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Functional community structure of shallow hard bottom communities at Easter Island (Rapa Nui)

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ABSTRACT. Important, often abrupt, and irreversible shifts associated with the degradation of ecosystem functioning and services are increasingly commonplace. Thus, a trait-based view of communities may be more insightful than that based solely on species composition, especially when inferring ecological responses to environmental change. This underscores the importance and urgency of establishing benchmarks against which future community changes and functional structure can be evaluated. As a first step toward setting these baselines and their current spatial variability, we here describe geographic and among-habitat patterns in the functional structure of shallow hard bottom communities, including fish assemblages, across the northeast and west coasts of Rapa Nui. We also document temporal patterns of change in dominant benthic functional groups that have taken place over the past 15 years at selected sites on this isolated Pacific island. Generally weak vertical zonation patterns were observed, with most striking differences due to the paucity of branching pocilloporid corals in shallow waters (<7 m), where massive corals of *Porites* predominate. We identified three main 'groups' of sites in terms of the relative abundance of major functional groups and these did not follow geographic arrangement or strict coastline orientation. The similar spatial change in benthic and fish functional community structure documented here suggests there may be strong coupling with coastal oceanographic conditions that varies on scales of 1s-10s of km. Temporal patterns document relatively rapid recovery of total coral cover, largely via compensatory change in relative coral composition with an increase in *Porites* upon abrupt decline of *Pocillopora*, following extensive coral mortality caused by thermal stress (coral bleaching) in 2000. Moreover, coral abundance in shallow habitats increased beyond pre-disturbance levels (*i.e.*, 1999-2000). In contrast to shallow habitats, corals again suffered extensive mortality and reduced cover by 2005 at mid- (10-15 m) and deep (>15 m) habitats, with contrasting recovery. These results suggest depth-dependent disturbance regimes that differ in types and frequency of events, as well as capacity to recover. Overall, our results highlight the apparent resilience of the current system and provide a first-cut benchmark as to where management subsystems might be prescribed so as to spatially match ecosystem characteristics.

Keywords: functional groups, community structure, coral, fish assemblages, Easter Island, Chile.

Estructura funcional de comunidades que habitan sobre los fondos duros de Isla de Pascua (Rapa Nui)

RESUMEN. Importantes, abruptos e irreversibles son los cambios asociados con la degradación del funcionamiento de los ecosistemas. Por ello, una visión basada en las características funcionales de las comunidades puede entregar más información que aquella basada en la composición de especies, especialmente cuando el medio ambiente influye sobre respuestas ecológicas. Esto resalta la importancia y la urgencia de establecer parámetros y líneas base para detectar y evaluar posibles cambios futuros en la estructura funcional de los sistemas. Como primer paso hacia este tipo de línea base y su la variabilidad espacial actual, se describen los patrones a escala geográfica en la estructura funcional dentro de los hábitat en comunidades someras de fondos rocosos, incluyendo ensambles de peces y comunidades macrobentónicas a través de la costa noreste y oeste de Rapa Nui. También se demuestran cambios en los patrones temporales de los grupos bentónicos funcionales dominantes en los últimos 15 años en algunos puntos de esta aislada isla del Pacífico. Generalmente se observa una zonación vertical débil, con una notable diferencia debido a la escasez de corales arborescentes como *Pocillopora* en aguas someras (<7 m profundidad) donde corales masivos como *Porites* son predominantes. Según la abundancia relativa de los grupos funcionales, se determinaron tres agrupaciones de

sitios muestreados no consistentes con la disposición geográfica o con la orientación costera. El patrón similar de cambios espaciales en la estructura funcional comunitaria bentónica y de los ensambles de peces sugiere la existencia de acoplamiento con las condiciones oceanográficas costeras que varían a escalas de 1s-10s de km. Los patrones temporales indican una rápida recuperación en la cobertura de corales, principalmente a través de un cambio compensatorio en la composición relativa del coral con un aumento de *Porites* respecto a una abrupta disminución de *Pocillopora*, después de sufrir una elevada mortalidad de los corales en el año 2000, a causa del estrés térmico (blanqueamiento de los corales). Por otra parte, aumenta la abundancia de los corales en hábitat someros respecto a los niveles previos a la perturbación (*i.e.*, 1999-2000). En contraste con el hábitat somero, los corales nuevamente sufrieron una extensiva mortalidad reduciendo su cobertura en el 2005 en hábitat de profundidades medias (10-15 m) y profundas (>15 m) con recuperación contrastante. Estos resultados sugieren regímenes de perturbaciones dependientes de la profundidad, los cuales difieren tanto en la frecuencia de ocurrencia como en la capacidad de recuperación. En general, nuestros resultados destacan la resiliencia aparente del sistema actual y proveen una primera guía para el manejo de subsistemas dentro de la isla que se asemejan a aquellos patrones entregados por las características de los ecosistemas circundantes de fondo rocoso de Rapa Nui.

Palabras clave: grupos funcionales, estructura comunitaria, corales, ensambles de peces, Isla de Pascua, Chile.

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INTRODUCTION

The occurrence of ecological regime shifts (also referred to as phase shifts, alternate stable states or tipping points), which evoke change in the internal governing dynamics and feedbacks of an ecosystem (Hughes, 1994; Scheffer *et al.*, 2001; Levin & Lubchenco, 2008; Hughes *et al.*, 2010; Barnosky *et al.*, 2012), has become increasingly commonplace in all ecosystems of our planet. Since such rapid wholesale changes to community structure can dramatically alter the very ecosystem functions/services on which humans rely, there is good reason for the growing concern not only by scientists, but by the population at large. Causes are complex, usually involving the interaction of two or more major drivers of change, but often appear to be associated with weakening or outright loss of key functional groups of species, which through varied mechanisms can increase system resilience and/or vulnerability to human-related disturbance (Scheffer *et al.*, 2001). The demonstrated relationship between species and functional group diversity on ecosystem functioning has reinforced the idea that a trait-based view of communities may be more meaningful/insightful than that based solely on species composition, especially when inferring ecological responses to environmental change (Stuart-Smith *et al.*, 2013). Toward this endeavor, characterizing the temporal variability or persistence, as well as spatial organization of functional community structure, is indeed a critical step for early detection of warning signals of an imminent regime shift and/or propagation of localized regime shifts to larger scales (Hughes *et al.*, 2010; Fung *et al.*, 2013).

Coral reef ecosystems living near the limit of individual species thermal tolerances appear to be

undergoing global degradation, as symbolized by the seemingly increasing occurrence of dramatic regime shifts from hard coral dominance to a state dominated by fleshy macroalgae (Done, 1992; Hughes, 1994; Nyström *et al.*, 2000; Bellwood *et al.*, 2004). While studies have demonstrated the interaction of multiple causes (*e.g.*, increased run off and sea surface temperature) induced by human damage, changes in grazing regimes associated with depleted herbivore abundances (*e.g.*, from over-fishing) appear to be a common and critical denominator in most documented examples of extensive coral mortality that follows bleaching induced, for instance, by anomalously high temperature events (*e.g.*, Hughes, 1994; Jackson *et al.*, 2001; Wellington & Glynn, 2007; Baker *et al.*, 2008; Edwards *et al.*, 2014). Indeed, fast-growing macroalgae can rapidly colonize and inhibit coral recovery and thus reduced herbivory has been invoked as a critical symptomatic driver of eroding reef resilience and coral-macroalgal regime shifts (McCook *et al.*, 2001; Jompa & McCook, 2002; Diaz-Pulido *et al.*, 2009). Despite the demonstrated connection between variation in diversity and abundance of functional groups and community resilience (Cheal *et al.*, 2010), few studies have documented changes to functional structure over relevant landscape and inter-annual timescales.

Rapa Nui, or Easter Island, is the most isolated island in the Pacific Ocean, so the existence there of relatively depauperate (species poor) communities with high levels of endemism is not surprising. The comparatively brief history of scientific studies of Rapa Nui's coral reef communities, along with compilations of taxonomic inventories, were previously reviewed for marine benthic flora by Santelices & Abbott (1987), for invertebrates by Castilla & Rozbaczylo (1987) and

Glynn *et al.* (2003, 2007), and for nearshore fishes by Castilla & Rozbaczylo (1987); Ojeda & Aviles (1987) and Sepúlveda (1987), with notable recent updates on zooxanthellate corals (Glynn *et al.*, 2007) and fishes (Randall & Cea, 2011).

The ecology of shallow, subtidal, hard bottom communities around the island is still poorly studied. General benthic community surveys were first made by DiSalvo in the mid 1980's (DiSalvo *et al.*, 1988), but were not quantitatively surveyed again until the late 1990's (Hubbard & Garcia, 2003; Glynn *et al.*, 2007). Apart from our own irregular surveys since 1999 (see below), a recent expedition supported by the Chilean government and the National Geographic Society, and other foundations (Waitt Foundation, Oceana Chile), surveyed and compared benthic communities of Rapa Nui to nearby Salas y Gómez Island, documenting important between-island differences in community structure driven largely by the relatively lower fish abundances and scarce apex predators observed at Rapa Nui (Friedlander *et al.*, 2013). Based on anecdotal reports, personal observations and differences among earlier quantitative surveys, Hubbard & Garcia (2003) suggested that shallow water communities around the island undertook an important shift in dominance from macroalgae (particularly *Sargassum*) to coral reefs sometime during the early-mid 1980s. This is particularly notable in light of the opposing trajectory of coral loss described for much of the world's coral reef communities over the past 30 years (Hughes *et al.*, 2007). This further underscores the importance and urgency of establishing baselines against which future community changes and functional structure can be evaluated.

As a first step toward setting these baselines and their current spatial variability, we here describe geographic and among-habitat patterns in the functional structure of shallow hard bottom communities, including fish assemblages, across the northeast and west coasts of Rapa Nui. We also document temporal patterns of change in dominant benthic functional groups that have taken place over the past 15 years at selected sites on this Pacific island. The patterns reported here could also provide guidelines for the much-needed management and conservation plans for this isolated ecosystem.

The system

Rapa Nui lies at the eastern edge of the Subtropical Counter Current and Polynesian Triangle, corresponding to the austral limit of coral distribution. Like many high-latitude subtropical reef-building coral communities (*e.g.*, Veron & Done, 1979), significant limestone reef structures are rare. However, incipient reef formations are observed, with the largest (approx. 7 m

thick) found at depth on the northeast sector of the Poike Peninsula (Hubbard & Garcia, 2003). Yet, in comparison to other subtropical areas, there is high coral cover at most sites, dominated by two of the 13 recognized species for the island, *Porites lobata* and *Pocillopora verrucosa* (Glynn *et al.*, 2003, 2007). Macroalgal cover is generally low in abundance around the island (Glynn *et al.*, 2007), despite relatively high species richness (Santelices & Abbott, 1987).

The fish fauna at Rapa Nui is generally species poor, with only 164 shore and epipelagic species (those that live offshore and near the surface) described (Randall & Cea, 2011). Geographic isolation, lack of lagoonal ecosystems and few protected bays offer plausible explanations of low species richness. Moreover, small-sized individuals characterize fish assemblages and there is notable lack of apex predators (sharks and jacks), with planktivores and herbivores dominating trophic structure (Friedlander *et al.*, 2013).

MATERIALS AND METHODS

Shallow hard bottom communities at six sites spaced 1–10's km apart across the northeast and west coasts were surveyed during irregular visits to the island between 1999–2013 (Fig. 1). All surveys were conducted during austral autumn months (April–May). Benthic communities were surveyed annually between 1999–2001 and 2010–2013 as well as 2005 for a total of 8 years. Not all sites and depths were sampled every year and thus we present temporal patterns of benthic communities only for four locations with the most complete records. Fish assemblages were surveyed annually between 2011–2013. Due to common heavy swell and wave action, combined with difficult access, it was not possible to undertake quantitative samples along the exposed southeast coast. Sites were composed of rocky outcrops openly exposed to oceanic swells and were selected to be as similar as possible in terms of geomorphology, slope, and local orientation. The greatest heterogeneity among sites occurred between the northeast and west coasts, which differ in orientation and wave exposure.

Benthic surveys

At each site, local numerical density of mobile benthic invertebrates (*e.g.*, sea urchins, snails, stars, crabs, limpets, etc.) and spatial cover of sessile species (*e.g.*, corals, macroalgae, sponges, barnacles, etc.) at shallow (<8 m), mid (10–15 m), and deep (17–23 m) zones were quantified at 2–3 rocky reefs using the standard transect-quadrat method, as described in detail in Wieters *et al.* (2009). A minimum of ten 0.25 m² quadrats, each with 81 systematic point grids, regularly placed along 50 m transects stretched parallel to the shoreline (along depth contour) were sampled and photo-

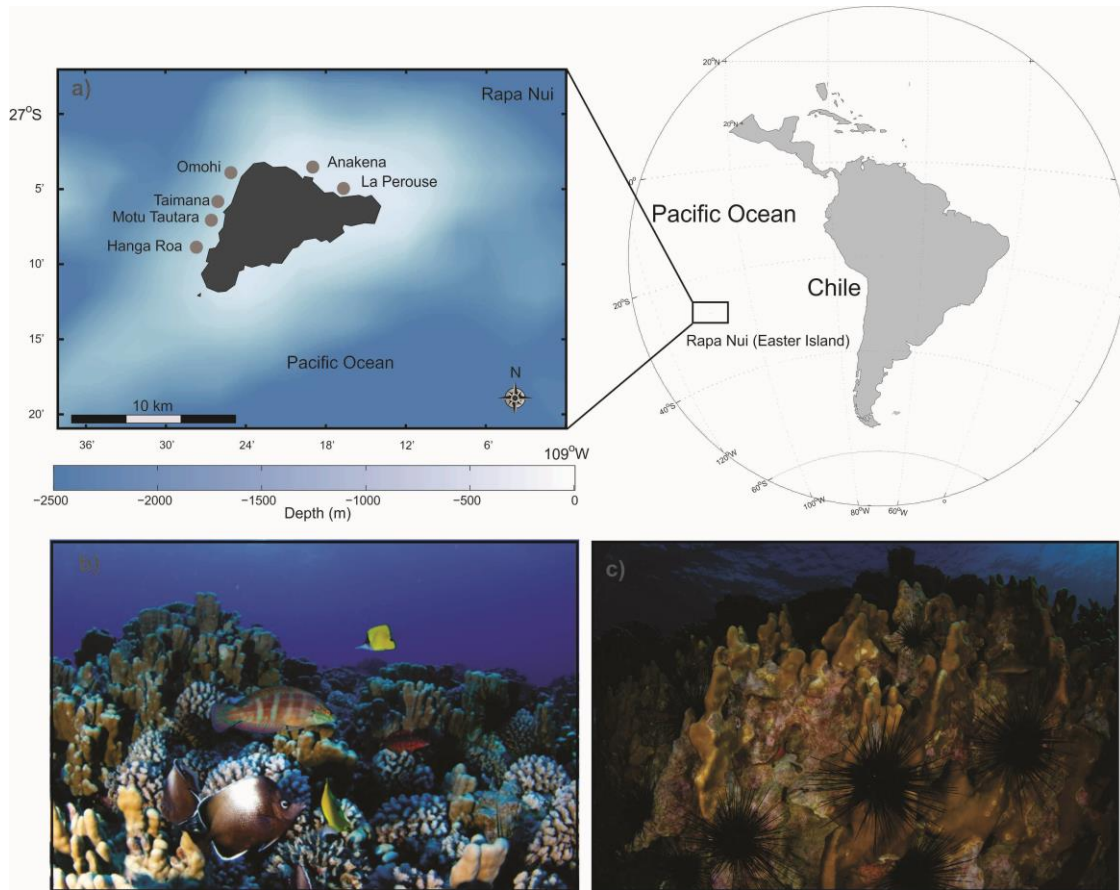


Figure 1. a) Map of Rapa Nui and study region indicating the positions of survey sites. Branching and massive corals typically dominate rock substrates, b) relatively high abundance of *Pocillopora* in mixed assemblages characterizes northwest coast sites whereas, c) large mono-specific patches of *Porites lobata* among smaller patches of mixed assemblages are relatively more common elsewhere.

graphed. Because of their large size and sparse or clumped distribution, densities of sea urchins were estimated by counting the number of individuals within a minimum of 15 randomly placed large 1 m² plots. Due to local geomorphology and topography, not all zones were present at all sites. Cover of species inhabiting primary space (attached to rock/reef surface) and secondary space (*i.e.*, epibiotic such as algae on corals) was estimated separately, so total cover could exceed 100%. All organisms were resolved to the lowest possible taxonomic level in the field. Areas obviously influenced by sediment abrasion were avoided to standardize suitable substrate habitat and avoid confounding among-site variability with habitat differences. To minimize potential observer-induced biases, ~75% of quadrats across all years were recorded by a single observer (EAW).

Fish surveys

At each study site, local composition and abundance of reef fish at shallow (5-15 m) and deep (15-25 m) zones

were quantified using unbaited video (years, 2011-2013) and underwater visual census (2013). All locations and sites were characterized by similarly low-medium-relief reefs (caves, ledges and overhang relatively scarce). Minimum underwater visibility during all surveys was 35 m. At each zone, an unbaited video camera (Go-Pro tm hero 2-3) was anchored with a 2 kg weight and deployed to record images parallel to the seafloor. A 10 m transect with weighted and vertically positioned, graduated PVC tubes of 30 cm height at every 1 m, was stretched directly in front of the camera to aid in quantification of individual fish size. Cameras were allowed to continuously record 25 to 35 min. Videos were reviewed on a large screen computer monitor. Species presence and the maximum number of individuals (MaxN, Willis *et al.*, 2000) belonging to each species in the field of view at one time were recorded. This provides a conservative estimate of relative density and avoids repeated counts of the same individuals. For each video clip, we obtained subsamples and the calculated area as delimited by tape transects and 20 cm tall tubes placed

3 m apart. We divided by area to standardize estimates to m^2 .

Underwater visual censuses (UVC) were conducted by a single SCUBA diver (APM) that swam along a randomly allocated 50 m strip transect placed perpendicular to the coastline. Observations were delayed 10–15 min after placement of transects to limit and standardize any potential disturbance to fish by the diver. Large (>20 cm TL) and small (<20 cm TL) fish were counted within 4 m or 2 m transect width, respectively, which was equally distributed to the left and right of the observer/diver. Underwater photography aided species identification (see Friedlander *et al.*, 2013). Two replicate transects, separated by 50–65 m, were conducted at each site \times zone combination. Fishes were resolved to lowest possible taxonomic level possible and categorized as endemic or non-endemic species as per Randall & Cea (2011).

We categorized species into one of 8 (benthic) or 5 (fish) functional groups based on a) morphological and anatomical traits related to maximum possible rate of biomass production (mass-specific growth; ability to quickly assimilate nutrient availability) and resistance to herbivory [algae; largely following Steneck & Dethier (1994) with grouping modifications similar to Broitman *et al.* (2001) and Wieters *et al.* (2009)] or b) trophic level and foraging strategy [invertebrates and fishes; DiSalvo *et al.* (2007); Halpern & Floeter (2008); Randall & Cea (2011)]. Benthic: 1) ephemeral algae, 2) corticated algae, 3) leathery algae, 4) crustose algae, 5) corals, 6) filter feeders, 7) herbivores, and 8) predators. Fishes: 1) herbivores, 2) planktivores, 3) invertivores, 4) omnivores, and 5) piscivores.

Data analysis

To compare abundances of functional groups among habitats, 1-way ANOVAs, with depth zone considered as a fixed factor and abundance per site and year as replicates were used. A completely factorial design with depth, site, and year was not possible due to incomplete information for several sites and/or years. To evaluate spatial consistency of differences in functional group abundance across depth (zones), a 2-way ANOVA was used, with zone considered a fixed factor and sites considered a random factor. Significant 2-way interaction required depth zone to be considered separately in further analyses of spatial patterns in functional group abundance (see Results).

To evaluate temporal consistency of among-site spatial patterns in mid depth (8–15 m) functional group abundance, a 2-way ANOVA with site and year (2012 or 2013) was used. Separate analyses were undertaken

for individual functional groups. In all cases a $\log(n+1)$ transformation was applied to meet ANOVA assumptions. Multivariate characterization of variability in benthic functional structure across the island was performed with principal component analyses (PCA) and non-metric multidimensional scaling (NMDS) with individual functional groups as dependent variables.

For each fish sampling method (video *vs* visual surveys), fish species richness (total number of species recorded), diversity (Simpson's Diversity Index) and numerical abundances (relative density of each species-individuals m^{-2}) were similar between depth zones, regardless of site and sampling year ($P > 0.05$ for main effect of Zone and Site \times Year interactions in 3-way ANOVA) and thus zones were pooled in further analyses (see below).

To assess potential methodological biases in characterization of fish assemblages, overall site-specific fish species richness was compared using unpaired t-test for the simultaneously recorded video and visual surveys conducted in 2013.

Multivariate characterization of variability in fish species composition across the island was performed with Jaccard or Bray-Curtis resemblance matrices with presence/absence (video and visual surveys) or abundance (visual surveys only) of individual species as dependent variables, respectively. To evaluate similarity in composition among sites, depth zones, and years, a three factor permutational multivariate analysis of variance was used for estimates based on presence/absence data. Among-site differences in composition based on abundance estimates were analyzed using a one factor permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001).

We performed a redundancy analysis (RDA) of the abundant species and functional groups for fishes and sea urchins against major sessile benthic functional groups. We selected this constrained method due to our *a priori* hypothesis of the possible effects of coral reef structure on abundances of reef fishes and sea urchins (*Diadema savignyi*). To test for associations among fish abundances and benthic functional structure, we performed the PERMANOVA routine among sites. We used the Hellinger transformation of the fish and point-count data; this transformation makes the data agreeable for the types of analyses performed here (Legendre & Legendre, 1998). We used RDA to graphically display the differences of the most abundant species among the study sites, and report the contribution of each constraint. All analyses were conducted using the R package 'vegan' (<http://www.r-project.org/>).

RESULTS

Benthic community functional structure

Zonation

In general (all sites and years pooled), total abundances of mobile and sessile organisms were similar across depths (mobile: $MS = 87.41$, $F_{1,43} = 0.24$, $P = 0.63$; sessile: $MS = 191.30$, $F_{1,43} = 2.65$, $P = 0.11$), with sessile organisms covering on average 66-87% of available substrate space. However, the relative contribution of some key functional groups differed (Fig. 2). Dominant space-occupying corals presented lowest cover at shallow (<5 m) and highest cover at mid (9-13 m) depth, which largely reflected the near absence of *Pocillopora* near the surface and its increasing relative contribution with depth (Fig. 2 insert). Likewise, ephemeral algae (largely *Lobophora* sp.) exhibited increasing abundance with depth, though average covers never reached greater than 10%. In contrast, leathery (mainly *Padina* sp.) and overall scarce (<3%) articulated (predominantly *Halimeda* sp.) algae were relatively more abundant at shallow depths. No clear pattern for benthic herbivores (predominantly the urchin *Diadema savignyi*) was observed across depth zones, whereas corallivore snails (*Coralliophora violacea*) were absent near the surface and most abundant at deeper locations.

Spatial structure across the island

Live coral consistently dominated substrates at all sites (60-80% cover), but showed significant among-site variation that persisted between years (Fig. 3, non-significant Site x Year interaction, see Table 1). Tukey tests revealed that differences were largely due to the significantly lower overall coral abundance at Taimana, which differed from Hanga Roa and northeast coast sites (Le Perouse, Anakena) that are characterized by large monospecific patches of *Porites lobata* among smaller patches of mixed assemblages. Relatively higher abundance of *Pocillopora* is found on the northwest coast (Tautara, Taimana, Omohi), where it commonly occurs in near pure stand patches and can reach similar abundance as *Porites* (e.g., Tautara; Fig. 3 insert). Algal abundance was generally low but varied significantly among sites and between years (Table 1). Regardless of year, dominant algal functional groups (primarily ephemerals but also articulated) presented peak abundances along the northwest tip of the island (Omohi, Taimana). Abundances of ephemerals and articulated macroalgae were higher during 2012 and 2013, respectively, at all sites (significant Time effect), but the spatial pattern persisted (non-significant Site x Time interaction). Crusts and leathery algae were absent from all but a few sites along the northwest coast, where they never reached greater than 2% cover

(Fig. 3). No clear patterns were observed for benthic herbivores (mainly sea urchins), though densities varied greatly among sites.

The multivariate characterization of benthic functional community structure showed marked spatial differentiation across the island, with geographic neighbors not always showing obvious similarity (Fig. 4). Important separation was observed between three groups of sites: 1) Anakena, Le Perouse, and Hanga Roa, 2) Omohi and Taimana, and 3) Tautara alone. The first two principal components explained 54% and 33% of the variation, respectively, with groups primarily separated on component 1 and secondarily (but still important) on component 2. PC1 reflected a combination of most all functional groups, with all but *Porites* being relatively similarly weighted. PC2 was most strongly weighted by *Porites* and ephemeral algae, followed by *Pocillopora*.

Temporal variation at selected sites

Temporal trends in total coral cover differed among depths (Fig. 5). While coral increased over time at our two shallow sites (Anakena and Hanga Roa), cover abruptly decreased in 2005, and remained low, at the relatively deep (>15 m) location of Taimana. The patterns in total coral cover were largely driven by massive *Porites*, particularly after 2000 when a sharp decline in branching corals (*Pocillopora*) was observed at most sites (Fig. 6). No clear temporal trend was observed at mid-depth (10-15 m) sites, although a notable decline in coral cover was again observed in 2005 at Taimana (Fig. 5). A trend to increasing abundance of articulated/calcified algae was observed at all sites, though overall cover was consistently low (<5%). No consistent temporal patterns were observed for crustose algae, which showed relatively high abundances at Tautara and Taimana during 2001. At all sites, cover of ephemerals increased and reached peak abundances during 2010, after which cover quickly decreased to near-absent again at all sites but Taimana. At all sites, leathery algae presented elevated abundances of relatively short duration (few years) between 2000-2005, with marked peaks at mid and deep locations of Taimana during 2005.

Fish species composition

Our fish surveys documented a total of 45 species from 25 families, with 24% of sighted species being endemic to the island (Table 2). The total number of species observed was similar between sampling methods ($P > 0.05$), with 36 (80%) recorded by visual census and 39 (87%) by unbaited video. However, unbaited video better captured the presence of those species that typically tend to avoid divers (butterflyfishes, girellids),

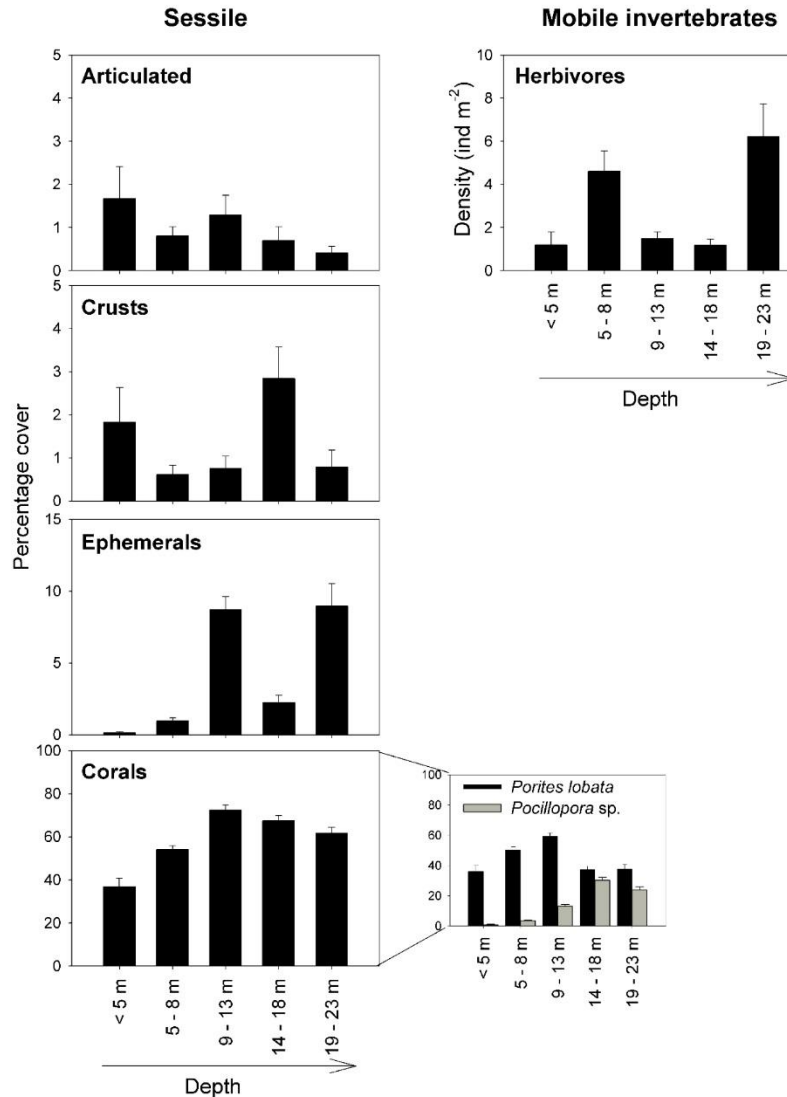


Figure 2. Mean percentage cover and density (\pm SE) of dominant sessile and mobile benthic invertebrate functional groups, respectively, across varying sub-tidal depth zones. Note the different y-axis scales used.

whereas visual census proved better in documenting the presence of relatively small cryptic species associated with complex microhabitats such as crevices (e.g., blennies). The distribution of species across functional groups was not even (Fig. 7). The numbers of species that comprised a given functional group (species richness) was strikingly lower for apex fish predators (piscivores), whereas invertebrate feeders were the most species-rich group.

Species composition of local fish assemblages showed significant spatial structure among sites, regardless of whether estimates were based on presence/absence (Permanova, $df = 6$, pseudo $F = 2.6$, $P < 0.001$) or abundances (Permanova, $df = 4$, pseudo $F = 2.8$, $P < 0.001$). In general, sites at the northwestern side of the island grouped together and differed from all

other sites. Spatial differences were largely due to variable presence and abundances of *Centropyge hotumatua*, *Acanthurus leucopareius* and *Chrysiptera rapanui*.

Abundances of individual functional groups

In general, total abundances of fishes (species/functional groups pooled) were low at all sites (0.4–1.5 ind m^{-2}), but varied significantly across the island (Kruskal-Wallis test, $df = 4$, $P < 0.05$), with overall highest densities observed at Taimana (1.5 ind m^{-2}) and Anakena (1.4 ind m^{-2}) and lowest at Omohi (0.4 ind m^{-2}). High among-site variability was common for individual functional groups (Fig. 8). Invertivores were most abundant at the northeast coast site of Anakena, where densities were at least twice that observed else-

Table 1. Two-way ANOVA tests of functional group abundances in relation to site and year. Bold values are significant at $\alpha = 0.05$.

	df	SS	F	P
Ephemerals				
Site	4	1226.64	3.94	0.0049
Year	1	1127.31	14.49	0.0002
Site x Year	4	415.81	1.34	0.2606
Error	116	11764.76		
Articulated				
Site	4	85.46	5.49	0.0005
Year	1	78.75	20.11	<0.0001
Site x Year	4	21.77	1.40	0.24
Error	107	416.65		
Crusts				
Site	4	5.05	1.87	0.1198
Year	1	3.19	4.73	0.0317
Site x Year	5	5.05	1.87	0.1198
Error	116	78.24		
Leathery				
Site	4	2.68	2.91	0.0244
Year	1	0.07	0.31	0.5774
Site x Year	4	3.11	3.38	0.0118
Error	116	26.67		
Corals				
Site	4	9974.70	6.59	<0.0001
Year	1	33.52	0.09	0.7665
Site x Year	4	740.54	0.49	0.7435
Error	116	43876.63		
Herbivores				
Site	4	0.10	0.52	0.7216
Year	1	0.02	0.45	0.5054
Site x Year	4	0.10	0.52	0.7216
Error	116	5.76		

where. Herbivorous fishes were strikingly more abundant at sites along the northeast coast and northwest tip (Taimana, Omohi) of the island. Piscivores, omnivores, and invertivore/piscivores were scarce at all sites, with the exception of Taimana where invertivore/piscivore abundance was relatively higher and similar to that observed for other functional groups. No clear geographic pattern was observed for fishes with planktivorous diets, which were highly variable among sites, reaching greatest densities of any functional group at Anakena and Taimana.

Fish correspondence with benthic functional community structure

Redundancy analysis (RDA) and permutation tests revealed strong, significant associations between fish functional structure and benthic functional community structure (Fig. 9a; df = 4, pseudo F = 2.9; P -value = 0.005). In general, herbivorous fishes were associated with branching corals (*Pocillopora*), while invertivores

were tightly associated with massive corals (*Porites*). Planktivores were associated with articulated and leathery algae. Benthic functional structure constrained more than 63% of the observed variation in total abundance of fish functional groups. No significant associations were observed for fish assemblage structure when based on individual species composition (Fig. 9b, df = 4, pseudo F = 1.2; P -value = 0.28).

DISCUSSION

Our results offer an important benchmark for understanding and recognizing future functional changes at the community level, placing them in light of existing spatial structure and temporal variability over the past 15 years. Our studies, like all available quantitative surveys for the island, were initiated/conducted after an apparent large shift in dominance from macroalgae to corals. Thus, we acknowledge our altered perception (*i.e.*, "shifting baseline", *sensu* Pauly, 1995) and its

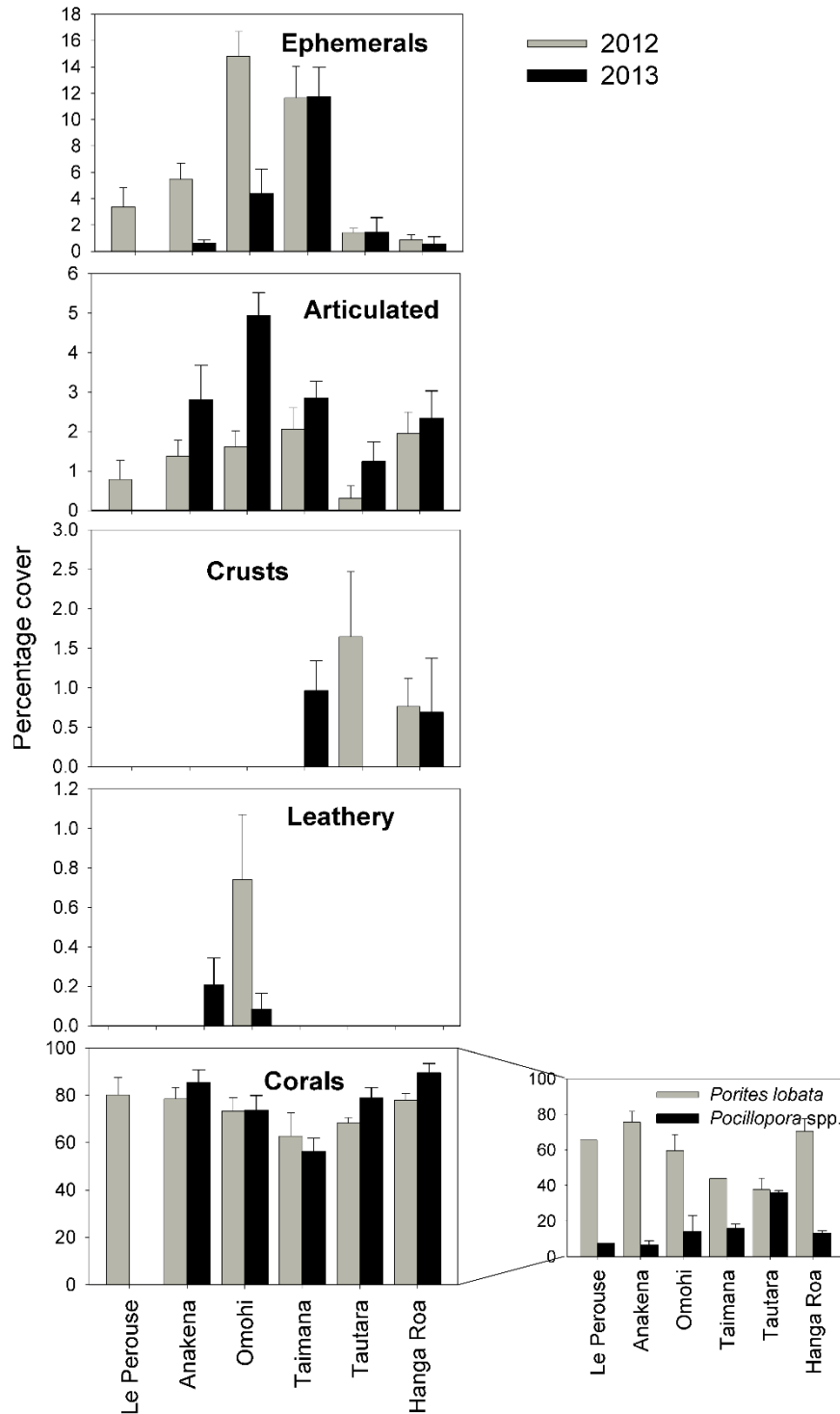


Figure 3. Mean percentage cover (\pm SE) of dominant sessile benthic invertebrate functional groups at mid-depth (10-15 m) at the different study sites. Note the different y-axis scales used. Shaded bars correspond to 2012 surveys, whereas black bars indicate surveys conducted in 2013.

limited potential use in determining some former "natural" or pristine condition (Dayton *et al.*, 1998; Jackson *et al.*, 2001; Myers & Worm, 2003). Instead,

we view this work as an important starting point to provide context for localized "snapshot" studies. This can help to provide a framework to generate testable

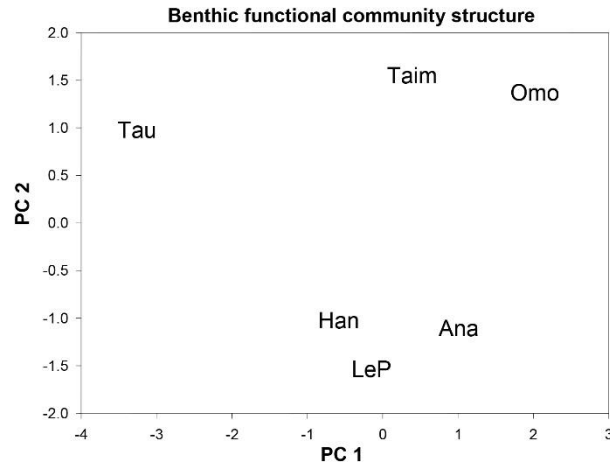


Figure 4. Relationship for the first two principal components obtained from Principal Component Analysis (PCA) of functional community structure at mid-depth zones (10-15 m) across Rapa Nui. Ana: Anakena, Han: Hanga Roa, LeP: Le Perouse, Omo: Omohi, Taim: Taimana, Tau: Tautara.

hypotheses about driving processes, assess subsequent change and, hopefully, trigger scientific support for locally-derived ecosystem-based conservation/management policy. Our results highlight the apparent resilience of the current system and the identification of geographic "compartments" of functional organization, providing a first-cut guideline as to where management subsystems might be prescribed so as to spatially match ecosystem characteristics.

Temporal patterns

We documented a consistent increase in coral abundance in shallow habitats over the past 15 years, despite naturally depauperate fish assemblages and intense fishing pressure that is likely most responsible for the low fish abundances, small body sizes, and skewed trophic structure (Friedlander *et al.*, 2013). Although data are restricted to only two shallow sites located on opposing coasts, field observations suggest the pattern is general to at least the northeast and west coasts of the island (no comparable data are available for the southeast coast). In light of the mass bleaching event of 2000 that caused high mortality of *Pocillopora* and had notable effects on this and total coral cover at most sites (Wellington *et al.*, 2001, Wieters, unpublished data, Fig. 6), the temporal trend reported here indicates high capacity for relatively rapid recovery of coral cover after disturbance. The rapid recovery from the large-scale disturbance was often associated with a change in relative coral composition, suggesting a compensatory response by massive *Porites*, which had suffered widespread bleaching but

overall little mortality (Glynn *et al.*, 2003). Similar changes in generic composition have been reported among other reefs showing capacity for rapid recovery from disturbance (*e.g.*, Adjerdoud *et al.*, 2009). Increase in coral cover beyond the pre-bleaching event was additionally enhanced by new recruitment that became most apparent after 2005, although regrowth/regeneration of remnants was also observed (Wieters, *pers. obs.*). In general, our results suggest that the current ecosystem at Rapa Nui is relatively "resilient", capable of absorbing stress and not losing its fundamental functional dynamics.

Small blooms of leathery macroalgae did follow coral mortality and disturbance, lasting at most a few years prior to about 2005. Given that all surveys were undertaken during the same months (Abril-May) each year, potential shorter-term seasonal effects are unlikely to confound the among-years pattern of algal abundances. The role of herbivory in recovery and community resilience must be interpreted with caution due to lack of temporal data for herbivorous fishes, as well as the difficulty in relating abundances of mobile fishes and benthic grazers (predominantly sea urchins *Diadema*) to actual grazing rates. However, the rather abrupt temporal changes with higher benthic grazer density following disturbance and during palatable macroalgal blooms suggest that sea urchin feeding activity may have been critical to control fast-growing macroalgae and enhance coral settlement and recovery. Indeed, on-going field experiments reveal a strong capacity for aggregative behavioral responses to macroalgal availability by urchins, adults of which can form slow-moving "fronts" (*e.g.*, Wieters, unpublished data). Future experimental studies teasing apart the role of diversity and identity of herbivores and whether/how these are modified by climate-induced bleaching stress are necessary and would provide critical insight into mechanisms of recovery, as well as provide insight into manageable attributes that drive functional vulnerability under scenarios of climate change.

Similar to that observed in shallow habitats, strong bleaching-induced declines in branching *Pocillopora* in 2000 with rapid, compensatory recovery of total coral cover was also observed at mid- to deep- locations at Taimana. However, recovery trajectories at depth were abruptly disrupted by 2005, when notable coral decline and peak abundances in leathery macroalgae were again observed. This time, the coral decline was largely due to decreased abundance in massive *Porites*. These results suggest important depth-dependent disturbance regimes with potentially greater types and frequency of disturbance at depth. Unfortunately, we have little idea of drivers and can only surmise that high-frequency upwelling or shoaling cold events, such as those we

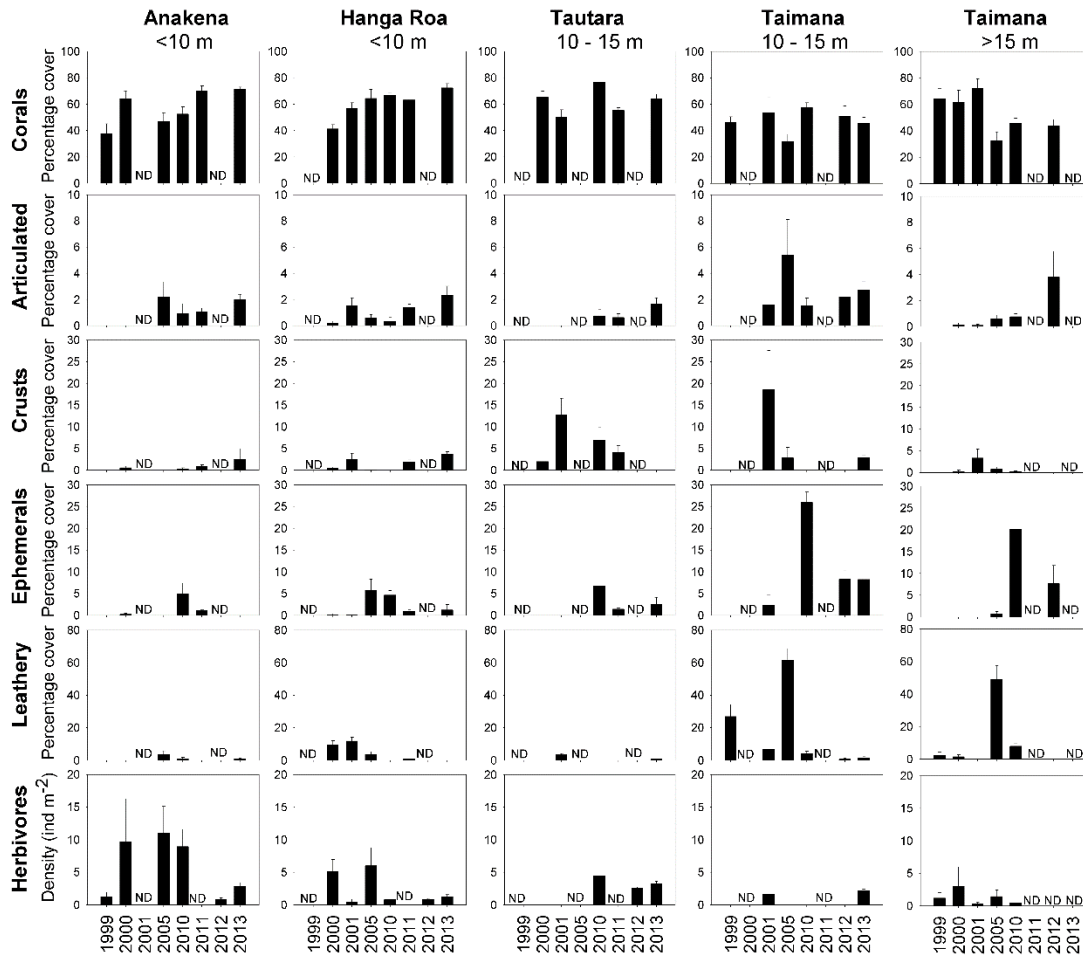


Figure 5. Mean percentage cover and density (\pm SE) of dominant sessile and mobile benthic invertebrate functional groups, respectively, across years at selected study sites of contrasting subtidal depth zones. Note the different y-axis scales used. ND: No data available.

have recently begun to document at Rapa Nui (Wieters, unpubl. data), might have been at play. Severe short-duration cold water events can indeed cause large-scale coral mortality (e.g., Lirman *et al.*, 2011) and have been observed with increasing depth elsewhere (Sheppard, 2009). Recovery also appeared depth-dependent, as corals at mid-depth had recovered to pre-2005 disturbance conditions again by 2010, whereas *Porites* (and total coral) abundances at the deeper location (approx. 20 m) have consistently remained lower (albeit similar to that prior to the 2000 bleaching event). Such hypotheses are amenable to experimentation.

Long-term monitoring is critical to evaluate fluctuations in community functioning and the impacts of current and future disruptive stresses. Our limited dataset covering 15-year time span is clearly short and requires longer view for interpretation. For example, the trend to increasing coral abundance in shallow habitats is even more dramatic when considering the

covers reported by DiSalvo *et al.* (1988) from their surveys in mid 1980's. According to long-term residents of the island, the rise to coral dominance was due to a combination of released competition and escape from predation following abrupt, large-scale mortality of once-thriving brown macroalgae (*Sargassum* and *Lobophora*) that had dominated space and provided habitat to corallivore fishes. The single corallivore fish species, the parrotfish *Leptoscarus vaigiensis*, was reportedly abundant in the late 1960s but was last sighted at the island in 1994 (Randall & Cea, 2011). As opposed to the now relatively common reports and demonstrations of coral-to-macroalgal phase shifts on coral reefs worldwide, persistent shifts of macroalgae-to-coral on coral reefs are, in general, extremely rare (but see Done, 1992; Idjadi *et al.*, 2006). Unfortunately, no quantitative data exist prior to the shift in dominance at Rapa Nui and we have little idea of potential driving mechanisms. Studies testing for alternate ecological

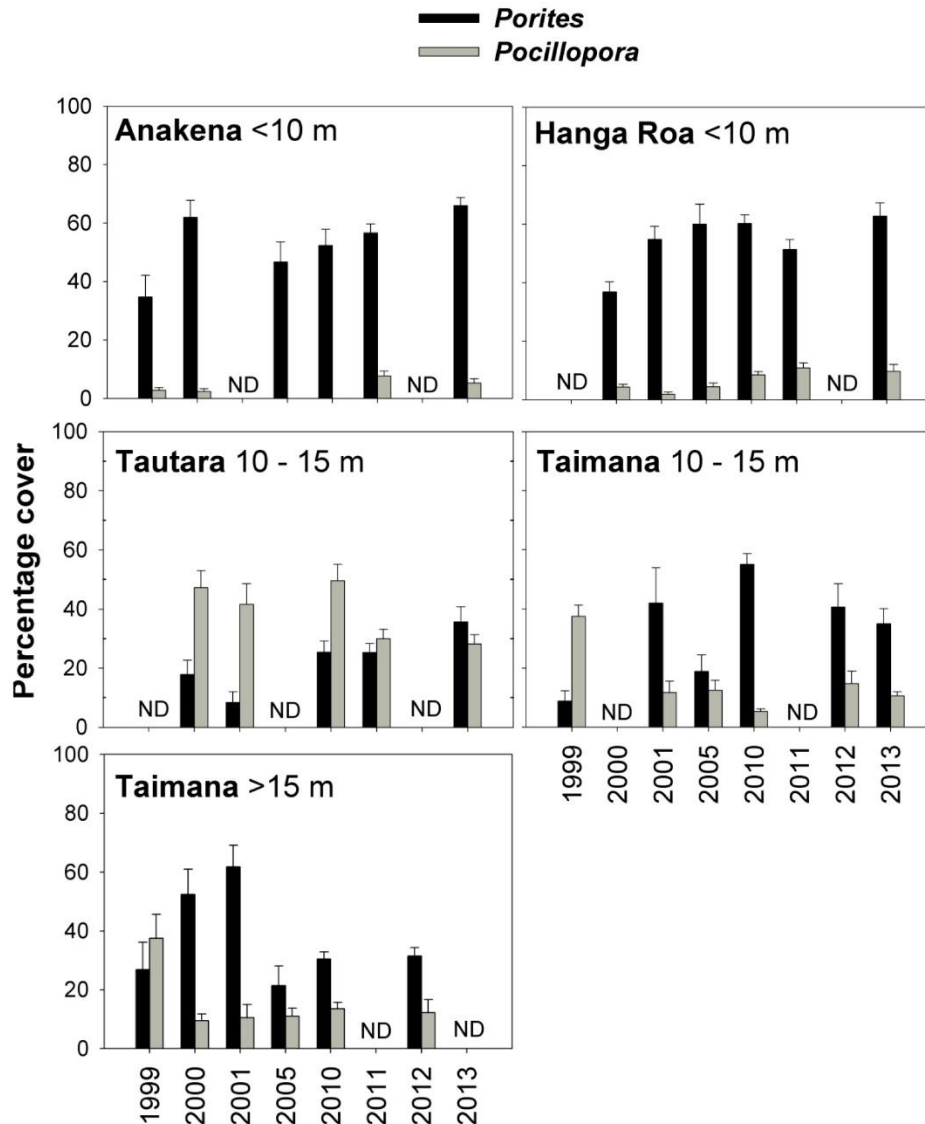


Figure 6. Mean percentage cover (\pm SE) of branching pocilloporid (grey bars) and massive *Porites* (black bars) corals across years at selected study sites of contrasting subtidal depth zones. Note the different y-axis scales used. ND: No data available.

feedback mechanisms that sustain coral or algal dominance at Rapa Nui are currently underway (Wieters, unpublished data).

Spatial structure: vertical zonation

Rapa Nui is directly exposed to open ocean conditions and large storm swells. Limestone reef structures do not reach the surface to buffer wave forces, and the coastline is characteristically steep. Shores are frequently wave-beaten and localized shelter habitat is scarce. Indeed, it is common to observe toppled and broken colonies (*pers. obs.*), which led Hubbard & Garcia (2003) to suggest waves are the principal factor limiting reef-building. Thus, extreme wave energy in shallow waters is likely responsible for the observed

reduced coral cover and absence of branching growth forms, which are known to be structurally more susceptible to wave-induced damage (*e.g.*, Madin & Connolly, 2006). Moreover, colonies of massive *Porites* in shallow waters are small relative to those found deeper, suggesting routine mortality and/or stunted growth. Alternatively, or additionally, *Porites* and *Pocillopora* may host specific symbiotic zooxanthellae (*Symbiodinium* spp.) that are differentially adapted to the depth-mediated light gradient (*e.g.*, Iglesias-Prieto *et al.*, 2004), and thus inhibitory physiological performance may play an important role in influencing the upper limit of depth distribution of *Pocillopora*. Indeed, photo damage and bleaching are more readily observed in *Pocillopora*

Table 2. List of fish species identified by contrasting survey methods and their assigned trophic functional groups.

Family	Species	Rapanui or common name	Trophic category	Video	Census	Endemic
Muraenidae	<i>Gymnothorax eurostus</i>	Kōreha puihi, Morena	Piscivore+invertivore	+	+	
	<i>Gymnothorax nasuta</i>	Kōreha, Morena	Piscivore+invertivore	+		+
Congridae	<i>Conger cinereus</i>	Kō'iro	Invertivore+piscivore	+	+	
Synodontidae	<i>Synodus isolatus</i>	Pāpa hakatara	Piscivore		+	+
Holocentridae	<i>Sargocentron wilhelmi</i>	Mārau hiva	Carnivore		+	+
Fistulariidae	<i>Fistularia commersonii</i>	Toto amo hiku kio'e, Pez Corneta	Piscivore+invertivore	+	+	
Aulostomidae	<i>Aulostomus chinensis</i>	Toto amo	Invertivore+piscivore	+	+	
Scorpaenidae	<i>Scorpaena orgila</i>	Nohu	Piscivore		+	+
Serranidae	<i>Acanthistius fuscus</i>	Kōpuku mangaro	Invertivore	+		+
	<i>Trachypoma macracanthus</i>	Kōpuku kava	Invertivore	+	+	
Priacanthidae	<i>Heteropriacanthus eruentatus</i>	Mata uira, Matahuira	Invertivore+planktivore		+	
Carangidae	<i>Pseudocaranx cheilio</i>	po'opo'o	Invertivore+piscivore	+	+	
Mullidae	<i>Mulloidichthys vanicolensis</i>	'a'avere	Invertivore	+	+	
Kyphosidae	<i>Girella nebulosa</i>	Māhaki, Nanue (c)	Omnivore	+		+
	<i>Kyphosus sandwicensis</i>	Nānue	Herbivore	+	+	
Chaetodontidae	<i>Chaetodon flavirostris</i>	Tipi tipi	Omnivore	+		+
	<i>Chaetodon litus</i>	Tipi tipi'uri	Invertivore		+	
	<i>Chaetodon pelewensis</i>	Tipi tipi	Omnivore	+		
	<i>Forcipiger flavissimus</i>	Tipi tipi hoe	Invertivore	+	+	
Pomacanthidae	<i>Hemitaeniarhynchus multispinosus</i>	Multispine butterflyfish	Planktivore	+		
	<i>Centropyge flavissimus</i>	Lemonpeel angelfish	Herbivore	+	+	
	<i>Centropyge hotumatua</i>	Kōtōti para	Herbivore	+	+	
Cirrhitidae	<i>Ircirrhitis wilhelmi</i>	Piliko'a	Piscivore+invertivore		+	
Pomacentridae	<i>Chromis randalli</i>	Māmata	Planktivore	+	+	+
	<i>Chrysiptera rapanui</i>	Māmata	Planktivore	+	+	
	<i>Stegastes fasciolatus</i>	Kōtōti	Omnivore	+	+	
Labridae	<i>Anampses caeruleopunctatus</i>	Mōri, Mārari	Invertivore	+	+	
	<i>Anampses femininus</i>	Pāhika	Invertivore	+	+	
	<i>Bodianus unimaculatus</i>	Matuku	Invertivore	+	+	
	<i>Cheilodactylus inermis</i>	Ure ure	Invertivore	+	+	
	<i>Coris debueni</i>	Tēteme	Invertivore	+	+	+
	<i>Pseudolabrus fuentesi</i>	Kōtea	Invertivore	+	+	
	<i>Thalassoma lutescens</i>	Mōri vaihi	Invertivore	+	+	
	<i>Thalassoma purpuraceum</i>	Kākaka, Ra'emea	Invertivore	+	+	
Gobiidae	<i>Pascua caudilinea</i>	Pascua Goby	Invertivore	+	+	+
	<i>Priolepis squamogena</i>	Scaledcheek goby	Invertivore	+	+	
Acanthuridae	<i>Acanthurus leucopareus</i>	Ma'ito	Herbivore	+	+	
Soleidae	<i>Aseraggodes bahamondei</i>	Rahai	Invertivore+piscivore	+	+	
Monacanthidae	<i>Aluterus scriptus</i>	Paoa	Omnivore	+	+	
	<i>Cantherhines dumerilii</i>	Kōreva	Omnivore	+	+	
	<i>Cantherhines rapanui</i>	Kōreva	Omnivore	+	+	+
Balistidae	<i>Xanthichthys mento</i>	Kokiri	Planktivore	+	+	
Ostraciidae	<i>Lactoria diaphana</i>	Momo tara	Invertivore	+	+	
Tetraodontidae	<i>Arothron meleagris</i>	Titeve kapovai, Pez globo	Invertivore	+	+	
Diodontidae	<i>Diodon holocanthus</i>	Titeve tara tara	Invertivore	+	+	
Total (%)				87%	80%	24%

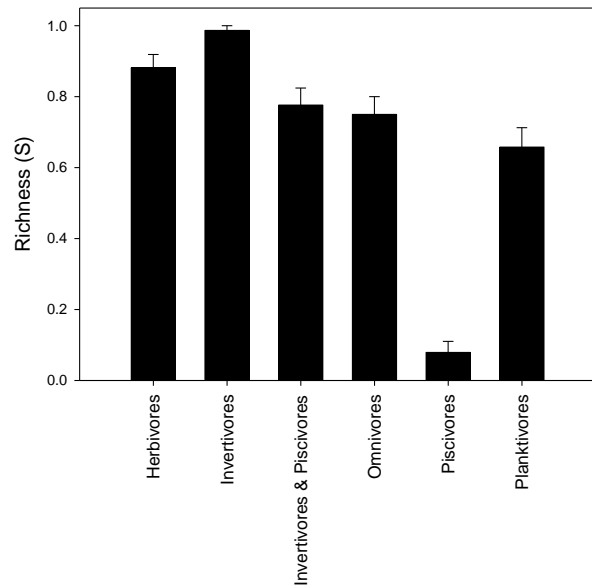


Figure 7. Number of fish species observed for each trophic functional group at Rapa Nui.

than *Porites* under the same depth and environmental conditions in the field (Wieters, unpublished data). Unfortunately, we currently have no information regarding the relative abundance of different *Symbiodinium* clades or how they vary across depths among species or functional groups. Reciprocal transplantation among depth zones could provide insight into the relative importance of holosymbiont characteristics and local environmental/physical factors influencing coral distribution.

In contrast to what is commonly described for coral reefs in similar depth ranges to those explored here (Huston, 1985), we did not observe important reductions in total coral abundance (cover) at deeper sites (>20 m). The persistently clear oceanic waters of Rapa Nui offer high light penetration and visibility (often >50 m) and thus our surveys were unlikely deep enough for irradiance to limit photosynthesis. Indeed, corals are frequently observed at >60 m depth (H. & M. García, *pers. comm.*).

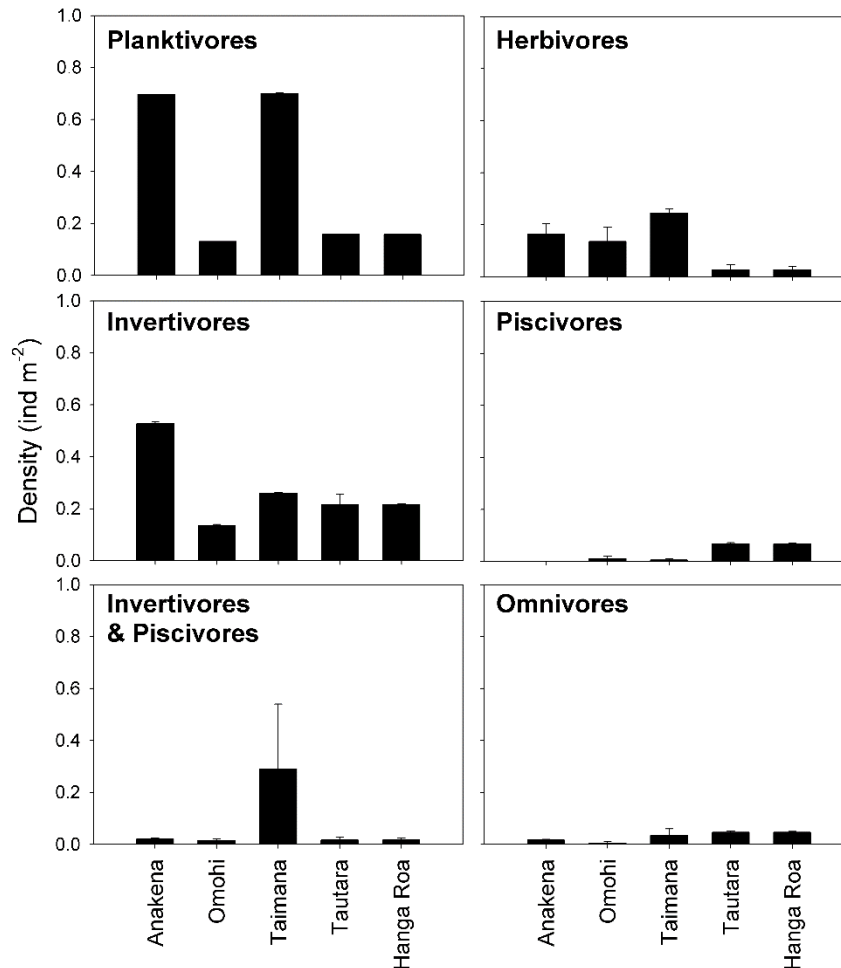


Figure 8. Mean density (\pm SE) of fish across study sites for each trophic functional group.

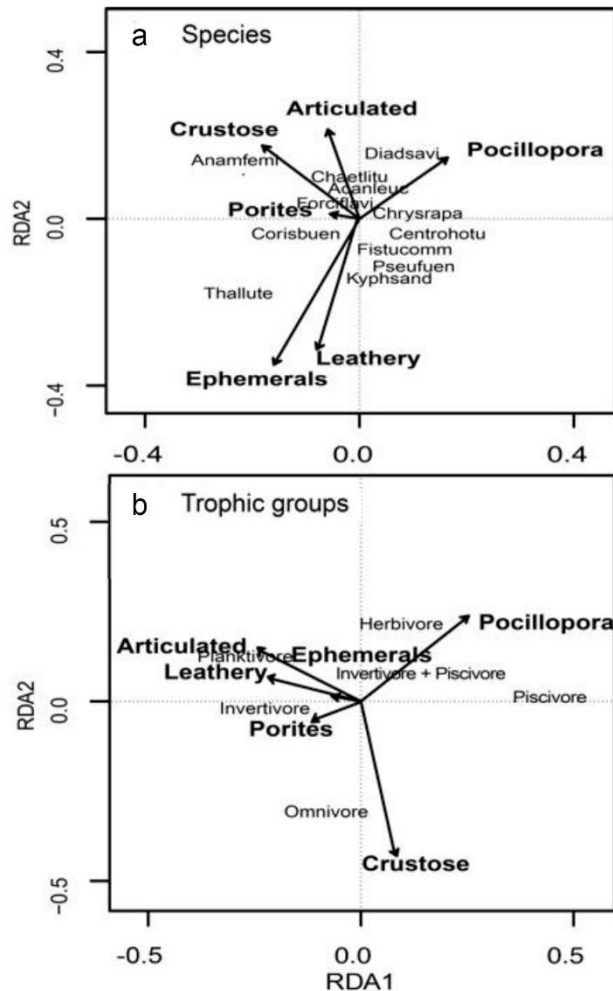


Figure 9. Relationship of the first two components of redundancy analysis (RDA) for the a) abundant species and b) functional groups, of fish and sea urchins against major sessile benthic functional groups (in bold). Species labels are based on the first four letters of their genus and species.

Neither wave action nor light availability is likely to explain the reduced cover of ephemeral macroalgae in shallow waters, since these early colonizers are usually favored by repeated disturbances that prevent successional development. Instead, herbivory and/or increased competition with the relatively more resistant and wave-tolerant articulated/calcified algae -that reach higher abundances in the shallows- seems more plausible. Alternatively, deeper sites could receive higher rates of nutrient replenishment, such as that supplied by upwelling/bores (*e.g.*, Leichter & Genovese, 2006), and promote ephemeral macroalgal growth (Smith *et al.*, 2004).

Spatial structure: among-site variability

Spatial patterns of functional community structure and similarity reflect shifts in the relative abundance of the

same set of species, rather than compositional changes. Site grouping structure did not strictly follow geographic characteristics, as neighboring sites were not always grouped together. For example, benthic communities of Hanga Roa grouped tightly with sites on the northeast coast (Anakena, Le Perouse) and Tautara was an outlier by itself despite its close proximity to Taimana, which grouped more tightly with Omohi. The surprisingly similar spatial grouping of fish functional assemblage structure further reinforces geographic patterns and suggests tight benthic-fish associations. Identification of distinct benthic regions or groups of sites can offer important insight into regularities and causes of change, as well as indicate the limits to which locally-derived ecological models apply (Navarrete *et al.*, 2005). Over large scales, the variability of the physical environment might "set the stage" for ecological interactions and functioning. Unfortunately, very little is known of the nearshore oceanographic conditions and how they vary around Rapa Nui. However, Andrade *et al.* (2014) recently described variation in satellite-derived temperature and chlorophyll-*a*, documenting important differences between the northwest and northeast coasts. The similar spatial change in benthic and fish functional community structure documented here suggests there may be strong coupling with coastal oceanographic conditions that varies on scales of 1s-10s of km. Such phenomena are of growing recognition and increasing interest around the world and warrant further study with emphasis on local *in situ* conditions.

Regardless of the underlying causes, identification of areas of distinct functional community structure has important implications for conservation and management, particularly when charged with the goal of upholding ecosystem functioning. Since spatial differences may reflect changes in regulating ecological processes, such information can help identify where to focus efforts or where different strategies might be most effective. Currently, the Chilean government is embarking on the implementation of a large no-take marine protected area east of Rapa Nui, Motu Motiro Hiva Marine Park, which includes the closest island of Salas y Gómez (see Friedlander *et al.*, 2013). Moreover, the native Rapa Nui population, with governmental and non-governmental agency support, is debating and developing cooperative conservation-driven management plans for the nearshore coastal habitats of the island. We hope this study can offer a rough, first-cut contribution to building ecological literacy for these decisions.

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