SPECIAL ISSUE ARTICLE

WILEY

The awakening of invertebrates: The daily dynamics of fishes and mobile invertebrates at Rapa Nui's multiple use marine protected area

Iván A. Hinojosa[1,2,3] | German Zapata-Hernández[2,3,4] | Amelia E. Fowles[5] | Carlos F. Gaymer[2,3,6] | Rick D. Stuart-Smith[5]

[1]Departamento de Ecología, Facultad de Ciencias, Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Universidad Católica de la Santísima Concepción, Concepción, Chile

[2]Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Coquimbo, Chile

[3]Departamento de Biología Marina, Millennium Nucleus for Ecology and Sustainable Management of Oceanic Islands (ESMOI), Coquimbo, Chile

[4]Programa de Doctorado en Biología y Ecología Aplicada, Universidad Católica del Norte, Coquimbo, Chile

[5]Institute for Marine and Antarctic Studies, University of Tasmania, Taroona, Tasmania, Australia

[6]Centro de Estudios Avanzados en Zonas Áridas, Coquimbo, Chile

Correspondence
Iván A. Hinojosa, Departamento de Ecología, Facultad de Ciencias y Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Universidad Católica de la Santísima Concepción, Chile.
Email: ihinojosa@ucsc.cl

Funding information
Chilean Millennium Initiative, Grant/Award Number: ESMOI; Comisión Nacional de Investigación Científica y Tecnológica, Grant/Award Number: PCHA/Doctorado Nacional/2015-21151249; Fondo Nacional de Desarrollo Científico y Tecnológico, Grant/Award Number: 3170392

Abstract

1. On shallow reefs, day-night activity patterns between fishes and invertebrates are presumed to reflect trade-offs between feeding and predation; however, quantitative data on daily community dynamics are scarce. Moreover, night surveys may contribute important information for biodiversity inventories or baselines that normally are not considered.

2. This study used standardized day–night visual surveys of fishes and mobile invertebrates on the same transect lines in Rapa Nui (Easter Island) and investigated how diel patterns vary between taxonomic and trophic groups.

3. Distinct differences between taxonomic groups were observed, with fishes being more abundant during the day (>twice), whilst invertebrate abundance and richness showed an opposite trend with higher numbers at night (>three times).

4. Analysis of trophic groups showed that herbivorous and planktivorous fishes were more abundant during the day. Carnivorous fishes did not show any trends. Top predators (Apex) were observed only at very low abundances. However, a replacement amongst carnivorous fish species between day and night was found, where labridae fishes were practically absent during nights.

5. Most of the mobile invertebrates remained concealed during the day, probably due to the influence of predation risk (labrid fishes). The results emphasize the need for consideration of nocturnally active invertebrates in biodiversity inventories or baselines of reefs, which focus heavily only on diurnal surveys.

6. Day–night reef surveys should be included in marine protected area planning and monitoring as this provides a better understanding of shallow benthic communities and helps inform proper management decisions.

KEYWORDS
biodiversity, community structure, coral reefs, marine protected areas, nocturnal fauna, predation risk

1 | INTRODUCTION

Multiple environmental cycles related to sun and moon phases modulate activity patterns (i.e. circadian, circatidal, circalunar, and seasonal) (Tessmar-Raible, Raible, & Arboleda, 2011), but they are ultimately believed to be primarily related to trade-offs between predation risk (Kronfeld-Schor & Dayan, 2003) and feeding (including activity patterns of prey). Sheltering in cracks and refuges of the reef and nocturnal emergence (Brewin, Brown, & Brickle, 2016) is a common strategy among small-bodied species vulnerable to predation. Such species may play important ecological roles and constitute an important component in the trophodynamics of shallow benthic communities (Boaden & Kingsford, 2012; Holzman, Ohavia, Vaknin, & Genin, 2007), but are generally missed or underestimated by most survey methods (Aguzzi et al., 2012; Azzurro, Pais, Consoli, & Andaloro, 2007).

Most coral reef fish studies have only considered species that can be surveyed during daylight hours, with only a few studies on nocturnal species (Annese & Kingsford, 2005; Bosiger & McCormick, 2014; Galzin, 1987). Nocturnal fishes can constitute about 25–44% of the species found in tropical reefs, and the biodiversity associated with coral reefs may therefore be consistently under-represented if only daytime surveys are undertaken (Boaden & Kingsford, 2012; Holzman et al., 2007). In general, the nocturnal species are those that feed on night-time active prey types such as plankton and/or micro-invertebrates, while herbivorous species tend to be largely diurnal (Hobson, 1965). Nevertheless, planktivorous fishes may be diurnal, nocturnal or both (Hobson, 1965; Hobson, 1991). Some tropical fishes also exhibit daily movement patterns across habitats (Hart, Clemons, Wakefield, & Heppell, 2010), with some species alternating between reefs, sand, and seagrass to feed or rest (Hitt, Pittman, & Nemeth, 2011), where the habitat configuration allows regular movements and spatial–temporal dynamics in the fish assemblages (Kruse, Taylor, Muhando, & Reuter, 2016). Also, differences in the fish assemblages could be due to refuge availability, prey abundances, predation risk, and rearing behaviour (Harvey, Dorman, Fitzpatrick, Newman, & McLean, 2012), creating important changes in the composition and structure of the assemblages (Azzurro et al., 2007).

For many mobile invertebrate taxa on reefs, nocturnal emergence plays an important role, changing the structure and trophic relationships of communities on a daily basis (Blackmon & Valentine, 2013). Generally, reduced predation risk at night has been suggested as the primary reason for nocturnal emergence for many invertebrates, as in shrimps (Clark, Ruiz, & Hines, 2003), urchins (Dee, Witman, & Brandt, 2012), and holothurians (Hammond, 1982). However, the influence of the predation risk on diel activities of coral reef mobile invertebrates has rarely been tested (Ory, Dudgeon, Duprey, & Thiel, 2014). Moreover, there are few studies that have evaluated changes in the whole community structure (i.e. including invertebrates and fishes) at a daily scale (e.g. Brewin et al., 2016).

The diel changes in the marine community structure have generally been neglected by sampling procedures due to a lack of adequate technology and/or sufficient resources to perform replicates of samples (Aguzzi et al., 2012). This has probably underestimated the diversity and the trophic relationships in marine communities (Myers, Harvey, Saunders, & Travers, 2016), leaving important gaps in the understanding of the effects of anthropogenic impacts on the diversity of fauna (diurnal and nocturnal) associated with coral reefs (Knowlton, 1992; Knowlton & Jackson, 2008). This is a key issue when planning conservation measures such as marine protected areas (MPAs), as they are generally based on daily surveys that do not only underestimate biodiversity, but also poorly explain the ecological processes that generate the observed biodiversity patterns and thus, conservation strategies could be inappropriately founded and the conservation goals neglected.

The aim of this study was to use co-located surveys of reef fishes and mobile invertebrates to describe day-night differences in richness, abundance and community structure, which should allow elucidating the fauna composition that may be missed in biodiversity inventories or baselines. Therefore, this study contributes to a better understanding of ecological patterns and processes which are important for conservation strategies of the shallow reefs.

1.1 | Rapa Nui reefs

Rapa Nui (Easter Island) is located at the eastern edge of the Polynesian Triangle and is the south-eastern limit of coral distribution in the Pacific. The coral composition is more similar to that in the Eastern Pacific than the broader Indo-West Pacific (Glynn et al., 2007). Biodiversity inventories have recorded 605 invertebrates and 216 fish taxa around the island, with 400 species of molluscs and crustaceans (Fernandez, Pappalardo, Rodriguez-Ruiz, & Castilla, 2014). The reef fauna is considered depauperate compared to other Polynesian islands, which have about 5–10 times more species (Randall & Cea, 2011). Due to isolation of Rapa Nui, there are high levels of endemism: 34% in molluscs, 33% sponges, 12% bryozoans, and 22% in coastal fishes (Fernandez et al., 2014), which increases to over 75% when considering biomass abundance (Friedlander et al., 2013). Coral cover is also quite high (>50%) in comparison to other subtropical areas with similar ocean climates, and it is dominated by only two scleractinian species, *Porites lobata* and *Pocillopora verrucosa* (only 13 species of coral have been recorded altogether at Rapa Nui) (Glynn et al., 2007; Hubbard & Garcia, 2003). Both coral species are found at depths of approximately 5–7 m, but with *Pocillopora* spp. dominating down to approximately 10–15 m, where *P. lobata* starts to progressively dominate as the depth increases (Hubbard & Garcia, 2003; Wieters, Medrano, & Perez-Matus, 2014). Recent surveys have documented that the long-spined sea urchin *Diadema savignyi* and the violet coral shell *Coralliophila violacea* are the most abundant mobile benthic invertebrates (Friedlander et al., 2013). The diurnal fish fauna is dominated by small individuals of planktivorous and herbivorous species, while apex predators such as sharks (e.g. *Carcharhinus galapagensis*) are practically absent (Friedlander et al., 2013), or present in low abundance at some sites (Morales et al., 2019). Herbivorous fishes tend to be associated with *Pocillopora* reefs, the

carnivorous fishes with *P. lobata*, and planktivorous species with articulated and leathery algae (Wieters et al., 2014). Although many species of macroalgae are known, macroalgal cover is generally low around the island (Santelices & Abbott, 1987). Recent surveys indicate that 10% of the reef substrate is covered with coralline crustose algae (Friedlander et al., 2013), and temporal and spatial variability in different algae groups (i.e. articulated, crustose, ephemeral and leathery) have been documented (Fernandez et al., 2014; Wieters et al., 2014).

Despite much recent effort to understand the structure and function of Rapa Nui, the ecology of subtidal communities remains poorly understood (Wieters et al., 2014) and there is limited knowledge of the nocturnal communities (DiSalvo, Randall, & Cea, 1988) and behavioural habits of the endemic species. Diel movements of individuals can influence the perception of population sizes and community composition, depending on the sampling time (Aguzzi et al., 2012). Present understanding of the reef communities at Rapa Nui may therefore be poorer than the survey effort may suggest, particularly if many of the endemic species are nocturnally active and poorly covered in daytime surveys. Therefore, to provide a more comprehensive knowledge of the reef communities at Rapa Nui, this study will add new information relevant to the potential contribution of nocturnally active species to its community composition.

The waters of Rapa Nui are presently protected by the recent declaration of a multiple-use MPA, but management planning is being developed for its full implementation (Paredes, Flores, Figueroa, Gaymer, & Aburto, 2019; Friedlander & Gaymer, in press). The present study will be an important contribution for conservation planning of the Rapa Nui multiple-use MPA and defining monitoring priorities for the reefs.

2 | MATERIAL AND METHODS

Change in the community structure between day and night was assessed at six sites from Easter Island; four sites on the western coast (Hanga Roa Sth, Hanga Roa SW, Manavai, and Motu Tautara) and two sites on the north coast (Anakena E1 and Anakena E2; Figure 1, Table S1). Standardized underwater visual census methods were conducted by three experienced divers (>100 dives) in March 2016 to record the fish and mobile benthic invertebrates (hereafter 'invertebrates') richness and their abundances (10 to 15 m depths, visibility >20 m). One 50 m long transect was conducted at each site during the day (between 1100 h and 1500 h). Transects were then replicated at the same GPS point, direction, and depth at night (between 2100 h and 0000 h). Reef life survey (RLS) methods were used to estimate densities and sizes of fish, and invertebrates (e.g. gastropods, sea cucumbers, sea stars, sea urchins, decapods) (Edgar & Stuart-Smith, 2014). Brittlestars and shrimps were also included in the visual census as they were obviously abundant and important components of the night-time invertebrate assemblage (RLS methods normally do not include these species). To conduct the RLS method properly, a diver deployed the 50-m transect line followed by two other divers counting fish and invertebrates respectively (i.e. a three-diver team). To estimate fish densities and sizes, fish
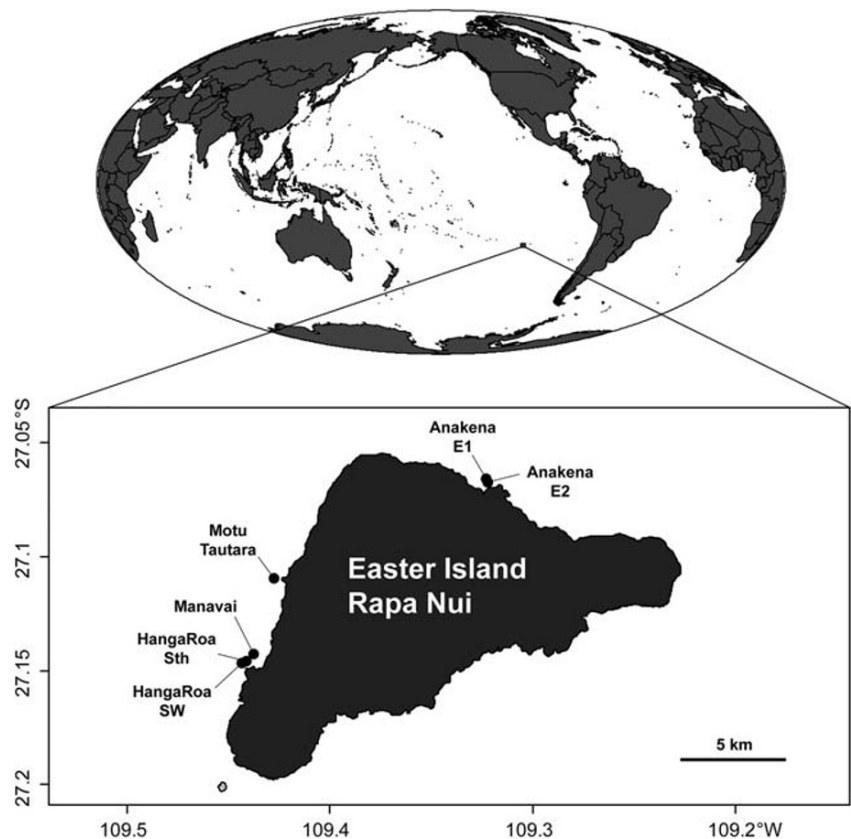

FIGURE 1 Sampling sites at Rapa Nui (Easter Island) where day and night visual surveys were conducted in March 2016

species sighted within 5 m from the transect line on either side were recorded by a diver who swam slowly along transect in the two directions (back and forward, 500 m^2 surveyed). The number and estimated size-category of each species was recorded according with size categories of 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 400, 500, 625 mm, and above, which represent total fish length. Digital photographs were taken by the diver who deployed the transect line to later confirm species identities. Invertebrates were surveyed along the same 50-m transect lines. The diver swam along the bottom recording all mobile invertebrates (>2 cm in size) on the reef surface within 1 m of the line on either side along the transect in the two directions (back and forward, 100 m^2 surveyed; detailed descriptions of methods are provided online www.reeflifesurvey.com and in Edgar and Stuart-Smith (2014)). Nocturnal dives were conducted using dive torches (500–1,200 lumens, 60° flood beam, Sola Dive 1200 S/F) allowing effective nocturnal visibility for more than 5 m. In a nocturnal exploratory dive, the torches were turned on and off to evaluate potential fish escapes, but no clear scape behaviour was observed. To relocate the same spot during night dives, there were surface buoys at the western sites, and underwater geographical marks (particular characteristics of the reef) were used at the northern sites.

No specific permissions were required as this was an observational study, and it did not involve manipulation of endangered or protected species.

2.1 | Statistical analysis

Fish abundance was expressed as number of individuals 500 m^{-2} and biomass was expressed as kg 500 m^{-2}. The biomass of individual fish was estimated using the allometric length-weight conversion: W = aTL^b, where parameters 'a' and 'b' are species-specific constants, TL is total length in mm, and W is weight in g. Length–weight fitting parameters were obtained from FishBase (www.fishbase.org) and the cross-product of individual weights and numerical densities was used to estimate biomass density by species. Fishes were categorized into four trophic groups (herbivore, planktivore [zooplankton consumers], carnivore [mostly benthic invertebrates], and apex predators) after Friedlander et al. (2013) and Wieters et al. (2014). Invertebrate abundances were expressed as number of individuals 100 m^{-2}. Fish and invertebrate richness are referred to the total number of species recorded per transect by the diver.

Paired Student t-test on Log (x + 1) data transformation was used to examine differences in fish and invertebrate abundances and richness, fish biomass, and fish trophic groups between day and nights surveys. Paired test was used to account for the lack of independence between day and night surveys at the same sites (Quinn & Keough, 2002).

Multivariate analyses were conducted in PRIMER v6 with PERMANOVA (Primer-E Ltd, Plymouth, UK). Fish and invertebrate species data were analysed separately. A one-way PERMANOVA was conducted to test the null hypothesis that community structure was not significantly different between day and night surveys (as a fixed

factor) utilizing fish and invertebrate abundance data (fourth root transformed). To test for difference in trophic groups between day and night surveys, a one-way PERMANOVA was conducted on fish trophic groups. Type III sums of squares was used as the design and calculations of the pseudo-F ratio and P-value were based on unrestricted permutations of the residuals under an unreduced model (Anderson, Gorley, & Clarke, 2008). Similarity of percentages (SIMPER) was used to determine the species most responsible for the percentage dissimilarities between day and night surveys, using Bray–Curtis similarity analysis of hierarchical agglomerative group average clustering. Principal coordinates analysis (PCO) was conducted to examine the relative differences in community structure between day and night surveys on fourth root transformed abundance by species using a Bray–Curtis similarity resemblance matrix. Eigenvectors of species most responsible for the separation among sites in ordination space were calculated using Spearman's correlation coefficients and displayed using vector diagrams on the PCO ordination overlaid on plot (Anderson et al., 2008). Similarly, another PCO was conducted but considering the fish trophic groups. Fourth root transformation on the data was used to normalize a Poisson distribution, which normally occurred with zero inflated observation in biological data (Anderson et al., 2008).

3 | RESULTS

Forty-three fish and 30 invertebrate taxa where found and identified on the transect surveys (Table S2 and S3). Fishes were more than twice as abundant during day surveys (285.0 ± 68.3 indiv. 500 m^{-2}, mean ± standard error) than during nights (122.2 ± 30.9 indiv. 500 m^{-2}; t = 3.22, df = 5; P = 0.024; Figure 2), however, differences in fish richness (18.2 ± 1.2 taxa at day and 14.0 ± 0.9 taxa at night; t = 2.49, df = 5, P = 0.055; Figure 2) and biomass (30.2 ± 16.1 kg 500 m^{-2} at days and 9.3 ± 1.6 kg 500 m^{-2} at nights; t = 1.66, df = 5, P = 0.159; Figure 3) were smaller. The opposite trend was observed in invertebrates where lower abundances were observed on diurnal surveys (224.5 ± 79.4 indiv. 100 m^{-2}) and higher abundances at nights (551.2 ± 56.8 indiv. 100 m^{-2}; t = −3.15, df = 5, P = 0.025; Figure 2), and lower richness in diurnal surveys (5.8 ± 0.6 taxa 100 m^{-2}) compared to nights (15.5 ± 1.3 taxa 100 m^{-2}; t = −8.90, df = 5, P < 0.001; Figure 2).

Fish and invertebrate abundances showed clear changes among day and night surveys (pseudo-F = 77.199; P = 0.001 and pseudo-F = 77.094; P = 0.002, respectively; Table 1). Similarity among sites during the day was 56.7% in fish assemblages (Table 2). The sunset wrasse Thalassoma lutescens (Mōri vaihi), the surgeonfish Acanthurus leucopareius (Ma'ito), the butterflyfish Chaetodon litus (Tipi tipi'uri) and the fuentesi's wrasse Pseudolabrus fuentesi (kōtea) contributed most to the similarity (48.8%; Table 2). Similarity among sites at night was 51.4% where the hawkfish Itycirrhitus wilhelmi (piliko'a) and the soldierfish Myripristis tiki (mārau) contributed most to this similarity (43.7%; Table 2). Concordantly, relatively high dissimilarity between sites at day and night surveys was found (67.7%) where T. lutescens
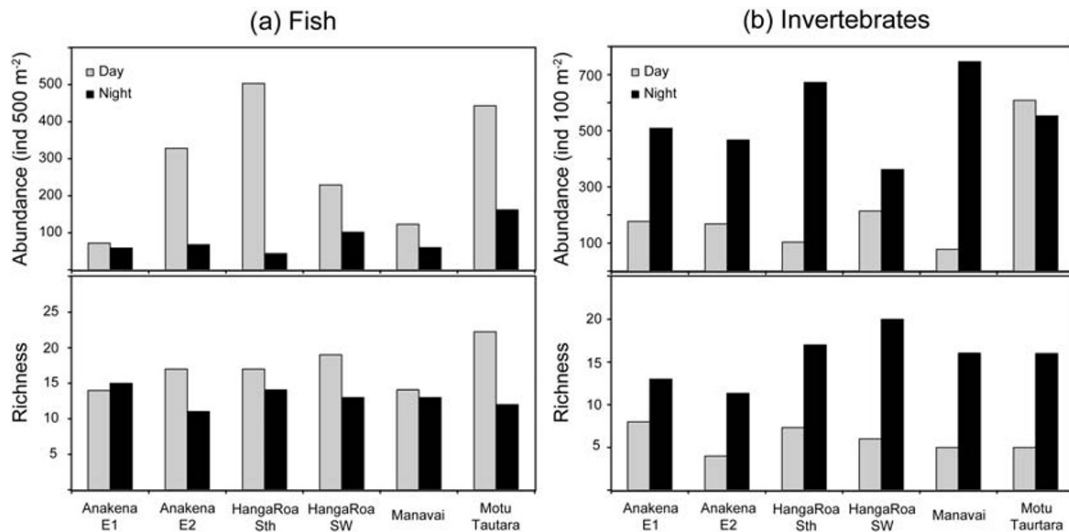
FIGURE 2 Abundance and richness of (a) fish and (b) invertebrate assemblages during day and night surveys in six coral reef sites around Rapa Nui
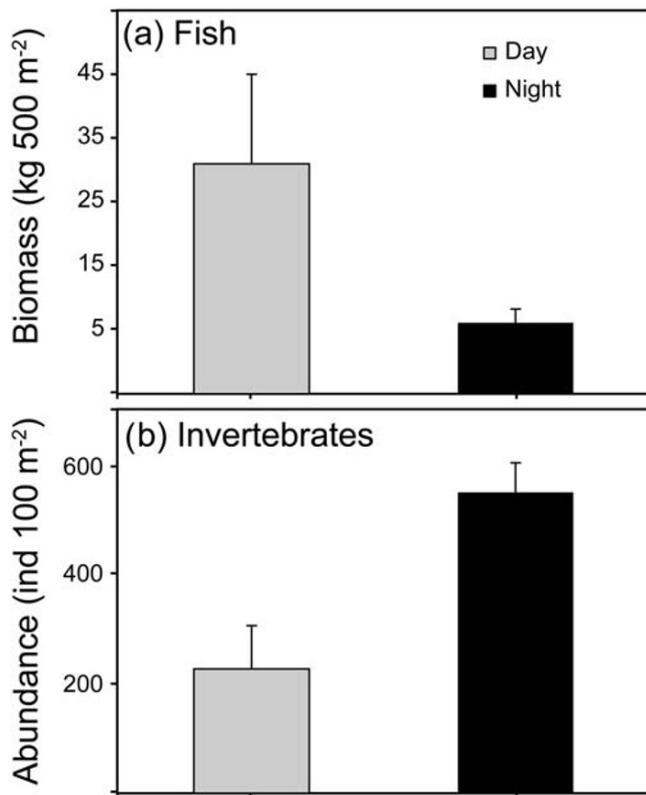

FIGURE 3 The average biomass of fish (a) and the average invertebrate abundances (b) during day and night surveys in coral reefs around Rapa Nui. Error bars represent the standard error

TABLE 1 Results of permutational multivariate analyses of variances (PERMANOVA) testing differences in the abundance of fish (a) and invertebrate (b) assemblages between day and night surveys at Rapa Nui, based on Bray–Curtis similarity matrices performed on fourth root transformed data

Source	df	SS	MS	Pseudo-F	P (perm)
a) Fish assemblage					
Day/night	1	7360.8	7360.8	77.199	0.001
Res	10	9534.8	953.5		
Total	11	16896			
b) Invertebrates assemblage					
Day/night	1	6795.6	6795.6	77.094	0.002
Res	10	8814.7	881.5		
Total	11	15610			

Abbreviations: MS, mean of squares; SS, sum of squares

(Mōri vaihi), *M. tiki* (mārau), the damselfish *Chrysiptera rapanui* (māmata), *A. leucopareius* (Ma'ito), *I. wilhelmi* (piliko'a), *P. fuentesi* (kōtea), and the feminine wrasse *Anampses femininus* (pāhika) contributed 42% of dissimilarity of the fish community structure (Table 2).

Invertebrate structure showed a similarity of 56.3% among day surveys, in which urchins *D. savignyi* and *Echinostrephus aciculatus*

contributed 63.9% of this similarity. During nocturnal surveys the community structure had a 61.1% similarity, where the brittlestar *Breviturma dentata*, the urchin *D. savignyi*, and the crab *Calcinus pascuensis* contributed 43.8% (Table 3). The dissimilarity between day and night surveys was 60% where the brittlestar, *B. dentata*, the violet coral shell, *C. violacea*, the guardian crab, *Trapezia punctimanus*, the rock shrimps, *Cinetorhynchus* sp., and the sea cucumber, *Stichopus monotuberculatus* contributed the most to the dissimilarity (37.5%; Table 2).

The first axis of the PCO on the fish assemblage explained 45.2% of the total variation and separated diurnal surveys well in ordination space from nocturnal surveys (Figure 4). The species most responsible for this separation in day surveys were the wrasses *P. fuentesi* (kōtea) and *T. lutescens* (Mōri vaihi). The species that accounted for most of the separation along Axis 1 of the PCO towards night surveys were the soldierfish *Plectrypops lima* (mārau kape) and the porcupinefish *Diodon holocanthus* (titeve tara tara). Relatively orthogonal to these

TABLE 2 Results of the similarity percentage analysis (SIMPER) on fish assemblage abundances (fourth root of abundance) between day and night at Rapa Nui

Group: Day surveys Average similarity: 56.73 Species	Trophic	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Thalassoma lutescens	Carnivore	2.95	8.57	8.22	15.11	15.11
Acanthurus leucopareius	Herbivore	3.36	7.30	1.98	12.88	27.99
Chaetodon litus	Carnivore	2.36	6.16	3.54	10.86	38.85
Pseudolabrus fuentesi	Carnivore	1.96	5.67	5.55	9.99	48.84
Chrysiptera rapanui	Planktivore	2.70	4.48	1.23	7.90	56.74
Itycirrhitus wilhelmi	Carnivore	1.86	4.02	1.71	7.09	63.83
Aulostomus chinensis	Apex	1.27	2.89	3.69	5.10	68.93
Heteropriacanthus cruentatus	Planktivore	1.29	2.85	2.73	5.02	73.95
Forcipiger flavissimus	Carnivore	1.40	2.62	1.20	4.61	78.56
Coris debueni	Carnivore	1.35	2.39	1.14	4.21	82.77
Anampses femininus	Carnivore	1.55	1.94	0.73	3.43	86.20
Gymnothorax eurostus	Carnivore	1.01	1.92	1.17	3.39	89.58
Mulloidichthys vanicolensis	Carnivore	0.96	1.54	1.16	2.72	92.30

Group: Night surveys Average similarity: 51.43 Species		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Itycirrhitus wilhelmi	Carnivore	3.37	12.02	3.26	23.37	23.37
Myripristis tiki	Planktivore	2.69	10.43	2.97	20.29	43.66
Chaetodon litus	Carnivore	2.50	7.56	2.00	14.70	58.36
Acanthurus leucopareius	Herbivore	1.15	2.87	1.09	5.59	63.94
Aulostomus chinensis	Apex	0.91	2.48	1.12	4.82	68.77
Diodon holocanthus	Carnivore	0.71	2.32	1.26	4.50	73.27
Forcipiger flavissimus	Carnivore	0.93	2.08	0.76	4.04	77.31
Sargocentron wilhelmi	Carnivore	1.29	1.80	0.48	3.50	80.81
Cantherhines rapanui	Carnivore	0.73	1.49	0.72	2.90	83.71
Arothron meleagris	Carnivore	0.65	1.33	0.75	2.59	86.30
Sargocentron hormion	Carnivore	0.78	1.28	0.46	2.50	88.80
Lactoria diaphana	Carnivore	0.53	1.26	0.78	2.45	91.25

Groups: Day & Night survey Average dissimilarity = 67.67 Species		Group day Av.Abund	Group night Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Thalassoma lutescens	Carnivore	2.95	0.00	5.52	6.25	8.16	8.16
Myripristis tiki	Planktivore	0.12	2.69	4.94	2.80	7.29	15.45
Chrysiptera rapanui	Planktivore	2.70	0.40	4.49	1.40	6.63	22.08
Acanthurus leucopareius	Herbivore	3.36	1.15	4.44	1.40	6.56	28.65
Itycirrhitus wilhelmi	Carnivore	1.86	3.37	3.18	1.45	4.69	33.34
Pseudolabrus fuentesi	Carnivore	1.96	0.30	3.16	2.68	4.66	38.01
Anampses femininus	Carnivore	1.55	0.00	2.70	1.24	3.99	42.00
Coris debueni	Carnivore	1.35	0.00	2.46	1.62	3.64	45.64
Decapterus muroadsi	Planktivore	1.38	0.00	2.40	0.72	3.55	49.18
Sargocentron wilhelmi	Carnivore	0.18	1.29	2.31	1.01	3.41	52.59
Chaetodon litus	Carnivore	2.36	2.50	2.14	1.40	3.16	55.75
Heteropriacanthus cruentatus	Planktivore	1.29	0.38	1.97	1.61	2.92	58.67
Cantherhines rapanui	Carnivore	0.75	0.73	1.82	1.24	2.69	61.36

TABLE 2 (Continued)

Groups: Day & Night survey Average dissimilarity = 67.67		Group day Av.Abund	Group night Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Species							
Gymnothorax eurostus	Carnivore	1.01	0.60	1.78	1.42	2.63	63.99
Forcipiger flavissimus	Carnivore	1.40	0.93	1.76	1.41	2.60	66.59
Mulloidichthys vanicolensis	Carnivore	0.96	0.00	1.72	1.41	2.54	69.13
Apogon kautamea	Carnivore	0.00	0.97	1.71	0.69	2.53	71.67
Sargocentron hormion	Carnivore	0.41	0.78	1.57	1.08	2.32	73.98
Thalassoma purpureum	Carnivore	0.90	0.00	1.55	1.21	2.30	76.28
Pseudocaranx cheilio	Apex	0.63	0.00	1.35	0.67	1.99	78.27
Aulostomus chinensis	Apex	1.27	0.91	1.23	1.34	1.82	80.09
Chromis randalli	Planktivore	0.18	0.60	1.22	0.94	1.80	81.89
Diodon holocanthus	Carnivore	0.12	0.71	1.21	1.51	1.78	83.68
Lactoria diaphana	Carnivore	0.23	0.53	1.11	1.33	1.64	85.31
Arothron meleagris	Carnivore	0.48	0.65	1.10	1.14	1.62	86.93
Plectrypops lima	Planktivore	0.00	0.53	1.00	1.20	1.47	88.41
Kyphosus sandwicensis	Herbivore	0.53	0.12	0.91	1.18	1.35	89.75
Gymnothorax porphyreus	Carnivore	0.30	0.30	0.90	0.60	1.33	91.08

species were the damselfishes *Chromis randalli* (māmata) and the hawkfish *I. wilhelmi* (piliko'a), more related to night surveys (Figure 4).

The PCO on the invertebrate assemblage also separated diurnal from nocturnal surveys in ordination space, where the first axis explained 53.6% of the total variation (Figure 5). Several species which appeared mostly during nocturnal surveys, such as crustaceans, holothurians, some molluscs and echinoids were responsible for this separation (Figure 5).

The fish trophic structure was different between day and night surveys (Pseudo-F = 3.901; P = 0.015; Table 4). Herbivorous species were more abundant and with higher biomass during the day (t = 3.85, P = 0.012; t = 3.23, P = 0.023, respectively; Figure 6). However, the differences between day and night surveys were less evident in apex predators, carnivores (secondary consumers) and planktivores, in both abundance (t = 1.14, P = 0.306; t = 0.09, P = 0.932; t = 1.30, P = 0.250, respectively) and biomass (t = 0.48, P = 0.634; t = 1.12, P = 0.312; t = −0.87, P = 0.424, respectively; Figure 6). The PCO separated day and night surveys, where 57.5% of the total variation was explained in the first axis (Figure 7). Herbivores were the most responsible for this separation of day surveys and planktivores for night surveys. The fish trophic structure at Hanga Roa SW during night survey was relatively isolated (orthogonal to first axis), and apex predators and carnivores explained this separation.

4 | DISCUSSION

This study shows an inverse activity pattern of fish and mobile invertebrate communities in the shallow reefs of Easter Island. Fishes concentrated their activity during the day, while invertebrates were less active, sheltering in cracks provided by the coral reefs. In contrast, invertebrate communities were more active during the night, when fish were less abundant.

4.1 | Shallow community structure dynamic

This study shows differences in the abundance of fish assemblages between day and night surveys at Rapa Nui, where fish were more than twice as abundant during the day than at night. A similar trend has been reported in others studies in the Mediterranean sea (Azzurro et al., 2007), Western Australia (Harvey et al., 2012; Myers et al., 2016), South Atlantic (Brewin et al., 2016), and Virgin Islands (Collette & Talbot, 1972). However, the richness and biomass of nocturnal fishes were not significantly different from diurnal surveys, because some diurnal species (i.e. mainly carnivores and herbivores) were replaced by others species that are strictly nocturnal (i.e. other carnivores and planktivores; Figures 2 and 6), probably specialized for detecting and capturing prey in the dark (Hobson, 1981).

The fish community structure changed among day and night surveys, where species that were predominantly diurnal such as *T. lutescens*, *P. fuentesi*, *A. femininus* (carnivores), *C. rapanui* (planktivore), and *A. leucopareius* (herbivore), and nocturnal fishes such as *M. tiki* (planktivore) and *I. wilhelmi* (carnivore) contributed with 42% of this dissimilarity (Table 2). *M. tiki* and *I. wilhelmi* contributed to the higher similarity among sites from the nocturnal surveys (43.7%), being the two most common fish species among the sites. The hawkfish *I. wilhelmi* has been seen immobile during the day on *Porites*

TABLE 3 Results of the similarity percentage analysis (SIMPER) based on the abundances (fourth root of abundance) of invertebrate assemblages between day and night at Rapa Nui

Group: Day surveys
Average similarity: 56.34

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Diadema savignyi	2.85	21.56	3.19	38.28	38.28
Echinostrephus aciculatus	2.06	14.41	3.35	25.58	63.86
Holothuria cinerascens	1.30	7.46	1.30	13.24	77.09
Coralliophila violacea	1.86	6.86	0.70	12.18	89.27
Calcinus pascuensis	0.91	3.65	0.78	6.48	95.75

Group: Night surveys
Average similarity: 61.07

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Breviturma dentata	3.84	12.39	4.78	20.28	20.28
Diadema savignyi	2.60	8.05	2.86	13.18	33.46
Calcinus pascuensis	1.97	6.28	7.81	10.29	43.75
Coralliophila violacea	1.87	5.24	3.26	8.58	52.33
Stichopus monotuberculatus	1.55	5.11	5.63	8.37	60.70
Echinostrephus aciculatus	2.04	4.26	1.05	6.98	67.68
Cinetorhynchus sp.	1.40	3.16	1.26	5.18	72.86
Naria englerti	1.11	2.96	1.36	4.84	77.70
Trapezia punctimanus	1.47	2.42	0.77	3.96	81.66
Polyplectana kefersteinii	0.90	2.30	1.36	3.77	85.43
Diadema paucispinum	1.43	2.18	0.70	3.57	89.01
Holothuria difficilis	1.17	1.80	0.79	2.94	91.95

Groups: Day & Night survey
Average dissimilarity = 59.96

| Species	Group day Av.Abund	Group night Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Breviturma dentata	0.70	3.84	8.31	2.26	13.86	13.86
Coralliophila violacea	1.86	1.87	3.80	1.71	6.35	20.21
Trapezia punctimanus	0.00	1.47	3.49	1.31	5.82	26.02
Cinetorhynchus sp.	0.00	1.40	3.46	1.86	5.77	31.80
Stichopus monotuberculatus	0.25	1.55	3.44	2.19	5.74	37.54
Diadema paucispinum	0.00	1.43	3.41	1.22	5.69	43.23
Holothuria cinerascens	1.30	1.22	3.28	1.47	5.47	48.70
Echinostrephus aciculatus	2.06	2.04	3.09	1.52	5.15	53.85
Calcinus pascuensis	0.91	1.97	2.91	1.52	4.85	58.71
Naria englerti	0.00	1.11	2.79	2.15	4.66	63.36
Holothuria difficilis	0.51	1.17	2.70	1.16	4.51	67.88
Ophidiaster easterensis	0.17	1.01	2.30	1.06	3.83	71.71
Polyplectana kefersteinii	0.00	0.90	2.21	2.13	3.69	75.39
Diadema savignyi	2.85	2.60	1.92	1.26	3.21	78.60
Conus miliaris	0.00	0.61	1.57	0.93	2.62	81.22
Holothuria nobilis	0.00	0.56	1.40	0.98	2.33	83.56
Breviturma longispina	0.00	0.50	1.19	0.68	1.99	85.54
Cinetorhynchus sp.	0.00	0.40	0.93	0.70	1.55	87.09
Holothuria sp.	0.00	0.36	0.85	0.69	1.42	88.52
Tripneustes gratilla	0.33	0.00	0.83	0.69	1.38	89.90
Calcinus imperialis	0.17	0.17	0.68	0.61	1.13	91.03
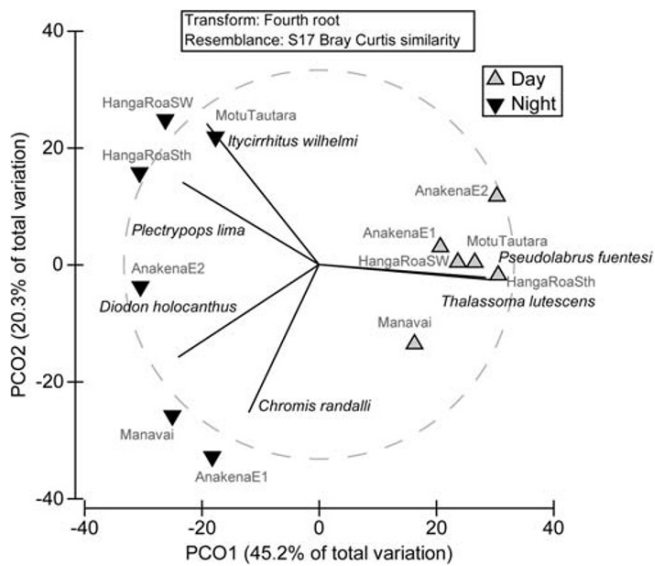
FIGURE 4 Plot of principal coordinates analyses (PCO) based on fish community structure using abundance – with species vectors (0.8 correlation). Species and sites are indicated in black and grey characters, respectively
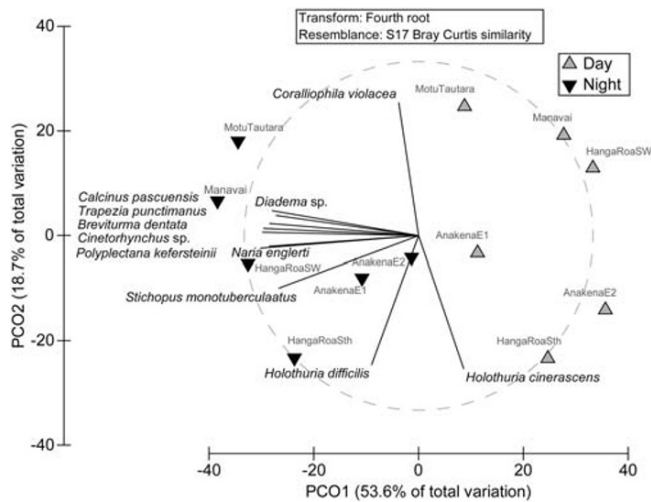

FIGURE 5 Plot of principal coordinates analyses (PCO) based on invertebrate abundances with species vectors (0.8 correlation). Species and sites are indicated in black and grey characters, respectively

reefs and their stomach contents contained small benthic crustaceans (DiSalvo, Randall, & Cea, 2007). This is similar to observations from the Mediterranean rocky reefs, where common prey of nocturnal predators are small mobile benthic invertebrates and planktivorous fishes that feed on large zooplankton close to substrate (Azzurro et al., 2007).

The invertebrate assemblage was more than three times richer and more abundant at night than in the day (Figure 2b). Most invertebrates remain inactive during the day under rocks, beneath sand, or in coral cracks, emerging at night to forage (Brewin et al., 2016). A

release of the predation pressure by fish at night has been used as an explanation of such increase in invertebrate abundances, as the activity of carnivorous fish decreases during night (Figure 6) (Aguzzi et al., 2012; Azzurro et al., 2007; Tessmar-Raible et al., 2011). However, some carnivorous fishes are specialized for feeding in the dark, including species of the families Apogonidae, Holocentridae, Clupeidae, Lutjanidae, and Serranidae (Azzurro et al., 2007).

Predators can exert strong selective pressure on their prey, determining different biological aspects including morphological, life history and behaviours (Bosiger & McCormick, 2014 and references therein). Some studies that report benthic invertebrates emerging during the night have been conducted on only single species (MacArthur, Hyndes, Babcock, & Vanderklift, 2008; Oppenheim & Wahle, 2013; Ory et al., 2014), assemblages of decapods (Aguzzi & Company, 2010; Aguzzi, Sbragaglia, Tecchio, Navarro, & Company, 2015; Nickell & Sayer, 1998), shrimps (Bauer, 1985), echinoderms (Nelson & Vance, 1979; Savy, 1987; Tuya, Martin, & Luque, 2004; Verling, Crook, Barnes, & Harrison, 2003), molluscs (Rueda, Urra, & Salas, 2008), and urchins and holothurians (Azzurro et al., 2007). However, reports of diel changes in invertebrate assemblages have been less common due to technical difficulties of nocturnal diving (Aguzzi et al., 2012). However, in a study conducted in Ascension Island by Brewin et al. (2016), a similar trend was reported, with several invertebrate species appearing only during the nights. These authors pointed out that several invertebrate species are simply hidden from view during the day but are present around the reef in refuges that are sub-optimal for accessing food resources. These authors suggested that the trophic ecology of reef species may be roughly partitioned between day and night and it may be a common trend in other places.

Among the most important invertebrates at night, the brittlestar *B. dentata* notably increased their abundance, emerging from their cryptic habitats (e.g. cracks provided mainly by massive *Porites* corals), probably to feed on detritus deposited on corals and coral mucus (Brewin et al., 2016). In addition, this species has been found in stomachs of diurnal carnivorous (e.g. *Coris debueni*, *T. purpureum*, and *Forcipiger flavissimus*) and other nocturnal fishes (*Cantherhines* spp. and *Arothron meleagris*) (DiSalvo et al., 2007), confirming that it is an important prey for diurnal and nocturnal predators in coral reefs at Rapa Nui.

Others less abundant invertebrate taxa were observed emerging at night, such as the echinoid *Lissodiadema lorioli*, the shrimp *Cinetorhynchus* sp., the crab *T. punctimanus*, two unidentified nudibranchs, and two holothurians (*Polyplectana kefersteinii* and *S. monotuberculatus*). These holothurians are important components of the reef ecosystem, emerging at night from their cryptic refuges to forage over the substrate (Brewin et al., 2016; Hammond, 1982). In addition, it is recognized that some holothurians can be strictly nocturnal, as has been reported for *Euapta lappa* at Discovery Bay, Jamaica (Hammond, 1982), and Ascension Island (Brewin et al., 2016). These holothurians have soft-bodies and slow-movement, and hence are susceptible to predation. Their nocturnal emergence could feasibly be hypothesized to be related to reducing predation risk (Brewin et al., 2016; Hammond, 1982).

TABLE 4 Results of permutational multivariate analyses of variances (PERMANOVA) testing differences in the biomass of trophic groups of fish assemblage between day and night surveys at Rapa Nui based on Bray–Curtis similarity matrices performed on fourth root transformed data

Trophic structure of fish					
Source	df	SS	MS	Pseudo-F	P (perm)
Day/night	1	548.1	548.1	3.901	0.015
Res	10	1405.3	140.5		
Total	11	1953.4			

Abbreviations: MS, mean of squares; SS, sum of squares
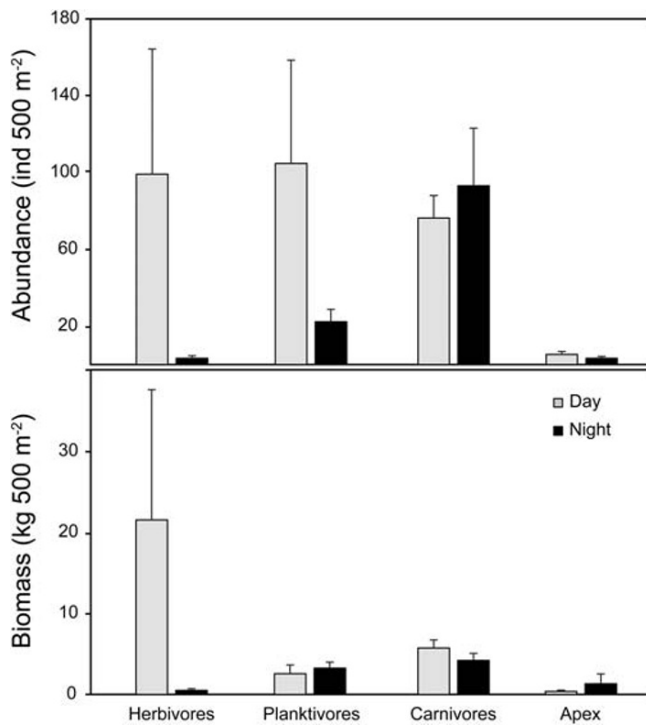
FIGURE 6 Diel changes in the trophic groups of fishes in terms of the average abundance and de average biomass. Apex = apex or top predator, Carnivores = invertivores. Error bars represent the standard error

Alternatively to predator avoidance, temporal niche partitioning has been put forward as an important mechanism to reduce competition among similar taxa thus permitting coexistence (Bosiger & McCormick, 2014; Brewin et al., 2016; Tessmar-Raible et al., 2011). Additionally, one lobster (*Panulirus pascuensis*) and two slipper lobsters (*Parribacus perlatus* and *Scyllarides roggeveeni*) also appeared only at night but they were only present outside of the quantitative transects. In the past, these three carnivorous species were conspicuous (DiSalvo et al., 1988), but were widely exploited in the past decades to satisfy the demands by tourists at Rapa Nui, reducing their abundance in both shallow and deeper waters (Gaymer et al., 2013). The effect of the fishery in removing these carnivorous species on the community structure has not been tested in Easter Island, but such
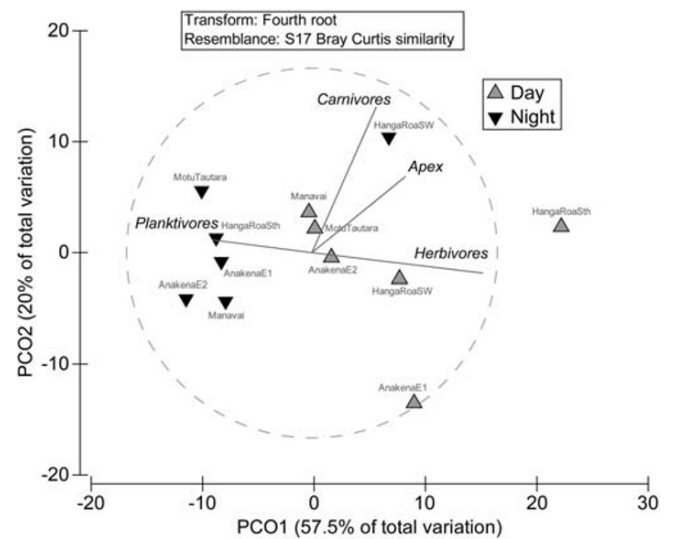

FIGURE 7 Plot of principal coordinates analyses (PCO) based on the biomass of trophic groups of fish assemblage). Species and sites are indicated in black and grey characters, respectively

trophic changes have generated strong impacts on the ecosystem dynamics elsewhere (e.g. catastrophic changes between alternative stable states) (Ling, Johnson, Frusher, & Ridgway, 2009; Mann & Breen, 1972).

4.2 | Fish trophic structure

Fishes may have the greatest effects on the benthic community structure and its dynamics (Friedlander et al., 2013). Clear differences were found in the fish trophic structure between day and night, and thus the impacts should differ accordingly. Other studies have suggested that differences in fish predatory impact between day and night are due to the replacement of some trophic groups by others (Collette & Talbot, 1972). Exceptionally, fish trophic structure at Hanga Roa SW during night was different to the other sites, owing to a single observation of the top predator *Conger conger cinereus* that accounted for most of this difference due to its large biomass.

Despite the lower richness of herbivorous fishes in this study, this trophic group was the most abundant, showed the greatest biomass, and was mainly associated to diurnal surveys. The surgeonfish *A. leucopareius* explained most of the abundance, followed by the Pacific rudderfish or chub *Kyphosus sandwicensis*. Also *A. leucopareius* contributed importantly in the similarity of diurnal surveys among sites. These results are similar to the observations of Friedlander et al. (2013) at Rapa Nui, where both species were the most important herbivores in terms of density and biomass. The herbivorous fishes from the Acanthuridae family, such as *A. leucopareius*, graze on turf algae during the day (Easton, Gaymer, Friedlander, & Herlan, 2018). In contrast, *K. sandwicensis* is a browser, typically seen forming schools and feeding on macroalgae such as *Lobophora variegata* and *Sargassum* sp. (Easton et al., 2018).

The diurnal and nocturnal planktivores possess different functional roles, where diurnal fishes typically feed on small prey of oceanic origin (transient zooplankton) and nocturnal fishes on large demersal zooplankton usually of coral reef origin (Marnane & Bellwood, 2002 and references therein). Among the planktivorous fishes, the Rapanui damselfish *C. rapanui* was an important consumer in diurnal surveys, and is characteristic of planktivorous pomacentrid species (Hobson, 1991). This species showed important abundances and biomass in previous diurnal surveys made at Rapa Nui (Friedlander et al., 2013), and is usually seen in aggregations feeding near the substrate, from tidepools to at least 60 m in depth on volcanic walls.

In contrast to *C. rapanui*, the soldierfish *M. tiki* (mārau) was the most abundant planktivorous fish at night, contributing 7.29% of the dissimilarity among diurnal and nocturnal fish community. This fish has been reported forming small aggregations hiding in caves during the day and emerging at night to forage upon zooplankton (DiSalvo et al., 2007; Randall & Cea, 2011), a common feature of holocentrid fishes (Gladfelter & Johnson, 1983). Previous surveys at Rapa Nui (DiSalvo et al., 1988, 2007) suggested that nocturnal planktivores of the families Holocentridae, Priacanthidae, and Apogonidae were the most important fishes around Rapa Nui. During the night, the demersal zooplankton (e.g. amphipods, isopods, decapod larvae, polychaetes) regularly emerge from coral reefs, being important food sources for nocturnal planktivorous fishes (Jacoby & Greenwood, 1989), playing an important role in coral reef trophodynamics (Carleton, 1993).

The carnivorous fishes such as the wrasses (Labridae family) *T. lutescens* (Mōri vaihi), *P. fuentesi* (kōtea), *A. femininus* (pāhika), *C. debueni* (tēteme), and *Thalassoma purpureum* (kākaka) were present only during day surveys. This group of fishes forage close to the substrate on a diverse group of small invertebrates with hard parts (e.g. brachyuran crabs, hermit crabs, molluscs, sea urchins, and brittlestars) (DiSalvo et al., 2007). Stomach content analyses conducted at Rapa Nui in wrasses such as *T. lutescens*, *P. fuentesi*, *A. femininus*, and *C. debueni* revealed mainly crustacean fragments, ophiuroid spines and mollusc shell fragments among other invertebrate fragments. The porcupinefish *D. holocanthus* (titeve tara tara) was more abundant during night surveys but was also active during the day. This species mainly feeds on crushed molluscs, hermit crabs (e.g. *Calcinus* spp.), and also on xanthid crabs, sea stars (*Ophidiaster easterensis* and *Leiaster leachi*), and polychaetes (DiSalvo et al., 2007), that have cryptic behaviour (DiSalvo et al., 1988). Similarly, the hawkfish, *I. wilhelmi* (pilikoʻa), that was mostly found during nocturnal surveys, frequently feeds on small crustaceans (DiSalvo et al., 2007).

The fish apex predators at Rapa Nui were found in relatively low abundance in the present study, as was observed by Friedlander et al. (2013) and Easton et al. (2018). This can be explained by high fishing pressure around the island associated with increased tourism in the last 3 decades (Gaymer et al., 2013). In contrast, apex predators represent almost half of the fish biomass at Salas & Gómez Island (Easton et al., 2018; Friedlander et al., 2013), where little fishing occurs and the ecosystem is protected by a marine park. With apex predators scarcer at Rapa Nui than at Salas & Gómez, carnivores and planktivores have a greater biomass at the former. This may represent a higher predation risk for small invertebrates at Rapa Nui, which may in turn help explain the invertebrate emerging at night.

4.3 | Future directions

Due to technical difficulties associated with night diving, most of benthic surveys at Rapa Nui and worldwide have been done during the day, providing a partial view of the shallow coral reef communities. Night surveys provide access to cryptic fauna that live in refuges during the day. Comparing day and night surveys has allowed us to have a more complete 'picture' of shallow benthic community structures and understand the species interactions that may shape them. This is the first attempt to evaluate the daily dynamic of community change at Rapa Nui. Future studies could include the seasonal variability of the benthic community structure, fish size distribution around the island, the effects of moon phases on the activity patterns of benthic and pelagic communities and potential changes in the ability of predators to detect prey (Hammerschlag et al., 2017). Nocturnal evaluation of benthic communities at Salas & Gomez would also provide useful insights, given the abundance of top predators in this pristine marine ecosystem, and their potential effects on daily dynamics. This is an important priority research topic to help inform the implementation of the Motu Motiro Hiva Marine Park, in the waters around Salas & Gómez (Gaymer et al., 2014).

Day–night reef surveys help to provide a full understanding of reef communities dynamics, thus they should be included at the outset of MPA planning worldwide, as this information is important when defining conservation goals and targets. Moreover, this type of survey should be implemented for monitoring MPA performance, and informing proper management decisions.

This study provides important scientific information for the management planning and implementation of the recently created Rapa Nui multiple-use MPA (Paredes et al., 2019), and could orientate future management strategies such as temporal area closures and specific regulations for artisanal fisheries.

Day–night reef surveys could be run as part of a citizen science programme in areas where certified divers frequently visit and undertake night dives, such as coral reefs (Hermoso, Martin, Stotz, Gelcich, & Thiel, 2019).

diver pioneers at Rapa Nui. Michel provided very constructive advice to decide the dive sites for this study.

ORCID

Iván A. Hinojosa https://orcid.org/0000-0002-9752-4374
German Zapata-Hernández https://orcid.org/0000-0003-3245-9118
Carlos F. Gaymer https://orcid.org/0000-0003-4395-9505
Rick D. Stuart-Smith https://orcid.org/0000-0002-8874-0083

REFERENCES

Aguzzi, J., & Company, J. B. (2010). Chronobiology of deep-water decapod crustaceans on continental margins. *Advances in Marine Biology*, *58*, 155–225. https://doi.org/10.1016/B978-0-12-381015-1.00003-4

Aguzzi, J., Company, J. B., Costa, C., Matabos, M., Azzurro, E., Manuel, A., ... Priede, I. G. (2012). Challenges to the assessment of benthic populations and biodiversity as a result of rhythmic behaviour: Video solutions from cabled observatories. *Oceanography and Marine Biology: an Annual Review*, *50*, 235–285. https://doi.org/10.1201/b12157

Aguzzi, J., Sbragaglia, V., Tecchio, S., Navarro, J., & Company, J. B. (2015). Rhythmic behaviour of marine benthopelagic species and the synchronous dynamics of benthic communities. *Deep Sea Research Part I: Oceanographic Research Papers*, *95*, 1–11. https://doi.org/10.1016/j.dsr.2014.10.003

Anderson, M., Gorley, R. N., & Clarke, R. K. (2008). Permanova+ for Primer: Guide to software and statistical methods: Primer-E limited. http://updates.primer-e.com/primer7/manuals/PERMANOVA+_manual.pdf

Annese, D. M., & Kingsford, M. J. (2005). Distribution, movements and diet of nocturnal fishes on temperate reefs. *Environmental Biology of Fishes*, *72*, 161–174. https://doi.org/10.1007/s10641-004-0774-7

Azzurro, E., Pais, A., Consoli, P., & Andaloro, F. (2007). Evaluating day-night changes in shallow Mediterranean rocky reef fish assemblages by visual census. *Marine Biology*, *151*, 2245–2253. https://doi.org/10.1007/s00227-007-0661-9

Bauer, R. T. (1985). Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bulletin of Marine Science*, *36*, 150–162. https://www.ingentaconnect.com/contentone/umrsmas/bullmar/1985/00000036/00000001/art00009#expand/collapse

Blackmon, D. C., & Valentine, J. F. (2013). Recurring nocturnal benthic emergence along the coral reef-seagrass interface in the Florida Keys National Marine Sanctuary: Evidence of a possible novel prey escape response. *Journal of Experimental Marine Biology and Ecology*, *448*, 220–227. https://doi.org/10.1016/j.jembe.2013.07.012

Boaden, E., & Kingsford, M. J. (2012). Diel behaviour and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs*, *31*, 871–883. https://doi.org/10.1007/s00338-012-0903-2

Bosiger, Y. J., & McCormick, M. I. (2014). Temporal links in daily activity patterns between coral reef predators and their prey. *PLoS ONE*, *9*, e111723. https://doi.org/10.1371/journal.pone.0111723

Brewin, P. E., Brown, J., & Brickle, P. (2016). Diurnal variation of fish and macrobenthic invertebrate community structure in an isolated oceanic island of the South Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, *96*, 737–747. https://doi.org/10.1017/S0025315415000892

Carleton, J. (1993). Zooplankton and coral reefs: An overview. *South Pacific Underwater Medical Society*, *23*, 102–107.

Clark, K. L., Ruiz, G. M., & Hines, A. H. (2003). Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *Journal of Experimental Marine Biology and Ecology*,

287, 37–55Pii S0022-0981(02)00439-2. https://doi.org/10.1016/S0022-0981(02)00439-2

Collette, B. B., & Talbot, F. H. (1972). Activity patterns of coral reef fishes with emphasis on nocturnal diurnal changeover. *Bulletin of Natural History Museum of Los Angeles Co.*, *14*, 98–124.

Dee, L. E., Witman, J. D., & Brandt, M. (2012). Refugia and top-down control of the pencil urchin *Eucidaris galapagensis* in the Galapagos Marine Reserve. *Journal of Experimental Marine Biology and Ecology*, *416*, 135–143. https://doi.org/10.1016/j.jembe.2012.02.016

DiSalvo, L. H., Randall, J. E., & Cea, A. (1988). Ecological reconnaissance of the Easter Island sublittoral marine-environment. *National Geographic Research*, *4*, 451–473.

DiSalvo, L. H., Randall, J. E., & Cea, A. (2007). Stomach contents and feeding observations of some Easter Island fishes. *Atoll Research Bulletin*, *548*, 1–22. https://doi.org/10.5479/si.00775630.548.1

Easton, E. E., Gaymer, C. F., Friedlander, A. M., & Herlan, J. J. (2018). Effects of herbivores, wave exposure and depth on benthic coral communities of the Easter Island ecoregion. *Marine and Freshwater Research*, *69*, 997–1006. https://doi.org/10.1071/MF17064

Edgar, G. J., & Stuart-Smith, R. D. (2014). Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, *1*, 140007. https://doi.org/10.1038/sdata.2014.7

Fernandez, M., Pappalardo, P., Rodriguez-Ruiz, M. C., & Castilla, J. C. (2014). Synthesis of the state of knowledge about species richness of macroalgae, macroinvertebrates and fishes in coastal and oceanic waters of Easter and Salas y Gomez islands. *Latin American Journal of Aquatic Research*, *42*, 760–802. https://doi.org/10.3856/vol42-issue4-fulltext-7

Friedlander, A. M., Ballesteros, E., Beets, J., Berkenpas, E., Gaymer, C. F., Gorny, M., & Sala, E. (2013). Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gomez, Chile. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23*, 515–531. https://doi.org/10.1002/aqc.2333

Friedlander, A. M., & Gaymer, C. F. (in press) Progress, opportunities, and challenges for marine conservation in the Pacific Islands. *Aquatic Conservation: Marine and Freshwater Ecosystem*. (this special issue).

Galzin, R. (1987). Structure of fish communities of French-Polynesian coral reefs. II. Temporal scales. *Marine Ecology Progress Series*, *41*, 137–145. https://doi.org/10.3354/meps041137

Gaymer, C. F., Stadel, A. V., Ban, N. C., Cárcamo, P. F., Ierna, Jr, J., & Lieberknecht, L. M. (2014). Merging top-down and bottom-up approaches in marine protected areas planning: experiences from around the globe. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(S2), 128–144. https://doi.org/10.1002/aqc.2508

Gaymer, C., Tapia, C., Acuña, E., Aburto, J., Cárcamo, P., Bodini, A., & Stotz, W. (2013). Base de conocimiento y construcción de capacidades para el uso sustentable de los ecosistemas y recursos marinos de la ecorregión de Isla de Pascua. Informe Final Proyecto SUBPESCA Licitación (4728-33).

Gladfelter, W. B., & Johnson, W. S. (1983). Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology*, *64*, 552–563. https://doi.org/10.2307/1939975

Glynn, P. W., Wellington, G. M., Riegl, B., Olson, D. B., Borneman, E., & Wieters, E. A. (2007). Diversity and biogeography of the scleractinian coral fauna of Easter Island (Rapa Nui). *Pacific Science*, *61*, 67–90. https://doi.org/10.1353/psc.2007.0005

Hammerschlag, N., Meyer, C. G., Grace, M. S., Kessel, S. T., Sutton, T. T., Harvey, E. S., ... Cooke, S. J. (2017). Shining a light on fish at night: An overview of fish and fisheries in the dark of night, and in deep and polar seas. *Bulletin of Marine Science*, *93*, 253–284. https://doi.org/10.5343/bms.2016.1082

Hammond, L. S. (1982). Patterns of feeding and activity in deposit-feeding holothurians and echinoids (Echinodermata) from a shallow back-reef lagoon, Discovery Bay, Jamaica. *Bulletin of Marine Science*, *32*,

549–571. https://www.ingentaconnect.com/content/umrsmas/bullmar/1982/00000032/00000002/art00015

Hart, T. D., Clemons, J. E. R., Wakefield, W. W., & Heppell, S. S. (2010). Day and night abundance, distribution, and activity patterns of demersal fishes on Heceta Bank, Oregon. *Fishery Bulletin*, *108*, 466–477.

Harvey, E. S., Dorman, S. R., Fitzpatrick, C., Newman, S. J., & McLean, D. L. (2012). Response of diurnal and nocturnal coral reef fish to protection from fishing: An assessment using baited remote underwater video. *Coral Reefs*, *31*, 939–950. https://doi.org/10.1007/s00338-012-0955-3

Hermoso, M. I., Martin, V., Stotz, W., Gelcich, S., & Thiel, M. (2019). How does the diversity of divers affect the design of citizen science projects? *Frontiers in Marine Science*, *6*, 239. https://doi.org/10.3389/fmars.2019.00239

Hitt, S., Pittman, S. J., & Nemeth, R. S. (2011). Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series*, *427*, 275–291. https://doi.org/10.3354/meps09093

Hobson, E. S. (1965). Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia*, *1965*, 291–302. https://doi.org/10.2307/1440790

Hobson, E. S. (1981). Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fishery Bulletin*, *79*, 1–30. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/1981/791/hobson.pdf

Hobson, E. S. (1991). *Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. The ecology of fishes on coral reefs* (pp. 69–95). San Diego: Academic Press.

Holzman, R., Ohavia, M., Vaknin, R., & Genin, A. (2007). Abundance and distribution of nocturnal fishes over a coral reef during the night. *Marine Ecology Progress Series*, *342*, 205–215. https://doi.org/10.3354/meps342205

Hubbard, D. K., & Garcia, M. (2003). The corals and coral reefs of Easter Island—A preliminary look. In *Easter Island* (pp. 53–77). Boston, MA: Springer. https://doi.org/10.1007/978-1-4615-0183-1_5

Jacoby, C. A., & Greenwood, J. G. (1989). Emergent zooplankton in Moreton Bay, Queensland, Australia—Seasonal, lunar, and diel patterns in emergence and distribution with respect to substrata. *Marine Ecology Progress Series*, *51*, 131–154. https://doi.org/10.3354/meps051131

Knowlton, N. (1992). Thresholds and multiple stable states in coral-reef community dynamics. *American Zoologist*, *32*, 674–682. https://doi.org/10.1093/icb/32.6.674

Knowlton, N., & Jackson, J. B. (2008). Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biology*, *6*, e54. https://doi.org/10.1371/journal.pbio.0060054

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology Evolution and Systematics*, *34*, 153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Kruse, M., Taylor, M., Muhando, C. A., & Reuter, H. (2016). Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve. *Regional Studies in Marine Science*, *3*, 49–57. https://doi.org/10.1016/j.rsma.2015.05.001

Ling, S. D., Johnson, C. R., Frusher, S. D., & Ridgway, K. R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 22341–22345. https://doi.org/10.1073/pnas.0907529106

MacArthur, L. D., Hyndes, G. A., Babcock, R. C., & Vanderklift, M. A. (2008). Nocturnally active western rock lobsters *Panulirus cygnus* forage close to shallow coastal reefs. *Aquatic Biology*, *4*, 201–210. https://doi.org/10.3354/ab00107

Mann, K., & Breen, P. (1972). The relation between lobster abundance, sea urchins, and kelp beds. *Journal of the Fisheries Board of Canada*, *29*, 603–605. https://doi.org/10.1139/f72-104

Marnane, M. J., & Bellwood, D. R. (2002). Diet and nocturnal foraging in cardinalfishes (Apogonidae) at one tree reef, great barrier reef, Australia. *Marine Ecology Progress Series*, *231*, 261–268. https://doi.org/10.3354/meps231261

Morales, N. A., Easton, E. E., Friedlander, A. M., Harvey, E. S., Garcia, R., & Gaymer, C. F. (2019). Spatial and seasonal differences in the top predators of Easter Island: Essential data for implementing the new Rapa Nui multiple-uses marine protected area. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*, 118–129. https://doi.org/10.1002/aqc.3068

Myers, E. M. V., Harvey, E. S., Saunders, B. J., & Travers, M. J. (2016). Fine-scale patterns in the day, night and crepuscular composition of a temperate reef fish assemblage. *Marine Ecology; an Evolutionary Perspective*, *37*, 668–678. https://doi.org/10.1111/maec.12336

Nelson, B., & Vance, R. (1979). Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Marine Biology*, *51*, 251–258. https://doi.org/10.1007/BF00386805

Nickell, L., & Sayer, M. (1998). Occurrence and activity of mobile macrofauna on a sublittoral reef: Diel and seasonal variation. *Journal of the Marine Biological Association of the United Kingdom*, *78*, 1061–1082. https://doi.org/10.1017/S0025315400044325

Oppenheim, N. G., & Wahle, R. A. (2013). Cannibals by night? In situ video monitoring reveals diel shifts in inter-and intra-specific predation on the American lobster. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 1635–1640. https://doi.org/10.1139/cjfas-2013-0099

Ory, N. C., Dudgeon, D., Duprey, N., & Thiel, M. (2014). Effects of predation on diel activity and habitat use of the coral-reef shrimp *Cinetorhynchus hendersoni* (Rhynchocinetidae). *Coral Reefs*, *33*, 639–650. https://doi.org/10.1007/s00338-014-1163-0

Paredes, F., Flores, D., Figueroa, A., Gaymer, C. F., & Aburto, J. A. (2019). Science, capacity building and conservation knowledge: The empowerment of the local community for marine conservation in Rapa Nui. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S2), 130–137. https://doi.org/10.1002/aqc.3114

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511806384

Randall, J. E., & Cea, A. (2011). *Shore fishes of Easter Island*. Honolulu: University of Hawai'i Press.

Rueda, J. L., Urra, J., & Salas, C. (2008). Diel and seasonal variation of a molluscan taxocoenosis associated with a *Zostera marina* bed in southern Spain (Alboran Sea). *Helgoland Marine Research*, *62*, 227–240. https://doi.org/10.1007/s10152-008-0111-1

Santelices, B., & Abbott, I. (1987). Geographic and marine isolation: An assessment of the marine algae of Easter Island. *Pacific Science*, *41*, 1–4. http://hdl.handle.net/10125/1012

Savy, S. (1987). Activity pattern of the sea-star, *Marthasterias glacial* is, in Port-Cros Bay (France, Mediterranean coast). *Marine Ecology*, *8*, 97–106. https://doi.org/10.1111/j.1439-0485.1987.tb00177.x

Tessmar-Raible, K., Raible, F., & Arboleda, E. (2011). Another place, another timer: Marine species and the rhythms of life. *BioEssays*, *33*, 165–172. https://doi.org/10.1002/bies.201000096

Tuya, F., Martin, J., & Luque, A. (2004). Patterns of nocturnal movement of the long-spined sea urchin *Diadema antillarum* (Philippi) in Gran Canaria (the Canary Islands, central East Atlantic Ocean). *Helgoland Marine Research*, *58*, 26–31. https://doi.org/10.1007/s10152-003-0164-0

Verling, E., Crook, A. C., Barnes, D. K., & Harrison, S. S. (2003). Structural dynamics of a sea-star (*Marthasterias glacialis*) population. *Journal of the Marine Biological Association of the United Kingdom*, *83*, 583–592. https://doi.org/10.1017/S0025315403007513h

Wieters, E. A., Medrano, A., & Perez-Matus, A. (2014). Functional community structure of shallow hard bottom communities at Easter Island (Rapa Nui). *Latin American Journal of Aquatic Research*, *42*, 827–844. https://doi.org/10.3856/vol42-issue4-fulltext-10

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.