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ORIGINAL PAPER

Diel changes in structure and trophic functions of motile benthic invertebrates on coral reefs at Rapa Nui (Easter Island)

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Abstract

Coral reefs are structurally complex habitats that provide diverse shelter for motile benthic invertebrates (MBI), including those with cryptic and nocturnal behaviors. In this study, diel changes in MBI structure (species composition, density, and biomass) and functions (trophic groups and isotopic diversity indices) were examined on coral reefs at Rapa Nui (27° S, 109° W). Diurnal and nocturnal surveys (March 2016) revealed that echinoderms were the dominant invertebrates throughout the diel cycle in terms of density, biomass, and their trophic role. The density and biomass of MBI were higher at night than during the day. Significant diel changes were detected in the structure of MBI and trophic groups, where the diurnal assemblages were mostly herbivores and the nocturnal assemblages were mostly detritivores. Moreover, the isotopic uniqueness index indicated that nocturnal MBI were trophically more redundant than their diurnal counterparts; consequently, the high nocturnal biodiversity did not necessarily increase trophic diversity. This time and trophic partitioning of MBI could have important consequences for energy transfer on the reefs and must be considered in future monitoring programs. Endemic taxa represented approximately a quarter of the species (26%), but had low density and biomass during both time periods, suggesting a modest influence on energy transfers on these coral reefs. However, their restricted geographic distribution and current low abundances could make these species vulnerable to extinction; therefore, management and conservation actions in the new multiple-use marine protected area of Rapa Nui should include these species.

Introduction

Coral reefs are one of the most productive and diverse ecosystems on Earth (Reaka-Kudla 1997). In general, research has focused on visually dominant taxa, such as corals, algae, and reef fishes (Stella et al. 2011). However, a high

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proportion of benthic fauna that lives in association with coral reefs exhibit cryptic behavior (the so-called *cryptofauna*), dominating the biodiversity and contributing considerably to the structure and functioning of reef communities (Stella et al. 2010; Glynn 2011; Enochs and Manzello 2012a). Cryptofauna remains difficult to study for several reasons, including the small sizes of the organisms, the use of structurally complex habitats (e.g., cracks and holes) during the day that are difficult to access, and the nocturnal behavior of several taxa (Ameziane 2006; Enochs 2010). These organisms also establish crucial trophic links for energy transfer through food webs (Enochs and Manzello 2012a), playing a critical role in the overall functioning of coral reef ecosystems (Glynn and Enochs 2011). They capture suspended and dissolved organic matter, feed on corals, graze on benthic algae, and prey on or are preyed upon by other organisms (e.g., epibenthic fauna, nekton, and reef fishes) (Enochs et al. 2011; Enochs and Manzello 2012b; Briand et al. 2016). Notably, some species that depend trophically on corals and live hidden within the coral matrix will diminish in density when corals are disturbed (Stella et al. 2011). Therefore, the loss of coral-associated fauna in response to natural and anthropogenic stressors could disrupt the functioning of coral reefs, due to the loss of key ecosystem functions, such as decomposition, bioturbation, nutrient recycling, protection, and availability of specialized habitats (Miller 2015). This may have negative impacts on coral reef food webs, with effects cascading through many trophic levels, even reaching apex predators (Birkeland 2015).

On coral reefs, motile benthic invertebrate assemblages (MBI) typically include polychaetes, mollusks, decapods, and echinoderms (Cortés et al. 2017). Most species belonging to these groups constitute potential or preferential prey for many other species in the coral reef systems (Glynn and Enochs 2011; Stella et al. 2011). However, predation risk may alter prey activity patterns, where prey species tend to be most active when predators are inactive, poorly efficient, or present at low densities (Dee et al. 2012). In this sense, important diel changes in fish assemblages have been recorded in tropical reef environments, where diurnal assemblages are typically dominated by carnivores, zooplanktivores, and herbivores, whereas at night, specialized nocturnal zooplanktivorous fishes tend to be more active (e.g., Hobson 1972; Galzin, 1987; Azurro et al. 2007; Holzman et al. 2007; Brewin et al. 2016; Hinojosa et al. 2021). Hence, some benthic invertebrate taxa could possess nocturnal behavior, which would minimize temporal overlap with their predators (Nelson and Vance 1979), thus reducing their detectability and potential consumption (Ory et al. 2014).

Global estimates indicate that > 60% of invertebrates may display nocturnal behavior (Hölker et al. 2010), so that perception of actual population size, composition, community structure, and functional roles of some taxa could be strongly biased depending on sampling times (Aguzzi et al. 2012). To date, existing information on diel activity patterns remains scarce for most rocky and coral reefs and, when available, it is mainly focused on fishes (e.g., Hobson 1965, 1972; Galzin 1987; Marmane and Bellwood 2002; Holzman et al. 2007; Myers et al. 2016), zooplankton (e.g., Loose and Dawidowicz 1994; Hays et al. 2001; Yahel et al. 2005) and more recently the interplay between fishes and invertebrates (Brewin et al. 2016; Hinojosa et al. 2021).

Coral reef structure and function are closely associated with energy sources and nutrient pathways throughout the marine food webs (Briand et al. 2015, 2016; McMahon et al. 2016; Fey et al. 2020). Stable isotope analyses (SIA) are important tools for tracing fluxes of energy and matter in terrestrial and marine ecosystems (Middelburg 2013). Owing to their potential usefulness for studying coral reef food webs (Yamamuro et al. 1995; Bierwagen et al. 2018), SIA have been increasingly used for several taxonomic groups, such as scleractinian corals (Aharon 1991; Nahon et al. 2013; Tremblay et al. 2015), clams, calcareous algae (Aharon 1991), urchins (Cabanillas–Terán et al. 2016), fishes (e.g., Wyatt et al. 2012; Letourneur et al. 2013; Briand et al. 2016; McMahon et al. 2016), invertebrates (e.g., Page et al. 2013; Davis et al. 2015; Kolasinski et al. 2016), and more recently for integrating invertebrate and vertebrate assemblages (e.g., zooplankton, soft-bottom and reef invertebrates, reef and pelagic fishes, and seabirds; Zapata-Hernández et al. 2021). It is possible to explore various ecological attributes of the trophic structure of food webs, using community isotopic metrics based on species distribution in isotopic δ-spaces (Layman et al. 2007, 2011; Jackson et al. 2011). Additionally, multiple metrics of functional diversity enable quantification of the different traits present in a community (e.g., n-dimensional space based on functional traits) and their relative importance in terms of abundance, thus also providing a link between biodiversity and ecosystem functioning (Petchey and Gaston 2002). In this context, isotopic functional indices have been adapted to quantify different facets of food webs by combining abundance (density or biomass) and stable isotope composition of species (Cucherousset and Villéger 2015; Rigolet et al. 2015), allowing integration of information about the trophic structure, species interactions, and biomass partitioning within communities (Comte et al. 2016).

Rapa Nui (Easter Island) represents an endemism hotspot in terms of its marine biodiversity, due to its level of isolation, geologic history, and oceanographic features (Roberts et al. 2002; Boyko 2003), with levels of endemism of 34% for mollusks, 33% for sponges, 12% for bryozoans and 22% for coastal fishes (Fernández et al. 2014). Despite this, its biodiversity is impoverished compared to other Pacific islands (e.g., Hawai'i and the Galapagos Islands; Boyko, 2003; Fernández et al. 2014; Cortés et al. 2017). However, low sampling effort and lack of taxonomic studies may account for underestimation of current endemism levels, especially for some taxa (e.g., Annelida, Peracarida, and Ascidacea; Boyko 2003). Endemic taxa are usually assumed to have a high risk of extinction due to their restricted geographic ranges, and in some cases reduced abundances, making these species more vulnerable to environmental changes (Gaston et al. 2000).

Given the unique features of marine life in this Pacific area, the Multiple-Use Marine Protected Area (MU-MPA) of Rapa Nui was declared in June 2018. It covers an area of 579,368 km^2 in the southeast Pacific around Rapa Nui island and Motu Motiro Hiva (Salas y Gómez) islet, protecting both shallow- and deep-water environments (including shallow and mesophotic coral reefs as well as nearby seamounts and hydrothermal vents). Despite these marine conservation actions, ecological studies in the different environments around Rapa Nui have been scarce until recently (Fernández et al. 2014). For example, a pioneer study by DiSalvo et al. (1988) at Rapa Nui qualitatively described the shallow benthic community (at 15–60 m depth). Subsequently, the works of Friedlander et al. (2013) and Wieters et al. (2014) described community patterns and functional features of diurnal reef communities (focused mainly on fishes). More recently, Gusmao et al. (2018) studied ecological aspects of shallow (~10-m depth) soft-bottom infauna (meio- and macro-fauna), Hinojosa et al. (2021) investigated the diel community dynamics of reef fishes and invertebrates on coral reefs, and Zapata-Hernández et al. (2021) identified the main organic matter pathways supporting marine communities in the marine ecosystem of Rapa Nui. Despite this, the abundance of Rapa Nui endemic benthic invertebrates has been estimated only in diurnal communities, with only two endemic species evaluated (Friedlander et al. 2013), and when the fishing pressure on some endemic invertebrates (spiny and slipper lobsters, octopus, and gastropods) could have negatively affected their populations (Zylich et al. 2014). Moreover, other potential threats to marine biodiversity in the Rapa Nui MPA include mass tourism, plastic pollution, sewage pollution, and terrestrial runoff.

This study is the first to analyze the diel trophic structure of MBI on coral reefs around Rapa Nui, including species composition, abundance (density and biomass), and stable isotope measurements of species, and was conducted to understand the structural and ecological features of Rapa Nui coral reef communities. It provides comprehensive information about the nocturnal benthic fauna and relative abundance of endemic species. This information is useful for understanding the ecological role of species and for detecting potential changes in energy transfer throughout the ecosystem, as well as for biodiversity management, monitoring of marine communities, and as a support for ecosystem modeling for the MPA surrounding Rapa Nui.

Owing to a potential relaxation of predation risk at night, associated with a decrease in carnivorous fishes, and a greater dominance of zooplanktivorous fishes on temperate and coral reefs (Galzin 1987; Azurro et al. 2007; Holzman et al. 2007; Brewin et al. 2016; Hinojosa et al. 2021), we hypothesized that nocturnal MBI on Rapa Nui coral reefs differ in taxonomic composition and have higher abundances than diurnal assemblages have, and that this translates into different trophic functions during both periods. The aims of this study were (1) to quantify diel changes in the structure of MBI (composition, density, and biomass) on coral reefs at Rapa Nui, (2) to determine how diel differences in the MBI structure could change trophic groups and impact functional facets of coral reef communities, and (3) to evaluate the contribution of endemic taxa to MBI structure and trophic functioning of coral reefs in this remote island MPA.

Materials and methods

Study site

Rapa Nui (Easter Island; Latitude − 27.12°, Longitude − 109.37°) in the southeast Pacific is one of the most isolated inhabited places in the world and is 3800 km west of continental Chile and > 2200 km from the Pitcairn Islands, the nearest inhabited place (Boyko 2003). The island, which has a surface area of 163.6 km^2 (Arana 2014), is close to the center of the South Pacific Subtropical Gyre, which drives the most important circulation features around it (Andrade et al. 2014). Shallow reef communities are mainly dominated by two scleractinian corals with a wide bathymetric distribution range (i.e., *Porites lobata* and *Pocillopora verrucosa*), which cover ~ 80% of the bottom (Wieters et al. 2014). The shore fish fauna comprises ~ 220 species and is considered depauperate in comparison with other Pacific sites, which have five to ten times as many species, depending on the region (Allen 2008).

Structure of invertebrate assemblages

To assess the structure of MBI on coral reefs at Rapa Nui, sampling was conducted in March 2016 at six sites, using a SCUBA diving approach. Based on sea conditions, accessibility, and presence of coral reefs, four sites were selected off the western coast [Hanga Roa South (HRS), Hanga Roa South-West (HRSW), Manavai (HR), and Motu Tautara (MT)] and two sites off the northern coast [Anakena T1 (AK1) and Anakena T2 (AK2)] (Fig. 1). Reef Life Survey (RLS) methods (Edgar and Stuart-Smith 2014) were used to estimate the density of MBI (> 2 cm in size; e.g., gastropods, crustaceans, and echinoderms) during the day and night. Brittle stars and shrimps were included in the visual surveys

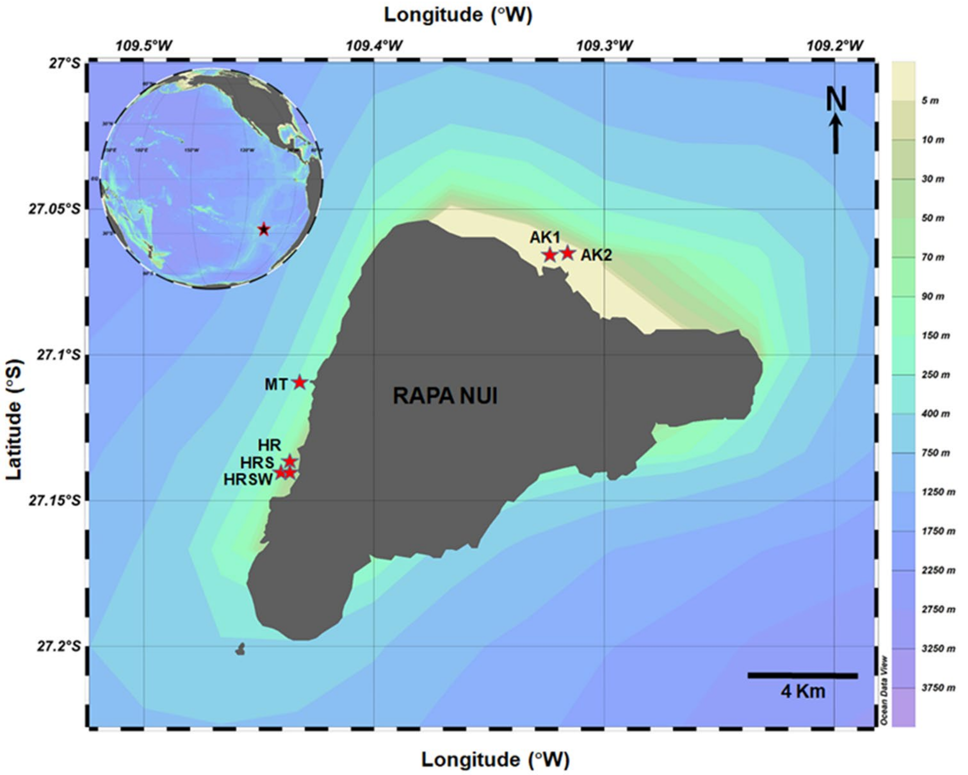

Fig. 1 Location of sampling sites in Rapa Nui (Easter Island) marine protected area. Hanga Roa South (HRS), Hanga Roa South-West (HRSW), Manavai (HR), Motu Tautara (MT), Anakena T1 (AK1), Anakena T2 (AK2). Stars represent sampled sites; color palette shows ocean depth ranges created using Ocean Data View software (Schlitzer 2018)

because of their numeric importance and possible relevance in the nocturnal invertebrate assemblages (the RLS method does not usually include these taxa). Digital photographs were also taken to enable post-survey corroboration of species identities. A 50-m shore-parallel transect line was deployed on the reefs at a depth between 10 and 20 m, due to previous non-significant differences found in the community structure of the coral reefs at depths of 10–20 m (Friedlander et al. 2013). Surveys were performed at each site during the day (at 1100–1500 h), then replicated at night (between 2100 and 2400 h) using the same GPS point, depth, and direction. The MBI were surveyed along the same transect lines, and density (ind 100 m^{-2}) was estimated by counting all individuals within a 2 m wide transect (divided into two blocks: one meter on either side of the transect line, surveyed backward and forward; further details about the methods are provided in www.reeflifesurvey.com and Stuart-Smith et al. 2018). To assess the trophic structure and partitioning of organic matter (biomass) within the MBI, samples of invertebrates were collected by divers (after determining the most abundant species from survey counts) and stored in plastic vials or bags for later taxonomic identification. In the laboratory, at Hanga Roa, Rapa Nui (no > 2 h after collection) the wet weight of all sampled species was determined using a digital balance. For each taxon, a mean value of wet weight was estimated based on available samples, and subsequently scaled up by its respective density in each transect, to obtain as estimate of wet biomass expressed in g 100 m^{-2}.

The sampled fauna was assigned to putative trophic categories based on the classification of Enochs and Glynn (2017): herbivore, carnivore (including predators and corallivores), suspension feeder, and detritivore (include detritus feeders and deposit feeders). The assignment to trophic categories was based on data from the literature related to the trophic ecology of the species, genus, or closest relative (e.g., Stella et al. 2011). As some species may incidentally ingest a wide spectrum of food items (e.g., algae, small invertebrates, and corals), the trophic categories were broad. Additionally, the geographic distribution range of species (i.e., endemic, Indo-Pacific, South Pacific, or unknown) was included for each taxon to assess contributions to the assemblage structure and trophic groups.

Stable isotopes analysis

In total, 84 samples of MBI were collected and kept frozen at – 20 °C until processed for SIA. For every individual sampled, ~ 10 mg of muscle was dissected under a stereomicroscope, washed with Milli-Q water, placed in pre-combusted vials, and dried in an oven (40 °C) for 48 h, then stored in a desiccator until analysis. Between the processing of each sample, the dissection tools were rinsed with methanol. Dried tissue samples were ground to a fine powder using an agate mortar and then small amounts (~ 0.5 mg) were placed in pre-weighed tin capsules and stored in a desiccator until the SIA were conducted. Carbonate-free samples were carefully taken (e.g., dissected from cheliped and abdominal muscles of decapods, the tube feet of sea stars, foot of gastropods; see Zapata-Hernández et al. 2016). However, samples of species containing calcium carbonate (i.e., holothurians) were split, and a subsample was acidified (using a solution of $PtCl_2$ in 1 N HCl) to remove inorganic carbonates. Nitrogen values were obtained from untreated subsamples.

The isotopic composition was analyzed at the School of Biological Sciences, Washington State University, using a Eurovector elemental analyzer (EA3000, Milan, Italy), coupled to an Isoprime isotope ratio mass spectrometer (IRMS, Micromass, Manchester, UK). The daily reference material was calibrated against the NIST (National Institute of Standards and Technology) standard reference material: Bovine Liver SRM 1577. Daily reference material was run between analyses of the unknowns and the values from the references in the sample run were used to calculate the values for the unknowns. Stable isotope ratios are reported in the δ notation as the deviation relative to international standards (Vienna Pee Dee Belemnite for carbon and air N_2 for nitrogen) using the following equation:

$$\delta X = \left[(Rsample/Rstandard) - 1\right]$$

where $X = \delta^{13}C$ or $\delta^{15}N$, and R is the ratio between heavy and light stable isotopes of each element ($^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively). The precision of the analysis is indicated by the standard deviation (SD) of ten replicate reference material analyses and typically was ± 0.1 ‰ for $\delta^{15}N$ and $\delta^{13}C$.

Lipid normalization was applied using C:N ratios (molar) as a proxy as lipids are ^{13}C-depleted relative to protein (DeNiro and Epstein 1977). This correction was made in every animal sample with C:N values > 3.5 (> 5% lipid content) using the following equation (Post et al. 2007):

$$\delta 13C' = \delta 13C + (0.99) \times (C : N) - 3.32$$

Voucher specimens of collected taxa were preserved in 95% ethanol and catalogued at Sala de Colecciones Biologicas Universidad Católica del Norte (SCBUCN), Chile.

Statistical analyses

To test for significant differences in species composition between the day and night assemblages (as a fixed factor), a permutational multivariate analysis of variance (PERMANOVA) was run for all taxa present in each transect using Euclidean distances as a dissimilarity measure. The *strata* option (i.e., randomizations restricted only within each site and not across sites) was applied to use sites as strata, given that day and night data at each site were not fully independent. Matrices of wet biomass (g 100 m^{-2}), densities (ind. 100 m^{-2}) and putative trophic group data were used. In all cases, non-metric multidimensional scaling analyses (NMDS) based on the Bray–Curtis dissimilarity metric with square root transformation were performed to visualize multivariate patterns of gradient variation across day and night. Since results based on biomass integrate aspects related to metabolism and organic matter transfer (Rigolet et al. 2015), presentation of results based on species biomass and putative trophic group gradients was chosen. Significant differences in the density and biomass of individual taxa present both day and night, and in the total density and biomass of MBI, were tested using Welch's *t* test (parametric) or Mann–Whitney *U* test (non-parametric), based on an initial analysis of the normal distribution of the data (Shapiro–Wilk test).

In addition, a series of metrics that quantify the isotopic functional diversity (IFD) in the δ-space (Cucherousset and Villéger 2015) were calculated for each block by transect (i.e., diurnal and nocturnal) to determinate the effects of MBI diel changes on the functional structure. Isotopic divergence (IDiv) was calculated using the sum of deviances and absolute biomass-weighted deviances of distances between all species and the gravity center of convex hull vertices. This measure represents how the biomass is distributed in a functional δ-space occupied by species (Cucherousset and Villéger 2015). The IDiv tends to be low when the most abundant species are distributed close to the center of the functional δ-space and higher when abundant species have extreme values (Villéger et al. 2008). Isotopic dispersion (IDis) was calculated using the biomass deviation to the average position of species in the δ-space divided by the maximal distance to the gravity center filled by the assemblage (Cucherousset and Villéger 2015). This measure quantifies the breadth of functional roles within an assemblage. The IDis tends to be low when most species and their respective biomasses are distributed close to the gravity center in the δ-space filled by an assemblage and higher when the biomasses are distributed far from the gravity center (Mouillot et al. 2013). Isotopic evenness (IEve) quantifies the regularity of species distribution and biomass along the shortest minimum spanning tree linking all species in the δ-space (Villéger et al. 2008; Mouillot et al. 2013; Cucherousset and Villéger 2015). This measure provides information about species packaging in the functional δ-space, being useful as a measure of equitability in the use of resources within assemblages. The IEve tends to be low when most species and their biomasses are packed within a small region in the δ-space and tends to be higher when species are evenly distributed. Isotopic uniqueness (IUni) was quantified using the biomass-weighted average of the nearest neighbor distance of each species divided by the maximum distance between two nearest neighbors (Cucherousset and Villéger 2015). This measure reflects the closeness of species in the δ-space (isotopic redundancy). Lower values indicate the presence of species with similar isotopic values and biomass, whereas higher values indicate the presence of species with higher biomass and isolated in the δ-space.

These metrics are mathematically independent of the species number used in assessments and account for species biomass; hence, integrating organic matter transfer and distribution throughout the food web (Cucherousset and Villéger 2015; Rigolet et al. 2015). All indices were calculated based on the biomass and stable isotope composition (δ^{13}C and δ^{15}N) of taxa from each transect. When stable isotope data were not available for a specific taxon at a particular site, data from other sites were used. Additionally, before IFD calculations were performed, the isotopic axes were scaled into a standardized multidimensional space to have the same range (e.g., 0–1; Cucherousset and Villéger 2015). Subsequently, to test for the fixed effects of time (day and night) on IFD indices, taking random effects (1|block/transect) into account, generalized linear mixed models (GLMMs) with a Gamma error distribution (link function "log") were fitted using maximum likelihood (Laplace approximation). Because GLMMs combine both fixed-effects parameters and random effects in a linear predictor via maximum likelihood (Bates et al. 2015), they are useful for ecological studies that include proportion data replicated across sites (Bolker et al. 2008). The effect of time in the models was assessed using likelihood ratio tests, which compare the difference in likelihood between a model with the factor and a model in which the factor is removed. This difference has a Chi-square distribution, thus a P value can be assigned.

All analyses were performed in the R statistical environment (R Core Team 2018), using the "adonis()" function for the PERMANOVA and "metaMDS()" function for the NMDS analyses from the "vegan" package (Oksanen 2018). For calculations of IFD indices, the "IDiversity()" function (Cucherousset and Villéger 2015) and the "glmer()" function were used to run GLMMs using the "lme4" package (Bates et al. 2015).

Results

Composition and abundance of motile benthic invertebrates

The MBI was composed of only three phyla (i.e., Mollusca, Arthropoda, and Echinodermata), totaling 27 taxa, including 13 echinoderms (i.e., five holothurians, four echinoids, two asteroids, and two ophiuroids), 6 gastropods, 1 cephalopod, and 7 crustaceans (Table S1). Only one taxon was surveyed exclusively during the day (i.e., *Tripneustes gratilla*), 16 taxa exclusively during the night, and 10 taxa both during the day and night (Table S1). Seven of these species are endemic to Rapa Nui (i.e., 25.9%), 14 are distributed around the Indo-Pacific (51.9%), 2 throughout the South Pacific (7.4%), and 4 had unknown distribution ranges (14.8%), because of their unspecified taxonomic status (Table S2).

Total density and biomass (mean ± SD) of the MBI were significantly higher for the nocturnal assemblages (550 ± 138 ind. 100 m^{-2} and $12{,}154 \pm 8670$ g 100 m^{-2}, respectively; Fig. 2) in comparison to diurnal assemblages (225 ± 194 ind. 100 m^{-2}and 5851 ± 3115 g 100 m^{-2}, respectively; Mann–Whitney U test, both $P < 0.05$, Fig. 2 and Table S1). In diurnal assemblages, the sea urchin *Diadema savignyi* and the gastropod *Coralliophila violacea* had the highest densities (87.8 ± 64.0 and 85.2 ± 148.8 ind. 100 m^{-2}, respectively; Fig. 2), followed by the sea urchin *Echinostrephus aciculatus* (27.7 ± 26.8 ind. 100 m^{-2}; Fig. 2). The highest biomasses in the diurnal assemblages were found for *D. savignyi* (2970 ± 2163 g 100 m^{-2}), followed by *C. violacea* (1149 ± 2007 g 100 m^{-2}) and *Holothuria cinerascens* (919 ± 1631 g 100 m^{-2}; Fig. 2). In the nocturnal assemblages, *H. cinerascens* had the highest biomass (3957 ± 8923 g 100 m^{-2}), followed by *Stichopus monotuberculatus* (2223 ± 1125 g 100 m^{-2}), *D. savignyi* (2170 ± 1694 g 100 m^{-2}) and *Breviturma dentata* (1268 ± 865 g 100 m^{-2}; Fig. 2). However, considering the density and biomass of species present during both day and night, only *B. dentata* showed significant differences (Welch's t test, $P < 0.05$, Table S1). For diurnal and nocturnal assemblages, the proportion of endemic species was 1.8% and 5.7% of total density, and 0.2% and 4.7% of the total biomass, respectively (Table S1).

Based on their densities, diurnal assemblages were represented mainly by carnivores and herbivores (both 39.9%), followed by suspension feeders (16.7%) and detritivores (4.2%) (Table S2). In contrast, nocturnal assemblages were characterized mainly by detritivores and suspension feeders (36.9% and 33.6%, respectively), followed by herbivores (22.6%) and carnivores (6.9%) (Table S2).

The endemic taxa contributed a low proportion to carnivore density and biomass (4.5% and 0.9%, respectively) to diurnal assemblages. In contrast, for the nocturnal assemblages, the endemics contributed a low proportion of the density and biomass of the herbivores (3.2% and 0.5%, respectively), but a higher proportion to the density and biomass of the carnivores (36.4% and 66.1%, respectively).

The PERMANOVA analysis showed differences for species biomass between the day and night assemblages ($F = 0.995$, $P = 0.031$), and the NMDS plots showed a high dissimilarity of species among adjacent sites in the diurnal surveys and less dissimilarity in the nocturnal assemblages (Fig. 3a). Moreover, a clear species gradient across both assemblages was observed, mainly due to the close association of *D. savignyi, E. aciculatus* and *C. violacea* with the diurnal surveys, whereas *B. dentata*, *S. monotuberculatus*, *Conus miliaris* and *Parribacus perlatus* were closely associated with the nocturnal surveys (Fig. 3a). In addition, the

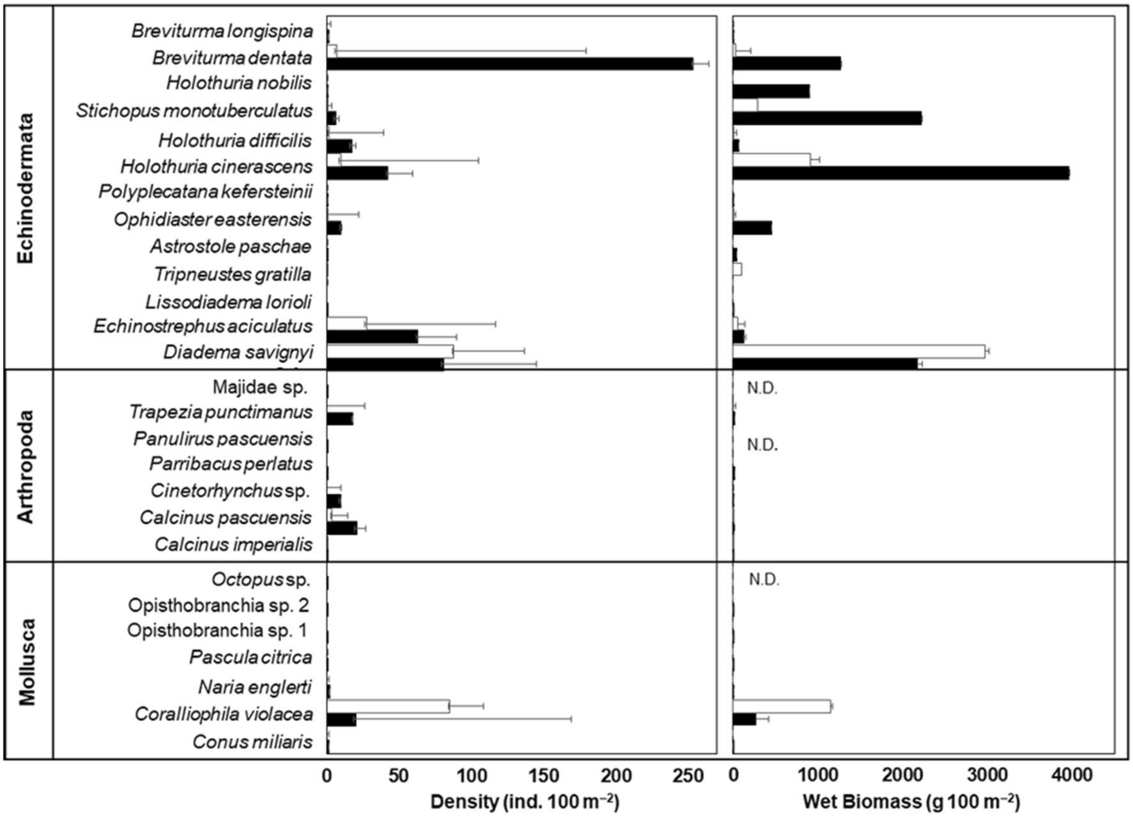

Fig. 2 Day (open bars) and night (filled bars) mean (±SD) densities (ind. 100 m^{-2}) and wet biomass (g 100 m^{-2}) of MBI assemblages (i.e., Echinodermata, Arthropoda, and Mollusca) on Rapa Nui coral reefs. Standard deviation error lines are presented. *N.D.* no data available

biomasses of the putative trophic groups showed significant differences between diurnal and nocturnal assemblages (PERMANOVA, $F = 1.630$, $P = 0.031$; Fig. 3b), with the herbivorous taxa more closely associated with the diurnal surveys and the detritivores more closely associated with the nocturnal surveys. Moreover, a similar pattern of dissimilarity between adjacent sites was detected for the trophic groups in the diurnal and nocturnal assemblages (Fig. 3b).

Stable isotopes composition of motile benthic invertebrates

The lowest δ^{13}C values (mean ± SD) were measured for *Naria englerti* (− 17.0 ± 2.5 ‰, $n = 7$), *Lissodiadema lorioli* (− 16.6 ‰, $n = 1$), *Trapezia punctimanus* (− 16.6 ‰, $n = 1$), and *Cinetorhynchus* sp. (− 16.0 ‰, $n = 1$). and the highest values for *T. gratilla* (− 12.0 ± 1.6 ‰, $n = 6$), *B. dentata* (− 12.3 ‰, $n = 2$), and *E. aciculatus* (− 12.6 ± 1.9 ‰, $n = 4$; Fig. 4). The lowest δ^{15}N values were measured for *T. gratilla* (4.8 ± 1.6 ‰, $n = 6$), *E. aciculatus* (4.9 ± 1.6 ‰, $n = 4$), and *D. savignyi* (5.5 ± 0.5 ‰, $n = 7$), and the highest values for *Cinetorhynchus* sp. (10.1 ‰, $n = 1$), *C. miliaris* (10.5 ± 1.2 ‰, $n = 3$), *T. punctimanus* (10.5 ‰, $n = 1$) and *P. perlatus* (11.1 ± 0.9, $n = 3$; Fig. 4).

Overall, the effect of survey time (day or night) on the isotopic diversity indices was not significant for IDiv, IDis, and IEve (GLMMs, $P > 0.05$; Table 1). Both the diurnal and nocturnal assemblages had higher IDiv values, which indicated that the biomasses of taxa were similarly distributed toward the borders of the convex hull in the δ-space (Fig. 5a, b). The lower IDis values indicate low variation in biomasses of taxa concerning the gravity center represented for all taxa in the δ-space (Fig. 5c, d). The IEve index values indicated that in both cases the biomass values tended to cluster in small regions of the δ-space (Fig. 5e, f). The IUni index, however, showed significant differences (GLMMs, $P < 0.001$; Table 1) between the diurnal and nocturnal assemblages, indicating that biomasses of the diurnal taxa were isolated from each other in the δ-space, in contrast to the nocturnal assemblages where biomasses were isotopically similar (Fig. 5g, h).

Discussion

The first qualitative study of shallow benthic communities at Rapa Nui, by DiSalvo et al. (1988), described the zonation patterns and composition of conspicuous taxa on coral reefs, where foraminifera and diverse invertebrate taxa (e.g.,

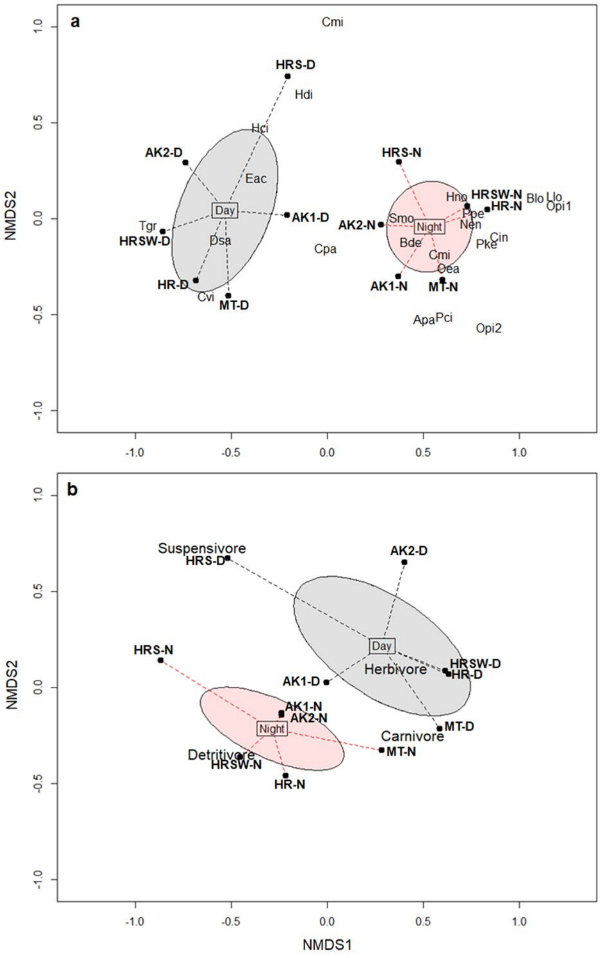

Fig. 3 Non-metric multidimensional scaling (NMDS) based on **a** biomass matrix of diurnal and nocturnal MBI assemblages (stress = 0.107) and **b** biomass of putative trophic groups (stress = 0.045). Black dots represent the position of transects in the multidimensional space and ellipses the standard deviation (SD) from the centroid representing the mean value for all transects (day or night). Black and red ellipses represent diurnal and nocturnal assemblages, respectively. Sampling sites (D: diurnal and N: nocturnal) include: Hanga Roa (HR), Hanga Roa South (HRS), Hanga Roa South-West (HRSW), Motu Tautara (MT), Anakena T1 (AK1) and Anakena T2 (AK2). Tgr: *Tripneustes gratilla*, Eac: *Echinostrephus aciculatus*, Hci: *Holothuria cinerascens*, Hdi: *Holothuria difficilis*, Dsa: *Diadema savignyi*, Hno: *Holothuria nobilis*, Cvi: *Coralliophila violacea*, Cpa: *Calcinus pascuensis*, Cim*: Calcinus imperialis*, Smo: *Stichopus monotuberculatus*, Llo*: Lissodiadema lorioli*, Nen: *Naria englerti*, Oea: *Ophidiaster easterensis*, Bde: *Breviturma dentata*, Apa: *Astrostole paschae*, Pke: *Polyplectana kefersteinii*, Pci: *Pascula citrica*, Cin: *Cinetorhynchus* sp., Cmi: *Conus miliaris*, Ppe: *Parribacus perlatus*, Opi1: *Opisthobranchia* sp. 1, Opi2: *Opisthobranchia* sp.2

Porifera, Cnidaria, Polychaeta, Crustacea, Mollusca, and Echinodermata) were described in detail. Thirty years later, the present study quantifies diel differences in the structure of MBI as well as the functional importance of Indo-Pacific and endemic invertebrate taxa on coral reefs at Rapa Nui.

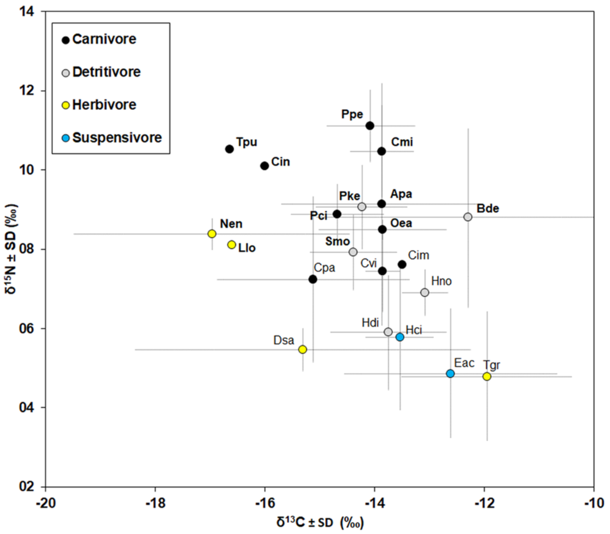

Fig. 4 Biplot of mean (± SD) δ^{13}C and δ^{15}N composition of motile benthic invertebrates (MBI) on coral reefs in the Rapa Nui marine protected area (all data available per species were pooled). Putative trophic groups for each species represented by different colors. Standard deviation error lines are shown ($n \geq 3$). Species codes in bold indicate mainly nocturnal taxa. Tgr: *Tripneustes gratilla*, Eac: *Echinostrephus aciculatus*, Hci: *Holothuria cinerascens*, Hdi: *Holothuria difficilis*, Dsa: *Diadema savignyi*, Hno: *Holothuria nobilis*, Cvi: *Coralliophila violacea*, Cpa: *Calcinus pascuensis*, Cim*: Calcinus imperialis*, Smo: *Stichopus monotuberculatus*, Llo*: Lissodiadema lorioli*, Nen: *Naria englerti*, Oea: *Ophidiaster easterensis*, Bde: *Breviturma dentata*, Apa: *Astrostole paschae*, Pke: *Polyplectana kefersteinii*, Pci: *Pascula citrica*, Cine: *Cinetorhynchus* sp., Tpu: *Trapezia punctimanus*, Cmi: *Conus miliaris*, Ppe: *Parribacus perlatus*

The MBI showed noticeable diel differences in species composition, density, biomass and trophic groups, while nocturnal taxa tended to be more diverse, abundant, and trophically more redundant than their diurnal counterparts. Currently, there are few examples of studies of MBI on coral reefs in other parts of the world that describe these structural differences. Despite this paucity, it is well accepted that several shallow benthic taxa have important diel changes in their activity patterns, such as the nocturnal behavior reported for shrimps (Ory et al. 2014), lobsters (MacArthur et al. 2008), gastropods, cephalopods (Rueda et al. 2008), sea urchins (Dee et al. 2012), and holothurians (Hammond 1982).

In the 1980s, echinoderms were recognized as the main component of nocturnal reef fauna at Rapa Nui (DiSalvo et al. 1988) and this study reinforces these findings, although taxa, such as *D. savignyi* and *E. aciculatus*, displayed similar densities and biomasses during both the diurnal and nocturnal surveys. A strictly nocturnal behavior has been observed in other diadematid urchins, such as *Diadema antillarum* in the South Atlantic (Tuya et al. 2004; Brewing et al. 2016) and *Diadema setosum* in the Red Sea (Lawrence and Hughes-Games 1972). Individuals of *D. antillarum* can

Table 1 Summary of mean isotopic functional diversity indices (*IDiv* isotopic divergence, *IDis* isotopic dispersion, *IEve* isotopic evenness, *IUni* isotopic uniqueness) and results of generalized linear mixed models (GLMMs)

Index	Day		Night		GLMMs				
	Mean	SD	Mean	SD	*df*	logLik	AIC	Chi-sq	*P*
IDiv	0.72	0.3	0.7	0.21	5	− 5.7	21.4	0.02	0.896
IDis	0.38	0.25	0.35	0.18	5	7.63	− 5.25	0.55	0.459
IEve	0.5	0.31	0.32	0.23	5	− 0.42	10.84	2.41	0.121
IUni	0.7	0.1	0.46	0.19	5	7.22	− 4.44	9.99	< 0.001

The standard deviation (SD), degrees of freedom (*df*), log-likelihood function (logLik) and Akaike´s information criterion (AIC) are included. Chi-square (Chi-sq) and *P* values from likelihood ratio tests (LRT) are also shown

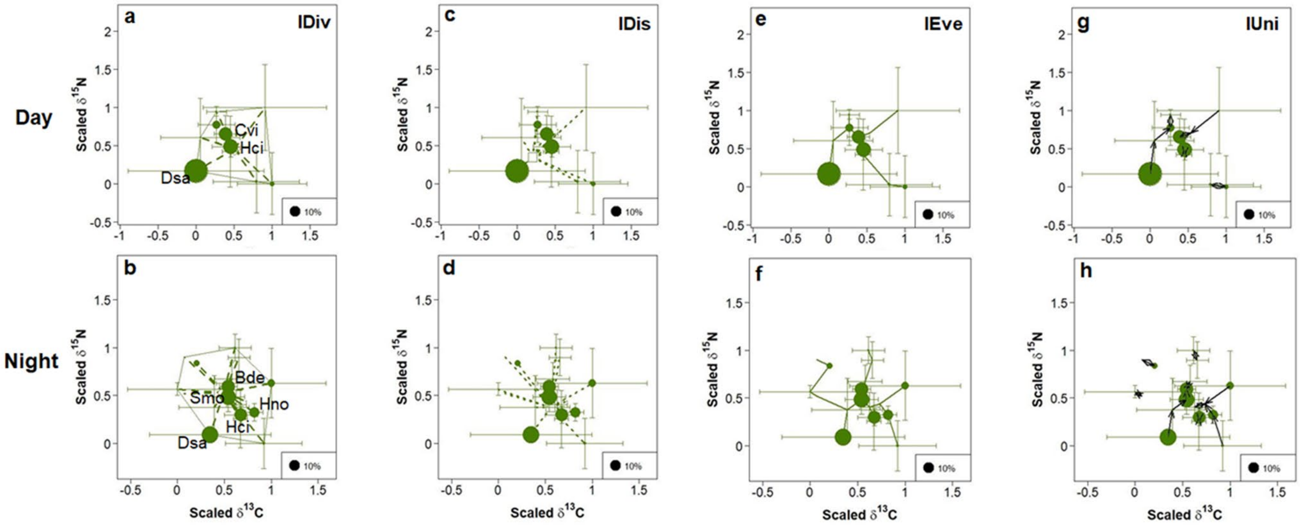

Fig. 5 Mean (± SD) of isotopic functional diversity indices in scaled isotopic space (δ^{13}C and δ^{15}N) for diurnal (upper panels) and nocturnal (lower panels) MBI assemblages. Isotopic divergence (**a**, **b**), isotopic dispersion (**c**, **d**), isotopic evenness (**e**, **f**), and isotopic uniqueness (**g**, **h**). Standard deviation lines are included in the figures. Sizes of point (species) represent magnitudes of mean values with respect to biomass (%) for taxa. For taxa with higher relative biomass (> 10%). Cvi: *Coralliophila violacea*, Hci: *Holothuria cinerascens*, Dsa: *Diadema savignyi*, Bde: *Breviturma dentata*, Smo: *Stichopus monotuberculatus*, Hno: *Holothuria nobilis*

display a homing behavior and the capacity to move short distances (range 1.0–5.1 m) from holes (Tuya et al. 2004). *Diadema savignyi* in the Rapa Nui MPA did not show such extreme cryptic behavior, as some individuals were observed moving around during the day, though there was an evident contrast with the nocturnal surveys where individuals were clearly more active. Birkeland (1988) mentions that in areas where their predators (e.g., fishes, lobster, and gastropods) are scarce or where echinoids are very abundant, sea urchins will forage freely during the day.

Only the ophiuroid, *B. dentata*, showed a significant diel increase in density and biomass, being dominant at night, but this nocturnal activity was highly variable among sites (254 ± 173 ind. 100 m^{-2}). Brittle stars are important components of the cryptofauna on reefs ecosystems (Aronson 1998), living in coral crevices and displaying nocturnal activity (Birkeland 1988). In some cases, species can have high densities (e.g., *Ophiocoma erinaceus* with up to 15,000 ind. m^{-2}; Chartock 1983), thus contributing substantially to the overall community biomass (Granja-Fernández et al. 2014). Likewise, holothurians are important nocturnal consumers that emerge from their cryptic or sandy habitats to feed at night (Hammond 1982). For both ophiuroids and holothurians, cryptic and nocturnal behaviors are usually considered a response to high predation risk (Hammond 1982; Birkeland 1988). This could also be the case for the coral reef communities at Rapa Nui, where planktivorous species dominate the nocturnal fish assemblages, whereas carnivorous species dominate the diurnal assemblages (Hinojosa et al. 2021). Therefore, it is expected that diel changes in predation risk could be influencing the structure of MBI, although further research is required to better understand predator–prey interactions and to evaluate their effects on specific invertebrate prey species.

The high variability of the assemblages among adjacent sites observed during the day, in contrast to at night, could be influenced in part by the species composition and abundance of fishes, which were 43% dissimilar among sites during the diurnal surveys (Hinojosa et al. 2021). In addition, the current low abundance of nocturnal predatory invertebrates, such as lobsters, could indirectly increase the densities of macroinvertebrates, such as sea urchins (Edgar et al. 2011). However, the structure of MBI on coral reefs may also change as a response to differences in the morphology of coral hosts (Stella et al. 2010), mutualistic relationships (Hay et al. 2004), coral reef degradation (Stella et al. 2011), substrate complexity (Nelson et al. 2016), and availability of microhabitats (Fraser et al. 2020). Consequently, more research is needed to understand how different habitat features could differentially benefit diurnal and nocturnal MBI and how this may affect the structure of MBI on coral reefs.

The biomasses of MBI have noticeable diel changes, shifting from diurnal assemblages predominantly constituted by herbivores and carnivores to nocturnal assemblages mainly composed of detritivores (Fig. 3b). Herbivorous species (mainly *D. savignyi*) were an important component of the diurnal assemblages, whereas detritivorous species (*S. monotuberculatus*, *Holothuria nobilis* and *B. dentata*) dominated the nocturnal assemblages (Fig. 3a). In general, the nocturnal taxa showed higher δ^{15}N values than those of the diurnal taxa, likely reflecting a trophic partitioning between diurnal and nocturnal assemblages. Both assemblages play important trophic roles in Rapa Nui reef ecosystem dynamics, associated with energy transfer from primary producers (e.g., macroalgae, zooxanthellae, and phytoplankton), and detrital pathways, to consumers of the upper trophic levels (Zapata-Hernández et al. 2021). In this sense, *D. savignyi* is an important grazer feeding not only on algae, but also on corals, invertebrates, and detritus (Muthiga and McClanahan 2007). The lower δ^{15}N values of this species and other herbivorous echinoids (i.e., *T. gratilla*; Fig. 4) suggest that they mainly incorporate organic matter from primary producers (e.g., macroalgae) and potentially transfer it to upper trophic levels when consumed by some reef fishes (i.e., *Coris debueni*, *Bodianus vulpinus* and *Thalassoma lutescens*) known to be occasional echinoid predators (DiSalvo et al. 2007). In contrast, lobsters, shrimps, crabs, gastropods, and asteroids are commonly recognized as important predators on coral reefs (Enochs and Glynn 2017), which aligns with the higher δ^{15}N values measured in the carnivorous taxa (Fig. 4).

Only two putative suspension feeder taxa (*H. cinerascens* and *E. aciculatus*) were represented in the MBI and they were the most important species in the nocturnal assemblages. The echinoid *E. aciculatus* is known for its sedentary behavior and is usually observed in boreholes catching drift algae (Birkeland 1988). However, during the Rapa Nui nocturnal surveys, individuals (~4 cm of test diameter) were observed wandering on the reefs. Kobayashi and Tokioka (1976) observed this rarely documented behavior when they found individuals browsing on algae-covered rocks. Therefore, it appears that *E. aciculatus* can also leave their holes at night to feed on benthic algae and are not exclusively drifting algae feeders as usually suggested (e.g., Asgaard and Bromley 2008). In addition, the individual analyzed had isotopic values close to those of *T. gratilla* (Fig. 4), suggesting a herbivorous diet. This behavior is likely a response to a lower risk of predation by other invertebrates (e.g., lobsters) and reef fish predators during the night. Palinurid lobsters are known to be important predators of juvenile sea urchins and small invertebrates on coral reefs (Sonnenholzner et al. 2009), exercising strong top-down control of benthic communities (Butler and Kintzing 2016). The current low abundance of lobsters on the Rapa Nui coral reefs could be determining the activity patterns of *E. aciculatus* juveniles during the night and driving their abundance, but could also be influencing the community structure and partition of biomass through the food web (Costello 2015). However, the present study did not consider systematic estimations of MBI size ranges during the reef surveys (e.g., for sea urchins), so these assertions still need to be tested. Future monitoring should evaluate the diel partitioning of select taxa through their ontogeny, to understand the influence of different size structures on the distribution of biomass and trophic structure of MBI.

Nocturnal detritivore holothurians likely emerge from their refuges to consume microorganisms, small metazoans, and detritus deposited on and between rocks and corals (Glynn and Enochs 2011). Similarly, during the night surveys in the present study, the brittle star *B. dentata* was observed to emerge from cryptic reef habitats to feed. This motile species is a versatile feeder, and its diet includes detritus, suspended particles, algae, and carrion (Chartock 1983; Glynn and Enochs 2011). Its δ^{15}N values were similar to those of other endemic carnivorous asteroids (e.g., *Ophidiaster easterensis* and *Astrostole paschae*; Fig. 4), likely reflecting a diet based on small metazoans (Glynn and Enochs 2011), demersal plankton (Kramer et al. 2013) or highly recycled organic matter. Ophiuroids can also be occasional prey for other macroinvertebrates (e.g., decapods and asteroids; Drolet et al. 2004) and reef fishes (Randall 1967; Glynn and Enochs 2011), with ophiuroid fragments occasionally found in the stomachs of both diurnal predatory fish, such as *Forcipiger flavissimus*, *Coris debueni*, and *Pseudolabrus fuentesi*, and nocturnal fish such as *Arothron meleagris* (DiSalvo et al. 2007). Therefore, these abundant nocturnal MBI taxa could be indispensable for organic matter uptake, nutrient cycling, and energy transfer to consumers at higher trophic levels (Birkeland 1988; Uthicke 2001), being important primary consumers in food webs on fringing coral reefs (Arias-González et al. 1997) and considered key for trophic functioning of coral reef ecosystems (Granja-Fernández et al. 2014).

Despite the higher number of species, density, and biomass of the nocturnal assemblages, in contrast to the diurnal assemblages, only the IUni index showed significantly lower values for nocturnal assemblages, suggesting a higher degree of trophic redundancy among the most abundant taxa (Cucherousset and Villéger 2015; Rigolet et al. 2015). This pattern is consistent with communities where, when certain species are removed (e.g., the predators; Cucherousset and Villéger 2015), the remaining species tend to share their functional roles more closely with other species (Mouillot et al. 2013). The wide occurrence of nocturnal detritivores observed in the present study can explain this pattern where other trophic groups (e.g., carnivores) were less represented. However, it is recognized that a number of factors may cause variation in the stable isotope composition of species (e.g., age, physiological condition, tissue type, diet quality, nutritional stress, and temporal shifts), all of which may influence the isotopic discrimination of organisms (Wyatt et al. 2012; Yeakel et al 2016; Gorokhova, 2018). Moreover, due to the environmental heterogeneity of isotopic baselines (Reddin et al. 2018; Fey et al. 2020), which could bias interpretation of trophic structure, results from isotopic metrics need to be interpreted with caution.

In the Rapa Nui MPA, endemic MBI represented 26% of the species composition assessed, being slightly more prevalent in the nocturnal assemblages. Despite this, the endemic taxa had the lowest density and biomass, whereas the Indo-Pacific taxa were dominant in the MBI assemblage structure and the isotopic diversity metrics. Therefore, the endemic MBI are considered to currently play a minor role in energy transfer (expressed as biomass) on coral reefs in the Rapa Nui MPA. However, it is important to note that at Rapa Nui, endemic nocturnal predators, such as the spiny lobster *P. pascuensis*, slipper lobsters (e.g., *P. perlatus*), and cephalopods (*Octopus* spp.), which can reach high biomasses, were scarcely seen during the visual surveys. This could be due to the intense fishing pressure in the last few decades that has decreased their populations (Friedlander et al. 2013; Zylich et al. 2014) as well as diver-light avoidance behavior during the nocturnal surveys (MacArthur et al. 2008 and references therein). Comparable results have been reported for the Galápagos Islands, where extensive reef assessment has indicated a low representation of endemic invertebrate taxa and a high presence of Indo-Pacific fauna (Edgar et al. 2004). Endemic invertebrate species at Rapa Nui are inherently at risk of local extinction because they have restricted distribution ranges and generally lower abundances. Additionally, the various anthropogenic-related threats (e.g., fishing, pollution, invasive species, and climate change) may increase the risk to their populations, thus conservation efforts should focus on these species. In addition, increasing the spatial and bathymetric coverage of reef surveys around Rapa Nui may provide more accurate estimates of the abundance and population status of endemic MBI taxa.

This study has demonstrated that the structure and trophic functioning of MBI changed in the short term (over 24-h cycles), indicating the great importance of the roles played by diurnal and nocturnal assemblages for coral reef functioning, because they exploit diverse and, to some degree, complementary resources (e.g., macroalgae, corals, and detritus), enabling more efficient organic matter transfer to upper trophic levels (Zapata-Hernández et al. 2021). Furthermore, MBI activity patterns could be incorporated as an important functional trait (*response trait*) in the face of environmental change (e.g., light pollution; Gaston et al. 2014) or by their influence on ecosystem functioning (*trait effect*; Villéger et al. 2017). However, this study represents just a one-time analysis of diel cycles over a short period. Consequently, it remains necessary to assess diel changes over a long period as well as considering the influence of other cycles (e.g., lunar, tidal, and seasonal) on the activity patterns of MBI. For accurate assessment of the effects of the new MPA at Rapa Nui on marine biodiversity, the implementation of diurnal and nocturnal long-term monitoring (e.g., monthly, seasonally and interannually) of all the benthic communities is essential in order to acknowledge community dynamics and their responses to environmental changes. Additionally, further knowledge on predator–prey interactions is clearly needed to assess the effects of fishing pressure (and potential predation-risk relaxation) on activity patterns of selected taxa that display higher densities (e.g., echinoids, and ophiuroids). Future research in the remote, non-anthropized Salas y Gómez islet (located ~ 400 km east of Rapa Nui) could provide an important baseline for contrasting the diel patterns of MBI in a scenario without fishing pressure and dominated by diurnal and nocturnal predators (Friedlander et al. 2013). Considering that the number of species of MBI may be higher at night, nocturnal surveys should be included in coral reef assessments to develop effective conservation management actions.

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Author contributions GZ-H and IAH conducted the field work and data collection. GZ-H, JS, and IAH contributed to the processing of the samples. GZ-H, RR, and YL conducted the data analysis. The first draft of the manuscript was written by GZ-H, YL, and JS and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest On behalf of all co-authors, the corresponding author states that there is no conflict of interest.

Ethics approval Sampling was performed under permission Res. Ext No. 41/2016 from SUBPESCA (Chile) to Universidad Católica del Norte, and approved by the scientific ethics committee of Universidad Católica del Norte, F.M. No. 70/2017.

Consent to participate Authors agree on their participation on this paper.

Consent for publication The authors agree to be co-authors on this paper on the order submitted.

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