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Effects of herbivores, wave exposure, and depth on benthic coral communities of the Easter
Island Ecoregion

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Abstract

The Easter Island Ecoregion consists of Rapa Nui (Easter Island), with a human population of ~5,600, and uninhabited Salas y Gómez (SyG). While the culture and terrestrial ecology of Rapa Nui have been well studied, we know little about the marine environment of these islands, particularly the interplay among herbivores, algae, and corals and how coral communities differ between islands, by wave-energy exposure, and with depth. To address the potential roles of herbivores, wave-energy exposure, and depth on the sessile benthic communities, we compared herbivorous fish biomass, sea urchin (*Diadema savignyi*) density, and algal and coral cover to identify patterns and potential relationships among these groups. We found significant differences between islands, with higher fish biomass, *D. savignyi* density, and cover of crustose coralline algae at SyG, which is much more exposed to high wave energy compared to Rapa Nui. In contrast, Rapa Nui had significantly higher cover of macro and turf algae. Turf and macroalgae were nearly absent from SyG, whereas the density of *D. savignyi* and biomass of the herbivorous fish *Kyphosus sandwicensis* were, ~28 and ~3 times greater, respectively, at SyG. Herbivores and wave-energy likely play important roles in structuring these benthic communities, especially for algal groups.

Additional keywords: coral, fishing impacts, trophic structure, community structure, *Diadema savignyi*

Running head: Effects on Easter Island Ecoregion benthos

Introduction

Rapa Nui (Easter Island) and Salas y Gómez (SyG) are the southeastern-most Polynesian islands and are the only two islands in the Easter Island Ecoregion (Gálvez-Larach 2009; Friedlander *et al.* 2013). The coral reef communities around these islands harbor high endemism of many taxa, but relatively low biodiversity compared to other coral reef communities around the world (DiSalvo *et al.* 1988; Boyko 2003; Raines and Huber 2012;). The island of Rapa Nui, with ~ 5,600 residents, has experienced high fishing pressure relative to the remote island of SyG (Castilla *et al.* 2014; Zyllich *et al.* 2014), which is uninhabited and included in the 150,000-km², no-take, Motu Motiro Hiva Marine Park (MMHMP) established by the Chilean government in 2010. Impacts from fishing at Rapa Nui have resulted in reduced abundance and biomass of apex predators and herbivorous fishes (Friedlander *et al.* 2013); however, little is known about the structure of the shallow benthic communities and the roles herbivore abundance, wave-energy exposure (hereafter wave exposure), and depth play in structuring these communities.

Benthic communities show a variety of changes in response to climate disturbances and fishing pressure (see Done 1999; Wismer *et al.* 2009; McClanahan 2014). Often these changes result in phase shifts from communities dominated by coral and crustose coralline algae (CCA) to ones dominated by macroalgae (Carpenter 1986; Steneck 1986; Hughes 1994). Decreased herbivory by fishes and sea urchins are often credited as the main factors for these phase shifts, whereas eutrophication and mesograzers are typically thought to play lesser roles (Hughes *et al.* 1987; Done 1992; De'ath and Fabricius 2010). Furthermore, high herbivore abundance and diversity after disturbances has been credited for resilience of some coral reef communities (Adam *et al.* 2011; Roff and Mumby 2012).

In addition to differences in grazing, differences in oceanic processes (e.g., wave and wind exposure) can affect community structure directly and indirectly (Steneck 1986; Friedlander *et al.* 2003). Rapa Nui and SyG have considerable between- and within-island differences in wave exposure (DiSalvo *et al.* 1988; Glynn *et al.* 2003; Hubbard and Garcia 2003), with greater exposure at SyG and the southeastern side of Rapa Nui due to the long-distance swells from storms originating off Antarctica and prevailing trade winds from the east-southeast. Wave exposure has been shown to play an important role in structuring communities on coral reefs (Dollar 1982; Grigg 1983; Grigg 1998); but not all communities differ with wave exposure (e.g., Williams *et al.* 2013). For example, coral reef communities with higher wave exposure may support greater biomass because more nutrients are transported through the system by the waves (Smith and Kinsey 1976; Grigg 1998; Hearn *et al.* 2001); however, coral cover may be low in high-energy environments for coral species not well adapted to these environments (see Sousa 2001).

Depth also plays an important role in structuring coral reef communities due to differences in light attenuation, temperature, wave energy, species composition, and other correlated factors (Steneck 1986; Denny and Wethey 2001; Friedlander *et al.* 2010). The effects of depth are often reef dependent due to differences in other factors, such as nutrient input, wave energy, reef structures, and species composition (Fox and Bellwood 2007; Williams *et al.* 2013).

To determine whether herbivore abundance, wave exposure, and depth play roles in controlling the sessile, benthic structure of the coral reef communities of Rapa Nui and SyG, we examined the relationships among herbivores, corals, and algae to determine whether those relationships differed within and between islands. To do so, we addressed the following questions: (1) does benthic community structure vary with depth, wave exposure, and island?,

(2) which groups/species vary with depth, wave exposure, and island?, and (3) what are the relationships among herbivore biomass, coral cover, and algal cover by depth, wave exposure, and island that could be driving these differences?

Materials and methods

Study sites

Rapa Nui (27°09' S, 109°22' W) is considered the most isolated inhabited island on Earth (DiSalvo *et al.* 1988). It is > 3500 km from the nearest large landmass, South America, and ~2000 km from the nearest inhabited island, Pitcairn. Salas y Gómez (26°28' S, 105°21' W), the nearest uninhabited island, is ~400 km to the east of Rapa Nui. Rapa Nui and SyG are the only two islands along the Salas y Gómez Ridge and are considered the southeasternmost part of Polynesia (Gálvez-Larach 2009; Friedlander *et al.* 2013). Both islands formed from volcanic activity associated with a hotspot over the Nazca Plate (Vezzoli and Acocella 2009) and are surrounded by fringing coral reefs. Water temperature ranges from 25°C in late austral summer to ~20°C in austral winter (Hubbard and Garcia 2003). The average temperature, based on satellite data (Andrade *et al.* 2014), is ~22.46°C at SyG and ranges from ~22.55°C to 22.7°C at Rapa Nui respectively from the southeastern to northwestern coasts. Limited temperature data from depths < 20 m are available, so temperatures among our stations could not be compared. Both islands have low nutrient levels, with an average of ~0.027 mg/m³ at SyG and 0.026-0.029 mg/m³ at Rapa Nui (Andrade *et al.* 2014). Mesoscale eddies may bring a short-term influx of nutrients to Rapa Nui during the austral spring and summer and during El Niño or La Niña events (Andrade *et al.* 2014).

Benthic and fish surveys were conducted at 10 and 20 m at each of ten stations around Rapa Nui and SyG in February-March 2011 (see Supplementary material Table 1; Fig. 1).

Survey sites were spread around both islands to provide representation of the benthic communities and degrees of wave exposure. These were the first surveys ever conducted at SyG. Because wave energy was not measured *in situ* and the resolution of available data (e.g., satellite altimetry data) is not fine enough to estimate differences in wave exposure among our stations and depths, we categorized the stations as either exposed, semi-exposed, or protected based on their location and known wave-exposure patterns (DiSalvo *et al.* 1988; Glynn *et al.* 2003; Hubbard and Garcia 2003). Swells and waves generally approach from the south, resulting in the northern (and western for Rapa Nui) coastlines of the islands being less exposed to wave energy. Wave-energy protection is minimal at SyG in comparison to Rapa Nui due to its smaller size (Hubbard and Garcia 2003), 0.15 and 163.6 km², respectively, and greater wind stress (Andrade *et al.* 2014). Therefore, wave exposure differs among islands such that Rapa Nui has protected sites but SyG does not.

Benthic surveys

We quantified sessile benthic taxa with point-line transects (every 20 cm along 10-m transects) oriented parallel to shore. Five transects were conducted per depth stratum and the average percentage cover of these transects were calculated for each station (see Supplementary material Table 2). Mobile macro-invertebrates were counted in five 50 × 50 cm quadrats placed haphazardly along either side of the same transects. Sea urchins were summed across quadrats (0.25 m²) with average number reported for each station (see Supplementary material Table 2).

Fish surveys

At each site, one diver tallied all fishes encountered within fixed-length, 25-m-belt transects. Transect bearings were determined haphazardly along isobaths and separated by 5 m. Large-bodied vagile fishes ≥ 20 cm total length (TL) were tallied within a 4-m wide strip

surveyed on an initial “swim-out” as the transect line was laid (transect area = 100 m²). Small-bodied, less vagile and more site-attached fish < 20 cm TL were tallied within a 2-m wide strip surveyed on the return swim along the laid transect line (transect area = 50 m²). Numerical densities of fishes were recorded to the lowest recognizable taxon and fish length was estimated to the nearest cm. Biomass in tons per hectare was calculated from the numerical densities multiplied by the individual body weights calculated using the allometric length-weight conversion: $W = aTL^b$, where a and b are species-specific constants, TL is total length in mm, and W is weight in g. Length-weight parameters a and b were obtained from FishBase (Froese and Pauly 2011) and other published sources (Letourneur 1998; Kulbicki *et al.* 2005).

Taxa selection

We focused our study on corals, algae, herbivorous fishes, and sea urchins (see Supplementary material Tables 2 and 3). Algae were separated into functional groups (Bruno *et al.* 2014): CCA, turf algae, and macroalgae (>2 cm height). Predatory fishes were excluded from the analyses because they were virtually absent at Rapa Nui (<2% of total fish biomass; Friedlander *et al.* 2013) and therefore were not sufficiently abundant to evaluate their potential effects on herbivore grazing. Fishes were determined to be herbivores if they had a trophic level <2.5 (see Supplementary material Table 3; Froese and Pauly 2011). When possible, we confirmed fish trophic status with observations of gut contents reported for individuals from Rapa Nui and SyG (DiSalvo *et al.* 2007; Randall and Cea 2010). No trophic level was reported in Fishbase for *Kyphosus sandwicensis* but Randall and Cea (2011) reported this species to feed on coarse benthic algae, such as *Lobophora* and *Sargassum* at Rapa Nui. The endemic angelfish *Centropyge hotumatua* had a trophic level of 2.8, but this was estimated from a congener, whereas Disalvo *et al.* (2007) reported its gut contents from SyG as filamentous turf algae and

two of the authors (CFG and AMF) observed it consuming turf algae on Rapa Nui. Herbivorous fishes were assigned to functional group (e.g., browser, grazer, scraper), and with the exception of *K. sandwicensis*, which is a browser, all other fishes in this study are functionally grazers. Herbivorous fishes with only one observation were only included in the count of total herbivorous fishes (see Supplementary material Table 3). Similarly, we included all three sea urchin species in counts of total urchins, but excluded *Echinometra insularis* and *Echinostrephus aciculatus* from additional analyses because they primarily consume drift algae, are generally found at shallower depths (≤ 10 m), are relatively rare (< 0.1 ind. m^{-2} at $< 33\%$ of the transects), and are cryptic during the day, making counts potentially inaccurate.

Statistical analyses

Fish biomass and sea urchin abundance were $\ln(x+1)$ transformed prior to statistical analyses. Percentage cover of sessile macro-invertebrates was logit transformed to maintain interpretability of the transformed data in comparison to arcsine square-root transformations, see Warton & Hui (2011). Values were transformed as $\ln((x+a)/(1-(x+a)))$, where a was the smallest non-zero value, with 6 then added to make all transformed values positive. Normality was examined using a Shapiro-Wilks W test, and Bartlett's test was used to examine homogeneity of variances (Snedecor and Cochran 1989). To explore community differences for the dominant taxa among islands, depth, and wave exposure, we conducted a principal components analysis (PCA) on the correlation matrix of the transformed data. For the PCA, we used the following groups as factors: macroalgae, turf algae, CCA, *Porites lobata*, *Pocillopora* spp., and herbivores by species. Further, a PERMANOVA analyses was run on these same groups to determine whether differences among stations significantly differed by island, depth, and wave exposure. We used the following settings for the PERMANOVA analysis in Primer v7

(Clarke and Gorley 2015): fixed factors = island, depth, and exposure; test = main and pairwise (for wave exposure); permutation method = permutation of raw data; sum of squares = type III (partial); and number of permutations = 9999.

If conditions of normality and homogeneity of variance were met, two-way, crossed ANOVAs were applied to the transformed data to test for taxon-specific differences between islands, depth, and the interactions among these factors. One-way ANOVAs were applied to test for taxon-specific differences with wave exposure. Student's t-tests were applied to identify pairwise differences for significant one-way ANOVAs. As suggested by Conover (1980), ANOVAs were applied to the raw and rank-transformed data if the conditions of normality and homogeneity of variances were not met. The raw data were used when the results agreed and the rank-transformed results used when they did not. All means are reported with standard error. Differences were significant at $p < 0.05$; however, in consideration of increased type I error due to multiple testing, whether results were significant after a sequential Bonferroni correction ($p < 0.05/n$), where n = ranking from largest to smallest p value from the 21 tests (Rice 1989), was also reported. When interactions occurred among depth and island, one-way ANOVAs were run after splitting the data by the interacting factor. Because grazing effects can differ by herbivore density and size (Tuya *et al.* 2004; Lokrantz *et al.* 2008), we also ran one-way ANOVAs to determine whether differences in sizes of the numerically abundant herbivores existed with depth, wave exposure, and island. ANOVAs were run in JMP® 11.2.0 (2013).

Results

Community structure differences by island, depth and wave exposure

PCA showed community structure to be generally well separated by island, and to some extent by wave exposure. The first two axes of the PCA explained 57.0% of the variability in the

coral reef community components examined (Fig. 2). Between-island differences were apparent with much of the variation in community structure between islands and within Rapa Nui being along axis 1, whereas differences within islands were observed along axis 2 (Fig. 2). Protected stations were separated from the other stations along axis 1; however, no differences between semi-exposed and exposed stations were apparent (Fig. 2). CCA, turf algae, macroalgae, and both coral taxa were the major loadings (± 0.6 or higher) on PCA axis 1, whereas *Diadema savignyi* and *P. lobata* were the major loadings on PCA axis 2 (see Supplementary material Table 4). PERMANOVA revealed no significant interaction among the factors and significant differences in station communities by island (pseudo-F = 8.47, $p < 0.0001$), depth (pseudo-F = 3.08, $p = 0.009$), and protection (pseudo-F = 2.53, $p = 0.0062$) with wave protected stations being significantly different than exposed (pseudo-F = 1.76, $p = 0.0120$), or semi-exposed stations (pseudo-F = 1.84, $p = 0.0141$).

Taxon/group differences by island, wave exposure, and depth

Herbivorous fish biomass and sea urchin density were significantly greater at SyG (Table 1). The majority of herbivorous fish biomass at SyG was due to *K. sandwicensis*, whereas, *Acanthurus leucopareius* contributed the most at Rapa Nui. Similarly, the primary contributor to sea urchin density was *D. savignyi*. The cover of CCA, the density of *D. savignyi*, and the biomass of herbivorous fishes (specifically, *Cirripectes alboapicalis*, *K. sandwicensis*, and *Stegastes fasciolatus*) were significantly higher at SyG (Table 1). In comparison, the biomass of the herbivorous fish *A. leucopareius*, the cover of the major macroalgal species, the total macro and turf algal cover, and the cover of *P. lobata* were all significantly higher at Rapa Nui (Table 1). The biomass of the endemic angelfish *C. hotumatua* and *A. leucopareius*, as well as the cover of turf algae, total macroalgae, and all species of macroalgae except *Zonaria stipitata* were

significantly higher at protected stations relative to semi-exposed and exposed stations (Table 2). In contrast, cover of CCA and density of total urchins and *D. savignyi* were significantly lower at protected stations relative to semi-exposed and exposed stations (Table 2). *P. lobata* had significantly less cover at exposed stations relative to semi-exposed and protected stations whereas cover of *Pocillopora* spp. increased with exposure (Table 2). *C. hotumatua* biomass, *P. lobata* cover, and *D. savignyi* density were significantly greater at 20 m (Table 1). A significant interaction between depth and island was only observed for *D. savignyi*.

Herbivore size differences

Mean test size (Table 3) of *D. savignyi* were marginally, but significantly, smaller at 20 m than at 10 m ($p < 0.0001$), and at the exposed sites compared to semi-exposed ($p < 0.0001$) and protected sites ($p = 0.0067$), however no significant difference was observed between islands ($p = 0.7297$). The island and depth patterns for the average TL of *K. sandwicensis* were as follows (Table 3): individuals were marginally but significantly larger at SyG and at 10 m than at Rapa Nui ($p < 0.0001$) and 20 m ($p < 0.0001$), and they increased significantly in size with exposure ($p < 0.0001$) such that individuals at exposed stations were significantly larger than at semi-exposed ($p = 0.0173$) and protected stations ($p < 0.0001$), which were also significantly different ($p = 0.0002$). The average TL (Table 3) of *A. leucopareius* had an opposite pattern to that of *K. sandwicensis* such that individuals were marginally but significantly larger at Rapa Nui and at 20 m ($p < 0.0001$) than at SyG ($p = 0.0026$) and 10 m ($p < 0.0001$). TL of *A. leucopareius* also differed with exposure ($p < 0.0001$) but no clear pattern with exposure was observed as individuals at exposed sites were significantly larger than those at protected stations ($p < 0.0001$) and semi-exposed stations ($p < 0.0001$) but individuals at protected stations were significantly larger than those at semi-exposed stations ($p < 0.0001$).

Discussion

Community structure was well separated by island and to some extent by wave exposure (protected stations being separated from the other stations) and depth (Fig. 2). Results indicate that differences in cover of turf algae, CCA, macroalgae, and coral taxa are the main contributors to community differences by island and wave exposure; whereas percentage cover of corals were the main contributors for community differences by depth.

Satellite-based temperature and nutrient data suggest that surface waters only differ slightly between islands, with $\sim 0.2^{\circ}\text{C}$ warmer average temperatures and comparable nutrient levels ($\pm 0.002 \text{ mg/m}^3$) at Rapa Nui compared to SyG (Andrade *et al.* 2014). Terrestrial inputs, although not measured, likely differ substantially as Rapa Nui lacks a sewage treatment plant, was deforested by the activities of early settlers (Hunt 2007), and has ~ 1100 times the surface area as SyG. Frequent rain events could also provide large influxes of terrestrial nutrients at Rapa Nui. Future studies should quantify nutrient input and investigate their potential role in these communities, especially as nutrient effects are often species specific and confounded by other correlated factors (Adey 1998; McCook 1999; Burkepile and Hay 2006). Other factors that may contribute to the observed inter-island differences in fish biomass, urchin density, and benthic cover include anthropogenic factors (e.g., increased sedimentation, overfishing, and destructive fishing practices), inter-island differences in wave exposure, and differences associated with evolutionary history and size of the islands (e.g., reef area and structure, recruitment limitation, and geographic location and associated differences in temperature and currents, terrestrial nutrient supply, and surface water productivity).

In addition to these factors, differences in competition for space may contribute to higher turf and macroalgal cover and lower CCA cover at Rapa Nui, and contrasting patterns of *P.*

lobata and *Pocillopora* by island and wave exposure. For example, CCA can negatively affect macroalgae settlement (see Diaz-Pulido and McCook 2004 and references therein), and macroalgae can negatively affect CCA cover through chemical and competitive interaction (see, e.g., Smith *et al.* 2006; O'Leary and McClanahan 2010; Barott *et al.* 2012). In addition, macroalgae can negatively affect the survivorship and recruitment of corals (Smith *et al.* 2006; Titlyanov *et al.* 2007; Burkepile and Hay 2010), although some coral species, including *P. lobata*, are superior competitors (McCook 2001). Our findings of greater CCA cover at SyG and lower macro and turf algal cover support the negative relationships among these groups. In addition, *S. obtusifolium*, *Halimeda* spp., and turf algae had the same patterns by island and by wave exposure as *P. lobata*, which supports it being a superior competitor to turf and macroalgae, whereas, *Pocillopora* spp. had opposite patterns by island and wave exposure, so turf algae and macroalgae may compete for space with this taxon.

As indicated by the opposite pattern of *D. savignyi* in comparison to macroalgae and turf algae, the density of *D. savignyi* may be an important factor for structuring the sessile communities. This pattern is consistent with previous studies at Rapa Nui that found *D. savignyi* to have patchy distributions (DiSalvo *et al.* 1988; Hubbard and Garcia 2003), with the seafloor almost barren of most algae, except for *Z. stipitata*, where *D. savignyi* is abundant (DiSalvo *et al.* 1988). Upon closer inspection, *D. savignyi* was ~84% less abundant at the stations where *S. obtusifolium* was present (i.e., protected stations at Rapa Nui) compared to those where it was absent (see Supplementary material Tables 2 and 3). Prior to 1983, *S. obtusifolium* was dominant in the littoral zone of Rapa Nui (DiSalvo *et al.* 1988); after which time, *D. savignyi* noticeably increased in abundance and may have contributed to the relative increase of coral cover and maintenance of relatively low *S. obtusifolium* cover (DiSalvo *et al.* 1988; Hubbard and

Garcia 2003). These observations are consistent with *S. obtusifolium* being resistant to grazing (Littler *et al.* 1983) and generally more abundant where grazing is relatively low (Fox and Bellwood 2007 and references therein).

The lack of strong correlations of herbivorous fishes to algal components suggests grazing by herbivorous fishes likely plays a lesser role than grazing by urchins in explaining differences in community structure; however, we did find a significant difference in total abundance of herbivorous fishes between the islands, which is primarily driven by *K. sandwicensis* having significantly (~28×) greater biomass at SyG in contrast to *A. leucopareius*, which had significantly (~10×) greater biomass at Rapa Nui (Table 1). *K. sandwicensis*, locally known as nānue, has historically been important to the local fishery at Rapa Nui (Randall and Cea 2010), and intense fishing pressure is likely an important factor contributing to its orders of magnitude lower biomass at Rapa Nui (Friedlander *et al.* 2013; Castilla *et al.* 2014; Zyllich *et al.* 2014). The greater abundance of *A. leucopareius* at Rapa Nui is possibly due to the relatively high cover of macro and turf algae at Rapa Nui (Friedlander *et al.* 2013), it being a less targeted species for fishing (Castilla *et al.* 2014; Zyllich *et al.* 2014), and predator release due to the near absence of large predators at Rapa Nui (Friedlander *et al.* 2013). The roles of these fishes differ due to their ecological function. For example, *K. sandwicensis* being a browser and known, based on gut contents, primarily to consume *Lobophora* (DiSalvo *et al.* 2007) may play an important role in controlling macroalgal growth and therefore in maintaining higher percentages of coral cover (see Green and Bellwood 2009). In contrast, *A. leucopareius* and the other herbivorous fishes are grazers or grazers/detritivores, which consume substantial amounts of turf algae, and therefore may indirectly limit macroalgal growth and recruitment (Green and Bellwood 2009). Future studies should focus on the grazing effects by these herbivores, whether

the grazing effects are on specific algal species or functional groups, the effect predation has on the herbivore grazing as predation on herbivores can cause complex trophic cascades (see McClanahan 2014), and the use of manipulative experiments to determine the impact of grazing by sea urchins and herbivorous fishes on percentage cover of algae and coral.

The direct effects of wave energy (Mach *et al.* 2007; Fong and Paul 2011) may prevent algae from settling or remaining attached to the substrate and could contribute to the patterns of higher cover of macroalgae and turf algae and lower cover of CCA at protected stations (Table 2, Fig. 2). Similarly, wave energy may contribute to higher cover of *Pocillopora* spp. at wave-exposed stations. Previous studies have demonstrated that *Pocillopora* spp. are opportunistic (Laboute 1985; Adjeroud *et al.* 2007), with high recruitment rates and potential for high dispersal, which make them an ideal species to colonize the relatively high-energy, shallow-water environments of these islands. Wave energy, specifically long-period Antarctic swell has been described as one of the primary controllers of coral community distribution and composition at Rapa Nui (Hubbard and Garcia 2003; Friedlander *et al.* 2013), which receives high wave energy throughout the year, especially from June through October. Hubbard & Garcia (2003) reported that waves over five meters were common on the southeastern side of Rapa Nui in August and September, with oceanic swells from the Antarctic reaching wavelengths up to 1.0–1.5 km. SyG is a small island (~700 m long) that provides little protection from these oceanic swells and wind waves and therefore experiences high wave energy on the leeward and windward sides of the island.

Broader impacts and conclusions

The coral reef communities of the Easter Island Ecoregion are being affected by local anthropogenic disturbances, as well as large-scale global impacts, and understanding the main

factors in controlling these communities is imperative to conservation and management. Here, we identified that the benthic communities differ substantially between the islands and that wave exposure appears to play an important role in controlling the distribution of coral species and algae; whereas depth appears to play a limited role at least for the depths we studied. Although we found several intriguing patterns with herbivore abundance, island, and wave exposure, we acknowledge that manipulative studies are required to determine the cause of the observed differences and whether the patterns are indicative of direct effects by or differences in other factors not evaluated in this study. Future studies should quantify the magnitude of these effects and how these effects differ with predation, site-specific wave energy, habitat complexity, and fishing pressure.

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510 Table 1. Mean $\pm$ SE and significance values ($p \leq 0.05$) for the two-way ANOVAs with factors island and depth. Means are reported in
511 tons ha⁻¹ for fish biomass, % for sessile benthic cover, and individuals per m² for density of mobile benthos. CCA = crustose coralline
512 algae, macroalgae = total macroalgae less turf algae, RN = Rapa Nui, SyG = Salas y Gómez, I - Island, D = depth, ns = not significant,
513 na = not applicable, 20 = 20 m, and 10 = 10 m.

	P value Interaction	Island			Depth		
	I vs. D	RN (n=20)	SyG (n=20)	P value	10 (n=19)	20 (n=21)	P value
<i>Centropyge hotumatua</i> ^a	ns	0.007 $\pm$ 0.001	0.006 $\pm$ 0.002	ns	0.003 $\pm$ 0.001	0.009 $\pm$ 0.002	0.0041 ^e
<i>Cirripectes alboapicalis</i> ^a	ns	0.0001 $\pm$ 0.00003	0.0007 $\pm$ 0.0002	0.0014	0.0005 $\pm$ 0.0001	0.0003 $\pm$ 0.0001	ns
<i>Kypbosus sandwicensis</i> ^a	ns	0.016 $\pm$ 0.007	0.444 $\pm$ 0.172	0.0143 ^e	0.371 $\pm$ 0.182	0.102 $\pm$ 0.050	ns
<i>Stegastes fasciolatus</i> ^a	ns	0.005 $\pm$ 0.002	0.011 $\pm$ 0.002	0.0429 ^e	0.010 $\pm$ 0.002	0.007 $\pm$ 0.002	ns
<i>Acanthurus leucoparius</i> ^a	ns	0.112 $\pm$ 0.037	0.012 $\pm$ 0.006	0.0151 ^e	0.053 $\pm$ 0.013	0.070 $\pm$ 0.037	ns
Total herbivorous fishes ^b	ns	0.140 $\pm$ 0.042	0.474 $\pm$ 0.175	0.0441 ^e	0.439 $\pm$ 0.182	0.188 $\pm$ 0.059	ns
<i>Porites lobata</i> ^a	ns	38.3 $\pm$ 5	23.8 $\pm$ 4.4	0.0351 ^e	22.0 $\pm$ 5.0	39.3 $\pm$ 4.2	0.0116 ^e
<i>Pocillopora</i> spp. ^c	ns	14.2 $\pm$ 2.4	20.4 $\pm$ 2.9	ns	21.7 $\pm$ 3.0	13.3 $\pm$ 2.3	ns
<i>Lobophora variegata</i> ^a	ns	9.9 $\pm$ 2.0	4.3 $\pm$ 0.8	0.0211 ^e	6.2 $\pm$ 1.2	7.9 $\pm$ 2.0	ns
<i>Stypopodium</i> spp. ^b	ns	2.8 $\pm$ 0.7	0.4 $\pm$ 0.3	0.0006	1.2 $\pm$ 0.4	2.0 $\pm$ 0.7	ns
<i>Zonaria stipitata</i> ^b	ns	1.0 $\pm$ 0.7	0.0 $\pm$ 0.0	0.0209 ^e	0.7 $\pm$ 0.7	0.3 $\pm$ 0.2	ns
<i>Halimeda</i> spp. ^a	ns	1.9 $\pm$ 0.4	0.0 $\pm$ 0.0	0.0002	0.9 $\pm$ 0.4	1.0 $\pm$ 0.3	ns
<i>Sargassum obtusifolium</i> ^a	ns	1.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0377 ^e	0.5 $\pm$ 0.4	0.8 $\pm$ 0.4	ns
Turf algae ^a	ns	3.9 $\pm$ 0.7	0.0 $\pm$ 0.0	<0.0001	1.6 $\pm$ 0.6	2.3 $\pm$ 0.7	ns
CCA ^a	ns	6.2 $\pm$ 1.5	31.6 $\pm$ 2.2	<0.0001	20.8 $\pm$ 3.3	17.1 $\pm$ 3.5	ns
Total coral ^b	ns	52.7 $\pm$ 4	44.5 $\pm$ 2.3	0.0455 ^e	43.9 $\pm$ 3.4	52.9 $\pm$ 3.1	ns
Total macroalgae ^d	ns	14.7 $\pm$ 2.8	4.6 $\pm$ 0.8	0.0022	8.7 $\pm$ 1.8	10.4 $\pm$ 2.7	ns
<i>Diadema savigny</i> ^c	0.0036	2.175 $\pm$ 0.386	6.488 $\pm$ 1.003	0.0004	3.042 $\pm$ 0.626	5.498 $\pm$ 1.013	0.0274 ^e

514	Total urchins ^a	0.0013	2.615 ± 0.508	6.998 ± 0.920	<0.0001	4.011 ± 0.684	5.526 ± 1.010	ns
515	^a ANOVA on raw data.							
516	^b ANOVA on rank-transformed data.							
517	^c ANOVA on ln(X+1)-transformed data.							
518	^d ANOVA on logit-transformed data.							
519	^e Using a sequential Boneforri correction ($p \leq 0.05/n$), where n = ranking from largest to smallest p value for the 19 tests (fauna), this result is not significant.							

520 Table 2. Mean $\pm$ SE and significance values ($p \leq 0.05$) for the one-way ANOVA and Student's t test for wave exposure. Means are
521 reported in tons ha⁻¹ for fish biomass, % for sessile benthic cover, and individuals per m² for density of mobile benthos. CCA =
522 crustose coralline algae, macroalgae = total macroalgae less turf algae, E = Exposed, SE = semi-exposed, Pr = protected, ns = not
523 significant, na = not applicable.

	Exposure			P value			
	E (n=22)	SE (n=12)	Pr (n=6)	Overall	E vs. SE	E vs. Pr	SE v. Pr
<i>Centropyge hotumatua</i> ^b	0.004 $\pm$ 0.001	0.008 $\pm$ 0.002	0.011 $\pm$ 0.003	0.0425 ^e	ns	0.0181	ns
<i>Cirripectes alboapicalis</i> ^a	0.0004 $\pm$ 0.0001	0.0002 $\pm$ 0.0002	0.0002 $\pm$ 0.0002	ns	na	na	na
<i>Kyphosus sandwicensis</i> ^a	0.366 $\pm$ 0.122	0.084 $\pm$ 0.166	0.022 $\pm$ 0.234	ns	na	na	na
<i>Stegastes fasciolatus</i> ^a	0.009 $\pm$ 0.002	0.010 $\pm$ 0.003	0.003 $\pm$ 0.004	ns	na	na	na
<i>Acanthurus leucoparius</i> ^b	0.059 $\pm$ 0.028	0.045 $\pm$ 0.038	0.104 $\pm$ 0.053	0.0215 ^e	ns	0.0061	0.0283
Total herbivorous fishes ^a	0.435 $\pm$ 0.124	0.140 $\pm$ 0.168	0.129 $\pm$ 0.238	ns	na	na	na
<i>Porites lobata</i> ^a	21.1 $\pm$ 4.1	41.3 $\pm$ 5.6	47.2 $\pm$ 7.9	0.0036	0.0065	0.0061	ns
<i>Pocillopora</i> spp. ^c	23.7 $\pm$ 2.2	11.6 $\pm$ 2.9	5.4 $\pm$ 4.1	<0.0001	0.0045	<0.0001	0.0374
<i>Lobophora variegata</i> ^a	5.6 $\pm$ 1.3	4.6 $\pm$ 1.8	17.5 $\pm$ 2.5	0.0003	ns	0.0001	0.0002
<i>Styopodium</i> spp. ^a	0.8 $\pm$ 0.4	1.0 $\pm$ 0.6	5.7 $\pm$ 0.8	<0.0001	ns	<0.0001	<0.0001
<i>Zonaria stipitata</i> ^a	0.2 $\pm$ 0.5	1.2 $\pm$ 0.6	0.3 $\pm$ 0.9	ns	na	na	na
<i>Halimeda</i> spp. ^a	0.3 $\pm$ 0.3	0.7 $\pm$ 0.4	3.8 $\pm$ 0.5	<0.0001	ns	<0.0001	<0.0001
<i>Sargassum obtusifolium</i> ^a	0.0 $\pm$ 0.3	0.1 $\pm$ 0.3	4.1 $\pm$ 0.5	<0.0001	ns	<0.0001	<0.0001
Turf algae ^a	1.1 $\pm$ 0.4	0.8 $\pm$ 0.5	7.2 $\pm$ 0.8	<0.0001	ns	<0.0001	<0.0001
CCA ^a	23.2 $\pm$ 2.9	19.6 $\pm$ 3.9	1.7 $\pm$ 5.6	0.0063 ^e	ns	0.0016	0.0130
Total coral ^a	45.0 $\pm$ 3.2	53.2 $\pm$ 4.3	52.7 $\pm$ 6.1	ns	na	na	na
Total macroalgae ^d	6.2 $\pm$ 1.6	6.9 $\pm$ 2.1	27.6 $\pm$ 3.0	0.0003	ns	0.0001	0.0003
<i>Diadema savigny</i> ^c	4.3 $\pm$ 0.8	6.4 $\pm$ 1.0	0.4 $\pm$ 1.5	0.0003	ns	0.0010	<0.0001

524	Total urchins ^a	4.9 ± 0.7	6.7 ± 1.0	0.5 ± 1.4	0.0046	ns	0.0102	0.0011
525	^a ANOVA on raw data.							
526	^b ANOVA on rank-transformed data.							
527	^c ANOVA on ln(X+1)-transformed data.							
528	^d ANOVA on logit-transformed data.							
529	^e Using a sequential Boneforri correction ($p \leq 0.05/n$), where n = ranking from largest to smallest p value for the 19 tests (fauna), this result is not							
530	significant.							

531 Table 3. Mean size $\pm$ SE for the most abundant herbivores. Means are reported in cm for the test diameter *Diadema savignyi* and TL
532 for fishes. E = Exposed, SE = semi-exposed, Pr = protected. Asterisks indicate means that are not significantly different from one
533 another between factor states; all other pairs significantly differed ($p < 0.02$).

	Island		Depth		Exposure		
	RN (n, range)	SyG (n, range)	10 (n, range)	20 (n, range)	E (n, range)	SE (n, range)	Pr (n, range)
<i>Diadema savignyi</i>	$3.58 \pm 0.07^*$ (269, 1-10)	$3.61 \pm 0.05^*$ (597, 1-7)	3.86 ± 0.07 (284, 1-12)	3.47 ± 0.05 (582, 1-10)	3.40 ± 0.06 (442, 1-10)	$3.78 \pm 0.06^*$ (412, 1-8)	$4.33 \pm 0.34^*$ (12, 1-12)
<i>Kyphosus sandwicensis</i> ^a	21.36 ± 0.36 (47, 18-30)	23.59 ± 0.08 (1043, 8-35)	23.82 ± 0.09 (798, 8-35)	22.58 ± 0.15 (292, 15-30)	23.61 ± 0.08 (941, 8-35)	23.05 ± 0.22 (128, 18-30)	20.86 ± 0.55 (21, 18-30)
<i>Acanthurus leucopareius</i>	14.69 ± 0.07 (719, 5-20)	14.04 ± 0.20 (84, 8-17)	13.93 ± 0.09 (376, 5-20)	15.24 ± 0.09 (427, 6-17)	15.52 ± 0.09 (360, 5-17)	13.25 ± 0.11 (233, 6-17)	14.62 ± 0.11 (210, 10-20)

534 ^aOnly one individual was 8 cm, all others were 15 cm or larger.

535 Figure captions

536 Fig. 1. Map of exposed (black circles), semi-exposed (medium gray circles), and protected
537 (light gray circles) sampling stations around Rapa Nui and Salas y Gómez and their positions
538 relative to South America and the Chilean EEZ. Additional station details are in see
539 Supplementary material Table 1.

540

541 Fig. 2. PCA plots of the variation in community structure among our stations by (A) island,
542 (C) wave exposure, and (D) depth. Communities are only well separated by island, primarily
543 along axis 1. Axes 1 and 2 respectively explain 37.0% and 20.0% of the variation. PCA
544 loadings are graphically illustrated in (B) and are reported in see Supplementary material
545 Table 4.