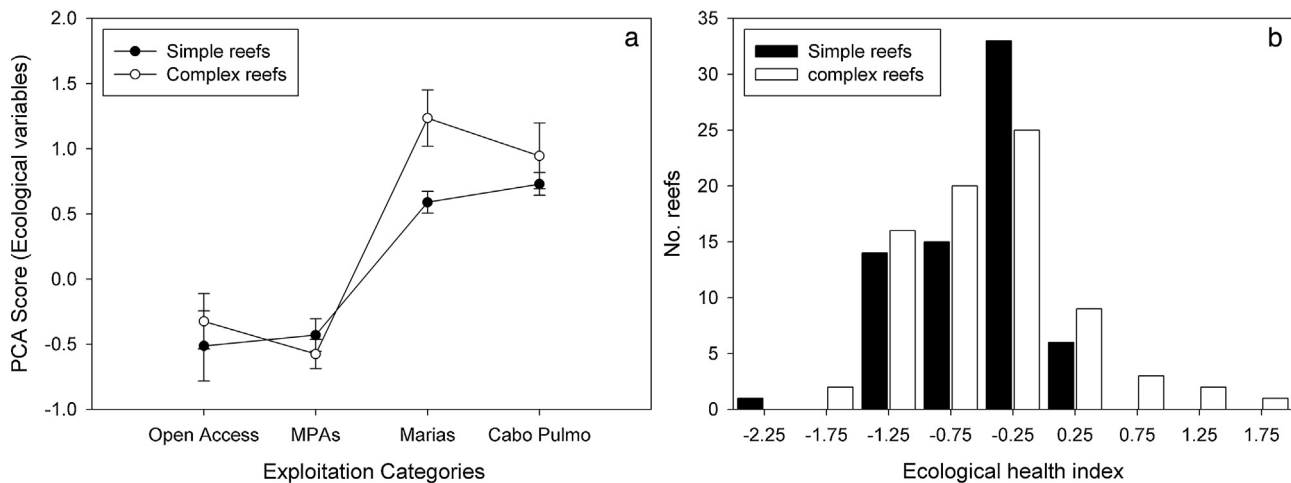


Fig. 2. Ecological health index. (a) Average scores of the simplified 5 indicators variables PCA against the four exploitation reef categories; (b) distribution of reefs along the gradient of values of the ecological health index.

piscivores increased significantly on the healthier reefs ($r^2 = 0.12$, $F = 11.8$, $P < 0.0001$). Carnivores showed a slight but significant tendency to increase towards the middle of the gradient of *IRH* values and a secondary tendency to decrease towards the negative values of the *IRH* ($r^2 = 0.06$, $F = 5.9$, $P = 0.004$).

4. Discussion

4.1. Direct applications of the health index

Reconstructing regional and global trends of reef assemblages have faced limitations mainly due to the different analytical approaches employed (Hughes et al., 2010). The results of our study show that five community-level indicators can provide a reliable estimation of the status of a given reef across an overall gradient of community assemblages, ranging from unprotected/high fishing pressure to protected/low fishing pressure rocky reefs. Our analysis also identified a minimum set of community indicators needed to assess reef health, predict sizes of some macro-invertebrates, and fish biomass. In addition, if we assume that each reef can be used to represent an ecological stage (from pioneer to climax community)

of the overall reefs, our index may be used to describe temporal changes in community structure as well. Although direct monitoring of fishes of high trophic levels (i.e., piscivores and carnivores) may be the simplest evaluation of a reef's health, often the biomass of these groups is so low (in comparison to the natural baseline) that trends through time are statistically unobservable, and resulting evaluations of management actions are ineffective. However, by presenting the whole gradient of reef states using the *IRH*, we are able to illustrate the whole process of degradation where shifts in the reef community assemblage are indicated by changes in the whole community, such as increasing average sizes, or increasing relative abundance of sea urchins or sea stars.

Our two baseline areas, CPU and MIA, were essential to avoid the shifting baselines problem and to set a benchmark for the evaluation of future studies on reef communities within the region, and base on the fish biomass values in other rocky reefs in the Tropical Eastern Pacific (Edgar et al., 2011; Edgar and Stuart-Smith, 2009), this *IRH* can be used to identify directional changes in reef health via shifts in simple community indicators. Furthermore, these indicators can be used in the assessment and informed management of reefs with limited data. Finally, the relationship we identify between fish biomass and simple community indicators may be

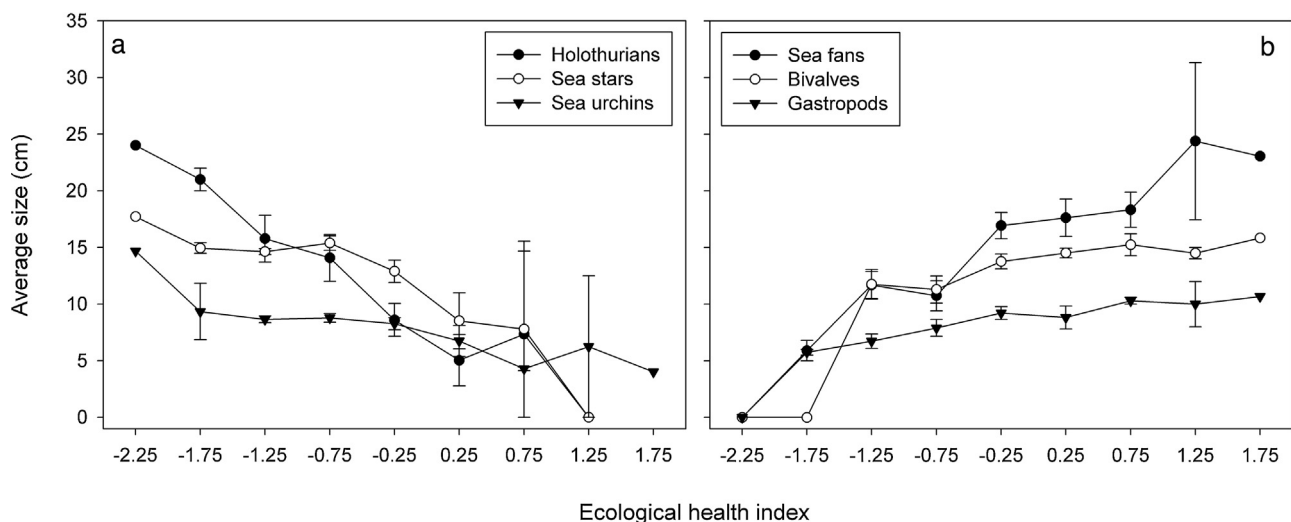


Fig. 3. Relationship between the average size of macro-invertebrates and the ecological health index. (a) Invertebrate groups that show a negative relationship between average size and reef health; (b) invertebrate groups that show a positive relationship between average size and reef health.

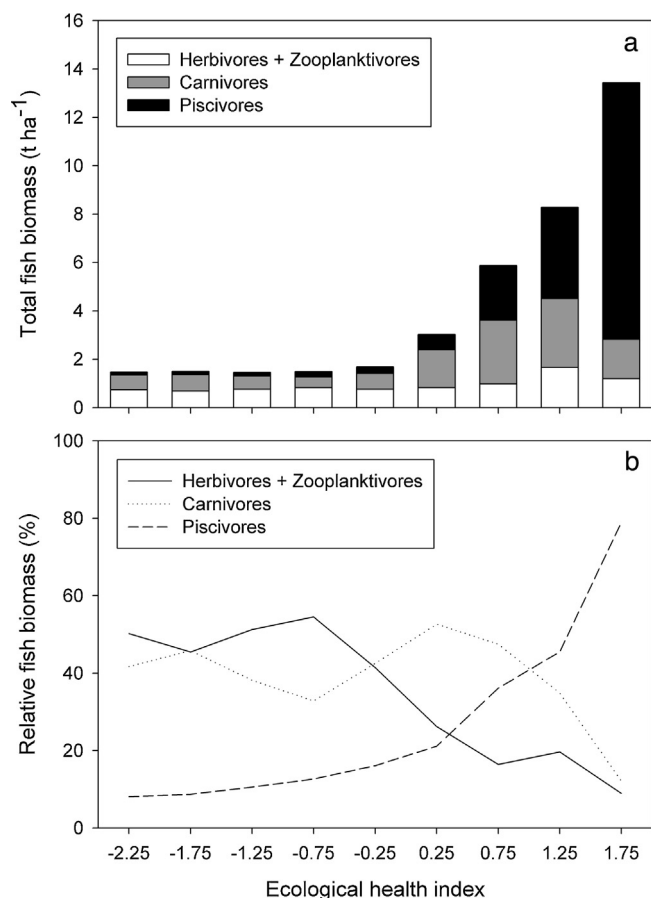


Fig. 4. Relationship between fish biomass, fish community structure and the ecological health index. (a) Absolute and (b) relative biomass of different trophic groups. All regression models were significant ($P < 0.01$).

useful in estimating fishable reef biomass and setting extraction thresholds and localized catch limits (Honey et al., 2010) as well as generating maps of actual and potential fish biomass, which can be used in turn to prioritize areas best suited for NTMRs (Knudby et al., 2011).

4.2. Ecological meanings

The decline of high trophic groups is likely to have long-term and cascading effects throughout community assemblages (Mumby et al., 2006). One notable change is the relative increase in the abundance of lower trophic groups due to the loss of top-down forces like predation and competition (Dulvy et al., 2000; Edgar et al., 2011). The ecological gradient detected in this study simply highlights different stages of the “fishing down the food web” phenomenon, i.e., the decline in average size and trophic level of harvested species (Pauly et al., 1998) within our study reefs. In protected reefs, the size of bivalves and gastropods was up to three times bigger than open access reefs. In the same way, more than 40% of the biomass in protected reefs may be represented by piscivores; while on reefs with intermediate health, more than 50% of the biomass was comprised of carnivores and, in unprotected reefs, more than 60% of the biomass was composed of zooplanktivorous and herbivorous fish.

Overlaying biomass pyramids onto the gradient of health (Fig. 4a) further demonstrates the effect of exploitation and the importance of proper baselines in interpreting our findings. The presence of inverted biomass pyramids have been documented in remote, isolated coral reefs (Friedlander and DeMartini, 2002;

Sandin et al., 2008) and in freshwater and marine plankton (Gasol et al., 1997; Moustaka-Gouni et al., 2006). However, here we have confirmed that the inversion of a biomass pyramid occurs within the gradient of IRH values. The inversion of the biomass pyramid is likely related to the higher growth and mortality rates of prey and higher longevity of predators, well-mixed populations with large prey turnover rates, and prey immigrations, and non-mixed populations where the prey can hide in refuges (Valentine and Heck, 2005; Wang et al., 2009). In any case, all of the aforementioned scenarios occur where reef communities are undisturbed, without the alteration of the community structure and function from overfishing.

4.3. Complex versus simple reefs

The index proposed here, coupled with a simple descriptor of the geomorphologic structure of the reef (complex vs simple), can predict the total fish biomass at each reef. Unprotected/high fishing pressure reefs of both types, complex and simple, all seem to support similar levels of biomass ($\sim 1\text{--}2\text{ t ha}^{-1}$). These levels of biomass increase, as expected, when a reef is protected, with complex reefs sustaining larger maximum levels of biomass (as much as $5\text{--}10\text{ t ha}^{-1}$) compared to simple reefs ($2\text{--}4\text{ t ha}^{-1}$). This difference in potential biomass strongly justifies the preferential establishment of NTMRs in complex reef systems rather than simple reefs (Palumbi et al., 2008). Additionally, our IRH gradient provides insight regarding the potential gains in total fish biomass that may result from the conservation (Micheli and Halpern, 2005) and protection of more complex reefs (Mora et al., 2011).

Since the costs of marine reserve enforcement are related to the size of the reserve and the distance of reefs from local, coastal administrations centers (Balmford, 2004), and not inherent geomorphologic structures of the reefs, the cost differences associated with protecting complex versus simple reefs are negligible. However, the magnitude and rate of recovery between both kinds of reefs are likely to be considerably different. Additionally, more complex interactions are present at complex reefs, where higher densities and total biomass of piscivores and carnivores can be recorded. Taking into account the importance of geomorphologic characteristics of reefs, complex rather than simple reefs, will be the ones that truly generate spillover effects into local fisheries and will mitigate the total cost of protective measures (Stobart et al., 2009). The characteristics of complex reefs are known to impact reef productivity (Friedlander et al., 2003), by directly influencing the standing stocks through nutrient inputs or, indirectly, by affecting larval delivery. Additionally, complex reefs are known to support higher abundances and biomasses of predatory reef fishes (groupers, jacks, snappers, etc.), which is related to their bathymetry, exposure to nutrient rich waters, currents for dispersal, etc. (Heyman and Kjerfve, 2008) compared to simple reefs. Future work must conduct cost-benefit analyses (including all elements of social capital and costs of protecting a community's fishing grounds) of the tradeoff between protection and initial reductions in local fishery yields to understand the optimal arrangement of NTMR reefs and effective management regimes for interconnecting areas.

Author contributions

OAo, EE, BE, TR originally formulated the idea. OAo, JM, ASR, IMO, CSO developed methodology. JM, ASR, IMO, CSO conducted fieldwork. OAo, EE, JM generated data analyses. OAo, EE, IMO performed statistical analyses, and OAo, EE, ASR, BE, TR wrote the manuscript.

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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.ecolind.2014.12.006>.

References

- Aburto-Oropeza, O., Balart, E.F., 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar. Ecol.* 22, 283–305.
- Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., Sala, E., 2008. Mangroves in the Gulf of California increase fishery yields. *Proc. Natl. Acad. Sci. U.S.A.* 105, 10456–10459.
- Aburto-Oropeza, O., Erisman, B., Galland, G.R., Mascareñas-Osorio, I., Sala, E., Ezcurra, E., 2009. Large Recovery of Fish Biomass in a No-Take Marine Reserve. *PLoS One* 6, e23601.
- Balmford, A., 2004. The worldwide costs of marine protected areas. *Proc. Natl. Acad. Sci.* 101, 9694–9697.
- Beaumont, N.J., Austen, M.C., Mangi, S.C., Townsend, M., 2008. Economic valuation for the conservation of marine biodiversity. *Mar. Pollut. Bull.* 56, 386–396.
- Cinner, J.E., McClanahan, T.R., Graham, N.A.J., Daw, T.M., Maina, J., Stead, S.M., Wamukota, A., Brown, K., Bodin, Ö., 2012. Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Global Environ. Change* 22, 1–9.
- Dulvy, N.K., Freckleton, R.P., Polunin, N.V.C., 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol. Lett.* 7, 410–416.
- Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., Reynolds, J.D., 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conserv. Biol.* 14, 283–293.
- Edgar, G.J., Banks, S.A., Bessudo, S., Cortés, J., Guzmán, H.M., Henderson, S., Martínez, C., Rivera, F., Soler, G., Ruiz, D., Zapata, F.A., 2011. Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern Tropical Pacific seascape. *Global Ecol. Biogeogr.* 20, 730–743.
- Edgar, G.J., Barrett, N.S., Stuart-Smith, R.D., 2009. Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. *Ecol. Appl.* 19, 1967–1974.
- Edgar, G.J., Bustamante, R.H., Fariña, J.M., 2004. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environ. Conserv.*
- Edgar, G.J., Stuart-Smith, R.D., 2009. Ecological effects of marine protected areas on rocky reef communities—a continental-scale analysis. *Mar. Ecol.—Prog. Ser.* 388, 51–62.
- Erisman, B.E., Galland, G.R., Mascareñas, I., Moxley, J., Walker, H.J., Aburto-Oropeza, O., Hastings, P.A., Ezcurra, E., 2011. List of coastal fishes of Islas Marías archipelago, Mexico, with comments on taxonomic composition, biogeography, and abundance. *Zootaxa* 2985, 26–40.
- Floeter, S., Halpern, B., Ferreira, C., 2006. Effects of fishing and protection on Brazilian reef fishes. *Biol. Conserv.* 128, 391–402.
- Friedlander, A.M., DeMartini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol.—Prog. Ser.* 230, 253–264.
- Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R., Rodgers, K.S., 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22, 291–305.
- Gasol, J.M., del Giorgio, P.A., Duarte, C.M., 1997. Biomass distribution in marine planktonic communities. *Limnol. Oceanogr.* 42, 1353–1363.
- Gower, J., 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53, 325–338.
- Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., 2008. Italian marine reserve effectiveness: does enforcement matter? *Biol.* 141, 699–709.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13, S117–S137.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952.
- Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., 1985. Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Revue d'écologie* 40, 467–540.
- Hawkins, J.P., Roberts, C.M., Dytham, C., Schelten, C., 2006. Effects of habitat characteristics and sedimentation on performance of marine reserves in St. Lucia. *Biol. Conserv.* 127, 487–499.
- Heyman, W.D., Kjerfve, B., 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science* 83, 531–551.
- Honey, K.T., Moxley, J., Fujita, R., 2010. From rags to fishes: data-poor methods for fishery managers. *Managing data-poor fisheries: case studies. Models Solutions* 1, 159–184.
- Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., Steneck, R.S., 2010. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25, 633–642.
- Jackson, D.A., 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology* 74, 2204–2214.
- Jennings, S., Blanchard, J.L., 2004. Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* 73, 632–642.
- King, J.R., Jackson, D.A., 1999. Variable selection in large environmental data sets using principal components analysis. *Environmetrics* 10, 67–77.
- Knudby, A., Roelfsema, C., Lyons, M., Phinn, S., Jupiter, S., 2011. Mapping fish community variables by integrating field and satellite data, object-based image analysis and modeling in a traditional fijiian fisheries management area. *Remote Sens.* 3, 460–483.
- Lester, S.E., Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. *Mar. Ecol.—Prog. Ser.* 367, 49–56.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C., Airoldi, L., 2011. Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26, 1–11.
- Mascareñas-Osorio, I., Erisman, B., Moxley, J., Aburto-oropeza, E.B.O., 2011. Checklist of conspicuous reef fishes of the Bahía de los Ángeles region, Baja California Norte, Mexico, with comments on abundance and ecological biogeography. *Zootaxa* 2922, 60–68.
- McClanahan, T.R., 2011. Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs—Maldives vs. Kenya. *Aquat. Conserv.: Mar. Freshwater Ecosyst.* 21, 186–198.
- McClanahan, T.R., Graham, N.A.J., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.* 17, 1055–1067.
- McClanahan, T.R., Graham, N.A.J., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H., Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc. Natl. Acad. Sci.* 108, 17230–17233.
- Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* 8, 391–400.
- Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecol. Appl.* 14, 1709–1723.
- Mora, C., Aburto-Oropeza, O., Ayala Bocos, A., Ayotte, P.M., Banks, S., Bauman, A.G., Beger, M., Bessudo, S., Booth, D.J., Brokovich, E., Brooks, A., Chabanet, P., Cinner, J.E., Cortés, J., Cruz-Motta, J.J., Cupul Magaña, A., DeMartini, E.E., Edgar, G.J., Feary, D.A., Ferse, S.C.A., Friedlander, A.M., Gaston, K.J., Gough, C., Graham, N.A.J., Green, A., Guzman, H., Hardt, M., Kulbicki, M., Letourneur, Y., López Pérez, A., Loreau, M., Loya, Y., Martínez, C., Mascareñas-Osorio, I., Morove, T., Nadon, M.-O., Nakamura, Y., Paredes, G., Polunin, N.V.C., Pratchett, M.S., Reyes Bonilla, H., Rivera, F., Sala, E., Sandin, S.A., Soler, G., Stuart-Smith, R., Tessier, E., Tittensor, D.P., Tupper, M., Usseglio, P., Vigliola, L., Wantiez, L., Williams, I., Wilson, S.K., Zapata, F.A., 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol.* 9, e1000606.
- Moustaka-Gouni, M., Vardaka, E., Michaloudi, E., 2006. Plankton food web structure in a eutrophic polymictic lake with a history in toxic cyanobacterial blooms. *Limnol. Oceanogr.* 51, 715–727.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sancheziro, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311, 98–101.
- Newman, M.J.H., Paredes, G.A., Sala, E., Jackson, J.B.C., 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecol. Lett.* 9, 1216–1227.
- Newton, K., Côté, I.M., Pilling, G.M., Jennings, S., Dulvy, N.K., 2007. Current and future sustainability of island coral reef fisheries. *Curr. Biol.* 17, 655–658.
- Palumbi, S.R., McLeod, K.L., Gruenbaum, D., 2008. Ecosystems in action: lessons from marine ecology about recovery, resistance, and reversibility. *BioScience* 58, 33–42.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Pielou, E.C., 1984. *The Interpretation of Ecological Data: A Primer on Classification and Ordination*. Wiley-Interscience, New York, NY, pp. 288.
- Pinca, S., Kronen, M., Magron, F., McArdle, B., Vigliola, L., Kulbicki, M., Andréfouët, S., 2011. Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island Countries and Territories. *Fish Fish.* 13, 361–379.
- Pollnac, R., Christie, P., Cinner, J.E., Dalton, T., Daw, T.M., Forrester, G.E., Graham, N.A.J., McClANAHAN, T.R., 2010. Marine reserves as linked social-ecological systems. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18262–18265.

- Rife, A.N., Erisman, B., Sanchez, A., Aburto-Oropeza, O., 2012. When good intentions are not enough . . . Insights on networks of “paper park” marine protected areas. *Conserv. Lett.* 6, 200–212.
- Roberts, C.M., 1995. Rapid build-up of fish biomass in a caribbean marine reserve. *Conserv. Biol.* 9, 815–826.
- Russ, G.R., Stockwell, B., Alcalá, A.C., 2005. Inferring versus measuring rates of recovery in no-take marine reserves. *Mar. Ecol. Prog. Ser.* 292, 1–12.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., Dayton, P.K., 2002. A general model for designing networks of marine reserves. *Science* 298, 1991–1993.
- Sala, E., Aburto-Oropeza, O., Reza, M., Paredes, G., López-Lemus, L.G., 2004. Fishing down coastal food webs in the Gulf of California. *Fisheries* 29, 19–25.
- Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the Northern line Islands. *PLoS One* 3, e1548.
- Stobar, B., Warwick, R., González, C., Mallol, S., 2009. Long-term and spillover effects of a marine protected area on an exploited fish community. *Marine ecology progress series* 384, 47–60.
- Tegner, M.J., Dayton, P.K., 2000. Ecosystem effects of fishing in kelp forest communities. *ICES J. Mar. Sci.* 57, 579–589.
- Turner, S., Thrush, S., Hewitt, J., Cummings, V., Funnell, G., 1999. Fishing impacts and the degradation or loss of habitat structure. *Fish. Manage. Ecol.* 6, 401–420.
- Tyler, E.H.M., manica, A., Jiddawi, N., Speight, M.R., 2011. A role for partially protected areas on coral reefs: maintaining fish diversity? *Aquat. Conserv.: Mar. Freshwater Ecosyst.* 21, 231–238.
- Valentine, J.F., Heck Jr., K.L., 2005. Perspective review of the impacts of overfishing on coral reef food web linkages. *Coral Reefs* 24, 209–213.
- Wang, H., Morrison, W., Singh, A., Weiss, H.H., 2009. Modeling inverted biomass pyramids and refuges in ecosystems. *Ecol. Modell.* 220, 1376–1382.
- Wantiez, L., Thollot, P., 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* 16, 215–224.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790.
- Zeller, D., Pauly, D., 2005. Good news, bad news: global fisheries discards are declining, but so are total catches. *Fish Fish.* 6, 156–159.