Research Article

Initial assessment of coastal benthic communities in the Marine Parks at Robinson Crusoe Island

Montserrat C. Rodríguez-Ruiz[1], Miguel Andreu-Cazenave[1], Catalina S. Ruz[2]
Cristina Ruano-Chamorro[1], Fabián Ramírez[2], Catherine González[1], Sergio A. Carrasco[2]
Alejandro Pérez-Matus[2] & Miriam Fernández[1]

[1]Estación Costera de Investigaciones Marinas and Center for Marine Conservation, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, P.O. Box 114-D, Santiago, Chile
[2]Subtidal Ecology Laboratory and Center for Marine Conservation, Estación Costera de Investigaciones Marinas, Pontificia Universidad Católica de Chile, P.O. Box 114-D, Santiago, Chile

ABSTRACT. The National Biodiversity Strategy developed in Chile aims to protect 10% of the surface area of the most relevant marine ecosystems. The waters around the Juan Fernández Archipelago were not protected until 2014, when a Multiple Use Marine Protected Area was created in the 12 nautical miles around the archipelago, which includes five marine parks in sites of high conservation value. Three of these parks are located around Robinson Crusoe Island. This study aims to define a baseline for monitoring the impact of the marine protected area and provides ecological information to improve the understanding of coastal marine ecosystems around Robinson Crusoe Island. In addition to a characterization of bathymetry and habitats, intertidal and subtidal communities were sampled using transects and quadrats within the marine parks. We quantified species richness and abundances, which were later organized into functional groups for algae and trophic groups for mobile organisms. Although species richness did not vary between sites nor among the habitats sampled, we observed important differences in species abundance and composition as well as in functional and trophic groups both between sites and habitats. Among our results, we highlight: a) the dominance of endemic algae in intertidal and subtidal (mainly corticated and corticated foliose) habitats, b) high abundances of macroinvertebrate herbivores in intertidal habitats and detrivores in subtidal habitats, c) dominance of invertivorous fish in the subtidal, which are the primary predators of mobile benthic organisms. This characterization includes both the inter and subtidal coastal communities of the Juan Fernández Archipelago.

Keywords: marine protected areas, biodiversity, conservation, Juan Fernández Archipelago.

Evaluación inicial de las comunidades costeras de los Parques Marinos en la Isla Robinson Crusoe

RESUMEN. La Estrategia Nacional de Biodiversidad de Chile fija como meta proteger el 10% de la superficie de los ecosistemas más relevantes del país. El área marina que rodea al Archipiélago Juan Fernández alcanzó protección en 2014 con la creación de un Área Marina Costera Protegida de Múltiples Usos de 12 nautical miles alrededor del archipiélago, que incluye cinco parques marinos en sitios de alto valor para la conservación. Tres de estos parques se ubican en la Isla Robinson Crusoe. Este estudio tiene como objetivos definir la línea base para el monitoreo del impacto del área marina protegida y aportar información ecológica para alcanzar un mayor entendimiento de los ecosistemas marinos costeros. Además de una caracterización batimétrica y de hábitats, se muestrearon las comunidades intermareales y submareales por medio de transectos y cuadrantes. Se contabilizó la riqueza y abundancia de especies que posteriormente se organizaron en grupos funcionales de algas y grupos tróficos de organismos móviles. A pesar que la riqueza de especies no mostró variaciones importantes entre los sitios y hábitats estudiados, se observaron importantes diferencias en la abundancia y composición de especies como también entre grupos funcionales y tróficos entre sitios y hábitats. Se destacan los siguientes resultados: a) dominancia de algas endémicas en ambientes inter y submareales (principalmente, corticales y corticales foliosas), b) altas abundancias de macroinvertebrados herbívoros en el intermareal y detritívoros en el submareal, c) dominio de peces invertívoros en el submareal, principales depredadores de organismos bentónicos móviles. Esta caracterización incluye a las comunidades costeras inter y submareales del Archipiélago Juan Fernández.

_____

Corresponding author: Miriam Fernández (mfernandez@bio.puc.cl)

INTRODUCTION

Marine Protected Areas (MPAs) are a conservation tool that can preserve ocean biodiversity and foster ecosystem services (Allison *et al.*, 1998; Lester *et al.*, 2009). In recent decades, the number and size of MPAs has increased in response to the evident decrease in abundances of exploited marine stocks, the failure of traditional strategies, and widespread habitat degradation (Worm *et al.*, 2006; Guarderas *et al.*, 2008). However, the establishment of MPAs faces a range of social and political resistance since they restrict fishers' access to coastal waters and external enforcement is costly. Thus, a range of MPAs types, allowing different levels of human uses, have been developed (Guarderas *et al.*, 2008).

Chile has followed this international trend, increasing the level of marine protection in the last decade through various conservation tools. The most restrictive type of area, and thus the one with the greatest potential for conflict, is the Marine Park (Fernández & Castilla, 2005; Tognelli *et al.*, 2009). These have been implemented in remote areas, where social resistance is minimal (*e.g.*, Francisco Coloane and Motu Motiro Hiva Marine Parks). Marine Protected Coastal Areas of Multiple Uses (MPCA-MUs) have increased significantly in area in the last decade. Between 2003 and 2013 Chile implemented 8 MPCA-MUs (Sierralta *et al.*, 2011). Although the MPCA-MUs reduce conflicts by allowing sustainable activities, most of them have not yet been implemented because agreement with local communities regarding uses (zoning) has not been reached. Thus, zoning the MPCA-MUs is of utmost importance, along with developing an effective monitoring program to assess the impact of protection. It is important to emphasize that Chile's meager investment in the conservation of biodiversity (Waldron *et al.*, 2013) is fundamentally focused on terrestrial habitats, while administrative plans or effective mechanisms of control and monitoring have not yet been implemented for the majority of MPAs (Fernández & Castilla, 2005).

Since Chile signed the Convention on Biological Diversity in 1994, efforts were made towards ecosystem conservation and the sustainable use of resources (CONAMA, 2005; Sierralta *et al.*, 2011). Within this context, the National Biodiversity Strategy was developed in 2003, establishing a mid-range goal of protecting 10% of the surface area of the country's most important ecosystems, a measure that is internationally considered appropriate for the protection of the biodiversity (CONAMA, 2005). Globally, Chile has achieved 50% of this goal in marine environments; however, a large imbalance remains in the protection of the most important ecosystems. While 20% of the Eastern and Salas y Gómez Biogeographic Region is protected others regions do not even reach 1% of their surface area protected. Furthermore, until 2014 some fragile and vulnerable ecosystems, such as the waters around the Juan Fernández Archipelago, were not under any sort of protection. The Juan Fernández marine ecoregion is internationally recognized for its biodiversity relevance, hosting one of the 11 sites prioritized as irreplaceable for marine conservation at a global level (Pompa *et al.*, 2011).

In 2014, three new MPCA-MUs were created (eleven MPCA-MU now established in Chile), one in the Juan Fernández Archipelago. In addition to the relevance of protecting a national and international priority site for marine conservation, the process by which this MPCA-MU was created is remarkable. This marine conservation initiative emerged from the Juan Fernández community, who worked together with scientists to generate a proposal to establish a new MPCA-MU in the Archipelago. After five years, the Ministry of the Environment accepted the proposal and established an MPCA-MU protecting 12 nautical miles (nm) surrounding the Archipelago. The proposal also identified five sites of high conservation value, which were declared no-take marine parks within the MPCA-MU. Three of these marine parks are located in the coastal areas of Robinson Crusoe Island: a) El Palillo (33°38'S, 78°49'W), a representative rocky coastal habitat already included as an area of interest for the protection of nature (Senderos de Chile), b) El Arenal (33°40'S, 78°56'W), the only sandy habitat on the island, that also hosts a colony of the Juan Fernández fur seal (*Arctocephalus philippii*), which is endemic to Chile, and c) Tierras Blancas (33°39'S, 78°54'W) that hosts one of the largest breeding colonies of the Juan Fernández fur seal on Robinson Crusoe Island. The others marine parks are located at Alejandro Selkirk Island (a major Juan Fernández fur seal settlement in the archipelago) and seamounts between both islands. The ecological information available for the three marine parks at Robinson Crusoe Island is scarce. El

Palillo is the only site with detailed information about intertidal communities (see Ramírez & Osorio, 2000), while only surveys of Juan Fernández fur seal populations are available at the other coastal sites (Osman, 2008). The difficulty of accessing these islands from the continent, as well as their rugged coasts, has limited the understanding of their marine communities and organisms. The creation of the MPCA-MU and the no-take marine parks generates an urgent need to appropriately characterize these coastal marine communities, both at the beginning of the conservation program and periodically afterwards to assess the impact of the protected areas.

Thus, the objective of this study is to generate an up-to-date set of baseline information for the marine communities of the three recently created marine parks in Robinson Crusoe Island, and more specifically to (a) record abiotic characteristics *in situ* that compliment extant cartographic information (bathymetry, habitat type), and (b) describe and compare (quantitatively and qualitatively) intertidal and subtidal algae, macroinvertebrate and fish communities.

MATERIALS AND METHODS

Study sites

The study sites were focused on the three marine parks established around Robinson Crusoe Island (Fig. 1). The site closest to the only human settlement (Juan Bautista) on the island was El Palillo (33°38'S, 78°49'W), located just 1 km from San Juan Bautista. The other sites, El Arenal (33°40'S, 78°56'W) and Tierras Blancas (33°39'S, 78°54'W), were located 22 and 20 km from the town, respectively, on the southern side of Robinson Crusoe Island (Fig. 1).

Characterization of abiotic factors

The abiotic characterization of the ecosystem was conducted using various sources of information depending on the study area. Bathymetric and substrate information was obtained by revising the extant information in official maps and records for the study area (Centro Nacional de Datos Hidrográficos y Oceanográficos de Chile (CENDHOC) and Servicio Hidrográfico y Oceanográfico de la Armada (SHOA), Chilean Navy). *In situ* observations of depth and substrate were carried out by divers or directly from boats. Direct observations and aerial images from Google Earth were also used to determine coastal substrate. The aerial images were particularly important for areas that were inaccessible by land, either due to geographic limitations (*e.g*., cliffs) or to the presence of fur seal colonies. Finally, layers of substrate and bathymetric information were created, extrapolating

the recorded data to the total area of the marine parks and adjacent coastline using GIS tools.

Bathymetric information was generated for the entire Juan Fernández Archipelago, using data points from CENDHOC and SHOA (Chilean Navy). These points were used to create a grid that allowed us to map the seafloor, from which depth isobars were interpolated. Later, the new bathymetric points were combined with depth information for the El Palillo, El Arenal and Tierras Blancas marine parks, which were taken from the surface with a Garmin Echo 200 echo sounder and from underwater with divers' digital depth meters. This information was then overlaid on the depth isobars, identifying bathymetric zones for each five meters of depth and correcting the previous depth curves. All of the compiled information was plotted in UTM coordinates, UTM zone 17, datum WGS84.

Marine community structure: species richness, abundance and endemism.

Inter and subtidal communities in El Palillo, El Arenal and Tierras Blancas were sampled between March 1 and 15, 2014 (see Fig. 1). The different habitats present at each site were sampled to quantify richness and abundance of sessile and mobile organisms. We registered species with more than 1 cm in total length. For rocky intertidal substrates, six to ten 10 m transects were carried out perpendicular to the coastline, spaced at least 10 m apart. Boulders were the most common habitat type and thus were sampled at El Palillo and El Arenal. At El Palillo there were cliffs and platforms in addition to boulders. At El Arenal soft substrates were also sampled. Intertidal samples were not carried out at Tierras Blancas because the entire study area hosted a colony of Juan Fernández fur seal, *Arctocephalus philippii* (one of the most abundant on the island; Osman, 2008). Five to ten quadrats of 0.25 m^2 were placed along each transect from the high to the low tide mark, spaced every meter for platforms and boulders. In cliffs only four quadrats without spaces were placed, covering the whole intertidal area. For the soft substrates in El Arenal, three 5 m transects were carried out, with samples directed specifically towards the mid and low intertidal. Along each transect two sediment core samples (7 cm diameter, 20 cm length) were taken up to 20 cm of depth in the mid and low intertidal zones. The sediment was sifted through a 0.5 mm mesh.

To estimate sessile organism richness and abundances we used quadrats with 81 intersection points. The points intersecting each species occupying the primary substrate (*i.e*., directly on the rock) were summed to estimate abundance (% cover). For mobile species, all individuals within each quadrat were counted. Crustose algae and amphipods were considered as one group given the scarce references for species identification. Species identification and counts
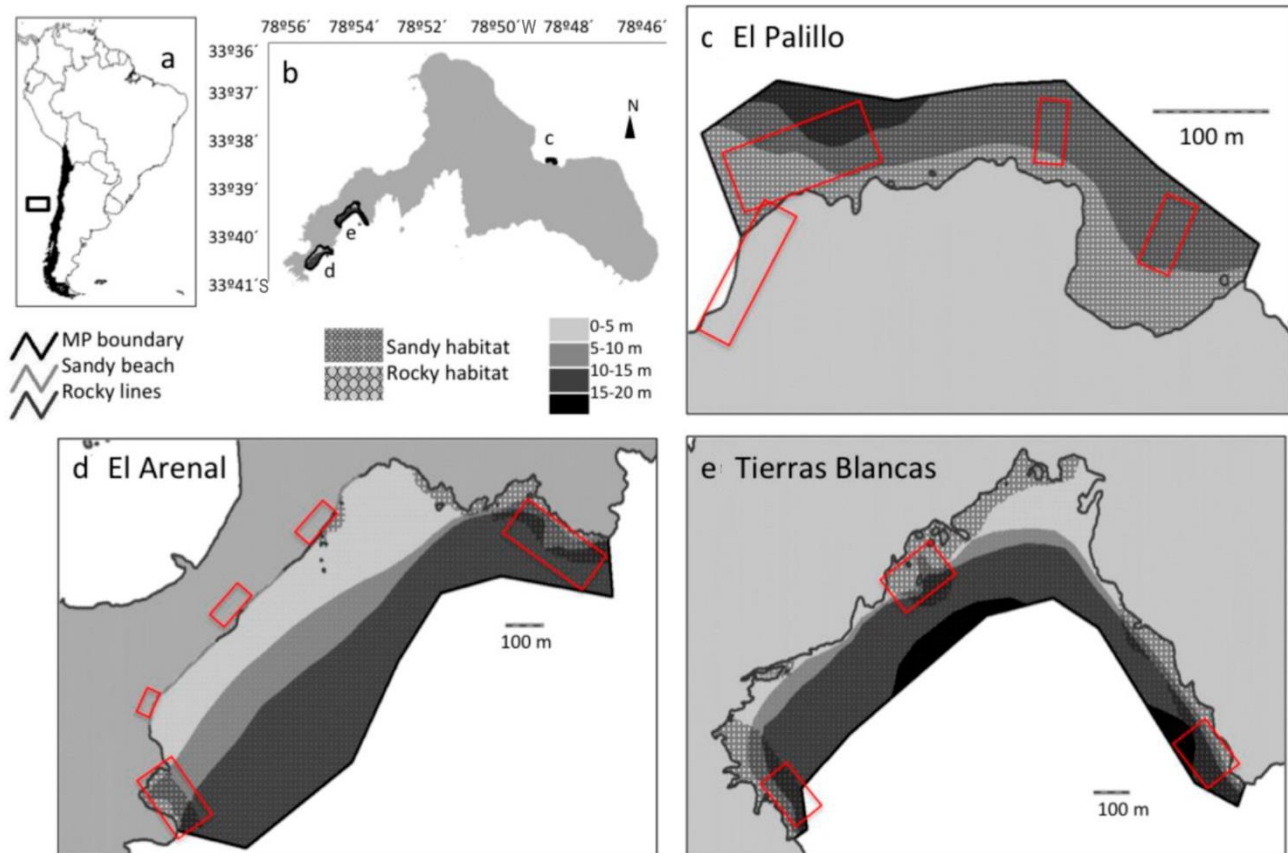
Figure 1. a-b) Location of the study area in South America, identifying the marine parks at Robinson Crusoe Island, with details of the sampling areas (red quadrats), substrate type and bathymetric profiles in c) El Palillo, d) El Arenal and e) Tierras Blancas.

were carried out *in situ* and unidentified organisms were collected and stored in 95% ethanol for further identification.

To characterize subtidal communities, macroalgae, macroinvertebrate (mobile and sessile) and fish (pelagic and benthic) were sampled by SCUBA diving. At each site, six to ten 50 m transects were carried out perpendicular to the coastline, from 2 to 15.5 m depth. Transects were spaced 30 m apart. Ten transects were carried out at El Palillo, six at El Arenal and seven at Tierras Blancas. To minimize observation error, the same four divers carried out all sampling through the study.

Similar to the intertidal sampling, abundances of sessile organisms (algae and macroinvertebrates) were obtained via 0.25 m² quadrats (81 intersection points), which were randomly placed in two points in each sampling station (four stations per transect). Sessile organisms were counted *in situ* and species were identified to the lowest taxonomic level possible. Unidentified organisms were collected and stored in

95% ethanol for later identification. Mobile macro-invertebrate richness and abundance was evaluated via visual censuses, where all individuals within 1 m on each side of the transects were counted. The sampled area of each transect was 100 m². Species identification was carried out *in situ*, and when necessary, some individuals were collected for later identification.

Coastal fish richness and abundances were measured through visual and photographic samples following a methodology previously used on Robinson Crusoe (see Ramírez *et al.*, 2013) and continental Chile (see Pérez-Matus *et al.*, 2007). Identification and size structure of fish species were carried out in 2 m on each side of the 50 m transects and 5 m in front of the diver. All individuals (adults and juveniles) larger than 5 cm in length were recorded. The total sampled area for each transect was 200 m². Juveniles and cryptic species (less than 5 cm total length) were recorded within 0.5 m on each side of the transects, covering a total area 50 m² per transect. Additionally, a stationary video camera (go-Pro hero 2) was placed at each transect to compare

the composition of fish species identified through the visual censuses. To avoid potential effects of fish behavior on abundance measurements, sampling was conducted between 10:00 and 16:00 h.

The algal species covering inter and subtidal rocky substrates were organized into different functional groups in order to understand the distribution of groups of species that have similar effects on ecosystem processes. The functional groups were determined following Steneck & Dethier (1994): a) foliose algae, b) filamentous algae, c) corticated foliose algae, d) corticated algae, e) articulated calcareous algae, and d) crustose algae. Similarly, mobile macroinvertebrates from the inter and subtidal habitats were classified into trophic groups based on Ramírez & Osorio (2000), Häussermann & Försterra (2009) and Willan *et al.* (2010): a) carnivores, b) herbivores, c) scavengers, d) detritivores, and e) omnivores. Finally, fish species were categorized by habitat based on Froese & Pauly (2014) and into trophic groups following (Ojeda & Avilés, 1987; Dyer & Westneat, 2010; Ramírez *et al.*, 2013): a) herbivores, b) planktivores, c) invertivores (carnivores that consume invertebrates), d) omnivores and e) piscivores.

Scientific literature and published reports were used to determine the level of endemism in inter and subtidal habitats (Levring, 1941; Etcheverry, 1960; Rozbaczylo & Castilla, 1987; Santelices, 1987; Sepúlveda, 1987; Pequeño & Lamilla, 2000; Pequeño & Sáez, 2000; Ramírez & Osorio, 2000; Donald *et al.*, 2005; Vega *et al.*, 2007).

Data analysis

Total abundances of mobile macroinvertebrates and fish were compared at the three sites with a one-way analysis of variance (ANOVA) followed by a *post hoc* Tukey test. Cochran C and Fligner-Killeenn tests were used to verify that the requirements of ANOVA, normality and homoscedasticity, were met (Crawley, 2007).

In order to compare species composition (abundance and richness) within and among sites in inter and subtidal habitats a series of permutational analyses of variance (PERMANOVA; Anderson, 2001) for sessile species, macroinvertebrates, fish, functional and trophic groups were performed. In each PERMANOVA a similarity percentage analysis (SIMPER) was used to determine which species contributed to the greatest differences in the analyzed parameters. For the intertidal, two additional PERMANOVAs were carried out: one to compare boulder habitats between El Palillo and El Arenal and one to determine the influence of different habitats and tide heights on the species composition within El Palillo.

RESULTS

Characterization of abiotic factors

In the intertidal, three rocky habitat types (cliffs, platforms and boulders) were identifieds. In addition, sandy bottom were also found in the intertidal zone. However, we were only able to sample all three habitats at El Palillo because the rough weather conditions prevented us from sampling cliffs at El Arenal and Tierras Blancas. In addition, we could not sample the platforms of El Arenal and Tierras Blancas that were occupied by colonies of fur seals. Thus, only boulders and sandy bottoms were sampled at El Arenal. In the subtidal there were two types of substrate, sand and rock. In El Palillo the subtidal substrate were primarily rocks, platforms and boulders, with a maximum depth of 15 m. Mobile rhodoliths beds characterized the subtidal (8-15 m) habitat at El Palillo. In El Arenal and Tierras Blancas the subtidal substrate was primarily sand with maximum depths of 15 and 20 m, respectively, though this could vary with the amount of sand deposited seasonally (Fig. 1). In both of these areas rocky substrate was only found as platforms in shallow waters.

Species richness and endemism

The total species richness of intertidal organisms was primarily explained by sessile organisms (mainly algae) and secondarily by mobile invertebrates (Figs. 2a, Appendix 1). For the intertidal, the total species richness for sessile organisms was 31, of which 27 were algae and only four were invertebrates. More specifically, in El Palillo total richness of sessile species was 26 (22 algae, 4 invertebrates). At this site, the richness of sessile species by habitat type was 11, 22 and 17 for cliffs, platforms and boulders, respectively (Fig. 2a inset, Appendix 1). At El Arenal there were 22 sessile species (20 algae, 2 invertebrates; Fig. 2a). Macroscopic organisms were absent from all the soft sediment samples from El Arenal. In the subtidal zone there were a total of 18 sessile species, of which 14 were algae and 4 invertebrates. More specifically, the total number of species for each site was 11, 15 and 15 for El Palillo, El Arenal and Tierras Blancas, respectively (Fig. 2b, Appendix 1).

Total richness of mobile organisms in the intertidal was 12, of which 10 were invertebrates (including amphipods as a group) and two were fish (Fig. 2a, Appendix 1). In El Palillo the total richness of mobile species was 10 (8 invertebrates, 2 fish), specifically 4, 7, and 6 for cliffs, platforms and boulders, respectively (Fig. 2a inset). At El Arenal the total richness of mobile organisms was 7 (all invertebrates including amphipods as a group; Fig. 2a). In the subtidal, total mobile inver-
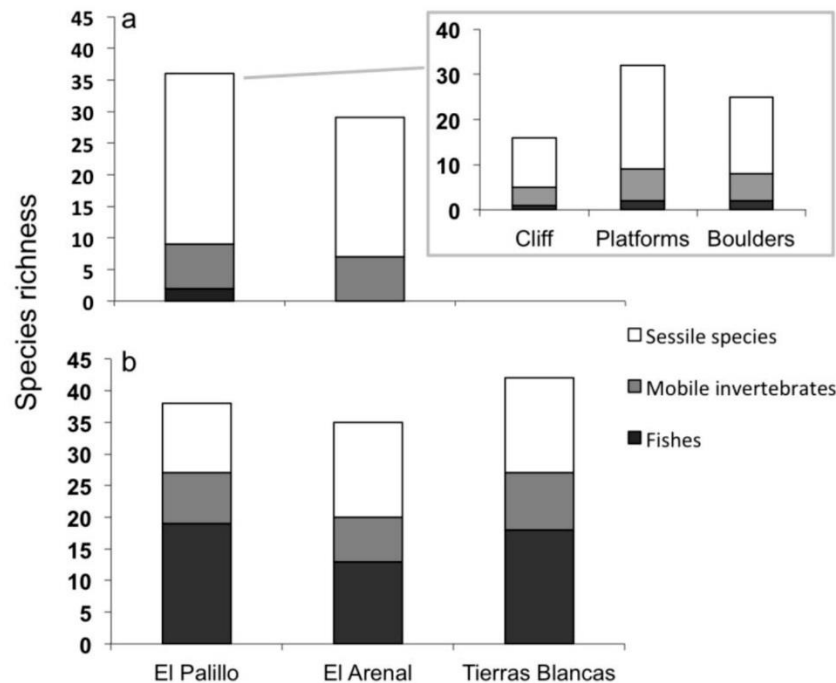
Figure 2. Richness of sessile organisms (algae and invertebrates), mobile macroinvertebrates and fishes in the three study sites in the a) intertidal, and b) subtidal habitats. Inset shows the principal habitats from El Palillo: cliffs, boulders and platforms.

tebrates (>2 cm) richness was 13, primarily represented by equinoderms, crustaceans and mollusks (Appendix 1). More specifically, the total number of species registered at El Palillo, El Arenal and Tierras Blancas was 9, 7 and 9, respectively (Fig. 2b).

Twenty four coastal fish species were recorded, representing 6 orders, 17 families and 22 genera. There are 10 benthic, 2 bentho-demersal, 8 bentho-pelagic, and 4 pelagic species. The family with the most representatives was Labridae with three species, followed by Carangidae, Chironemidae, Scorpaenidae and Serranidae with two species each. The total number of fish registered at El Palillo, El Arenal and Tierras Blancas was 20, 14 and 18, respectively (Fig. 2b, Appendix 1).

A total of 82 inter and subtidal species were found in the study area. El Palillo presented the highest richness with 67 species (31 sessile, 20 fish, 14 mobile macroinvertebrates). El Arenal had a richness of 58 species (31 sessile, 14 fish, 13 macroinvertebrates). Finally, the site with the lowest richness was Tierras Blancas with 41 species (15 sessile, 18 fish, 8 mobile macroinvertebrates) but it is important to note that this number does not include intertidal species (Appendix 1).

Out of all the species identified, five species of algae were endemic to the Juan Fernández Archipelago (*Codium cerebriforme*, *Codium fernandezianum*, *Chondriella pusilla*, *Liagora brachyclada* and *Padina fernandeziana*; Appendix 1). Of the mobile invertebrates found in the intertidal 36.4% were endemic to the Juan Fernández Archipelago (*Austrolittorina fernandezensis, Acmaea juanina, Plaxiphora fernandezi* and *Parvulastra calcarata*) and 18.2% were shared with the Desventuradas Islands (*Heliaster canopus* and *Holothuria* (*Mertensiothuria) platei*). Of all the subtidal invertebrate species, two were endemic to the Juan Fernández Archipelago (*A. fernandezensis* and *P. calcarata*), four were shared with the Desventuradas Islands (*Acantharctus delfini, Jasus frontalis, Astrostole platei, H. platei*), five had a wide geographic distribution and one opisthobranch could not be identified to the species level. With respect to fish, only three were endemic to Robinson Crusoe and the Juan Fernández Archipelago, 13 were shared with the Desventuradas Islands and 5 had a wide geographic distribution (Appendix 1).

Abundance and species composition

In the study area, the intertidal was clearly dominated by algae (Fig. 3), with a low abundance of sessile invertebrates (Fig. 4). The high intertidal was dominated by bare rock at all sites and algal cover never exceeded 2%. Algal cover progressively increased from

the mid to low intertidal, covering 50% and 80% respectively (Fig. 3). There was also a belt of barnacles (*Jehlius cirratus*) in the upper and mid intertidal; however, the majority of individuals were dead and thus the actual cover of live barnacles was low (1.5% cover). There were significant interactions between habitats and intertidal levels at El Palillo (PERMANOVA, df = 4, Pseudo*F* = 2.588, *P* = 0.00009). SIMPER analysis showed that the species that contributed to the differences between the high and mid intertidal were crustose algae (37%) and *Gelidium* sp.1 (25%); between the mid and low intertidal were crustose algae (20%), *Chaetomorpha firma* (16%) and *Chondracanthus intermedius* (16%); and between the high and low intertidal were crustose algae (18%), *C. firma* (18%) and *C. intermedius* (16%). In El Palillo, the most abundant sessile species in the mid intertidal were *Gelidium* sp.1 and crustose algae in all three habitat types (Figs. 3a-3c). Nonetheless, the low intertidal was dominated by different species in the three habitats: *C. intermedius*, *Corallina* sp. and *Jania rosea* dominated cliffs, *C. intermedius*, *Gelidium* sp.1 and crustose algae dominated boulders, and *C. firma* dominated platforms (Figs. 3a-3c).

There were significant differences in intertidal species composition in boulder habitats between El Palillo and El Arenal (PERMANOVA, df = 1, Pseudo*F* = 12.022, *P* = 0.00009). SIMPER analysis revealed that the species that mostly contributed to this difference were crustose algae (28%), *C. firma* (16%) and *Gelidium* sp.1 (14%). In the mid intertidal of El Arenal the cover of sessile organisms was more evenly split among various species (*i.e.*, crustose algae, *Ulva rigida* and *C. firma*) than in the boulders at El Palillo. The low intertidal of El Arenal was heavily dominated by *C. firma*, in contrast with El Palillo, where dominance was shared among various species (Figs. 3b, 3d). At El Arenal the average bare rock in the high intertidal was higher (97%) than in all studied habitats of El Palillo (Fig. 3d).

There were significant differences in the composition of subtidal algae between study sites (PERMANOVA, df = 2, Pseudo*F* = 7.8, *P* = 0.0001). Based on SIMPER analysis, the species responsible for these differences were *Distromium skottsbergii* which explained 23% of the difference between El Palillo and El Arenal, *Ulva* sp. which explained 18% between El Arenal and Tierras Blancas, and finally *D. skottsbergii* and *Litophyllum* sp. which explained 30% and 16% between El Palillo and Tierras Blancas, respectively. In the subtidal, corticated foliose algae exhibit high abundances, with *D. skottsbergii* showing the highest cover (37%) at El Palillo (Table 1). The algae *P. fernandeziana*, endemic to the Juan Fernández

Archipelago, also had a broad distribution, reaching 32% cover at El Arenal (Table 1). The crustose algae, *Litophyllum* sp., presented an extensive distribution, obtaining its maximum cover (20%) at El Palillo (Table 1). With respect to sessile invertebrates, unidentified vermetid gastropods had the highest abundance and distribution, reaching 27% cover at El Palillo (Table 1).

There were significant differences in the species composition of mobile invertebrates among intertidal habitats (PERMANOVA, df = 2, Pseudo*F* = 2.518, *P* = 0.0019) and intertidal levels (PERMANOVA, df = 2, Pseudo*F* = 3.008, *P* = 0.0003). Nonetheless, there was no significant interaction between habitat and intertidal levels (PERMANOVA, df = 4, Pseudo*F* = 1.370, *P* = 0.074). SIMPER analysis showed that the species that contributed the most to the differences among habitats were *A. fernandezensis* and *Leptograpsus variegatus* (47% and 13%; between boulders and cliffs, respectively), *A. fernandezensis* (58%; between cliffs and platforms), and *A. fernandezensis* and *L. variegatus* (46% and 12%; between boulders and platforms, respectively). SIMPER analysis also showed that the species that contributed most to differences among tide heights were *A. fernandenzesis* (60%; between high and mid), *H. platei* (33%; between high and low) and *L. variegatus* (18%; between mid and low). In the intertidal at El Palillo, the average abundance of mobile invertebrates (ind m^{-2}) was substantially higher on platforms than on cliffs and boulders (Fig. 4). In the high intertidal, the gastropod *A. fernandezensis* was the most abundant species on platforms and cliffs, while on boulders the most abundant species was *L. variegatus* (Fig. 4). In the mid intertidal the most abundant species were *H. canopus* on cliffs, *H. platei* and *L. variegatus* on boulders and *A. fernandezensis*, *P. calcarata*, *H. canopus*, *H. platei* and *L. variegatus* on platforms (Figs. 4a-4c). In the low intertidal, the most abundant species was *H. platei*, on cliffs, boulders and platforms. *Leptograpsus variegatus* was present in the low intertidal on platforms and boulders at low abundances (Figs. 4b-4c).

The abundance and composition of mobile species varied significantly between El Arenal and El Palillo for boulder habitats (PERMANOVA, df = 1, Pseudo*F* = 6.06, *P* = 0.00009). SIMPER analysis showed that the species that contributed most to differences among sites were *A. juanina* (37%) and *L. variegatus* (17%). At El Arenal the gastropod *A. juanina* was the most abundant specie at all tide levels, and *A. fernandezensis* was abundant only in the high zone (Fig. 4).

In subtidal habitats, the average abundance of mobile macroinvertebrates (ind 100 m^{-2}) was 156, 450 and 796 for El Palillo, El Arenal and Tierras Blancas, respectively. These differences were significant (ANOVA, df = 2, *F* = 7.8, *P* = 0.003), with Tierras Blancas showing the
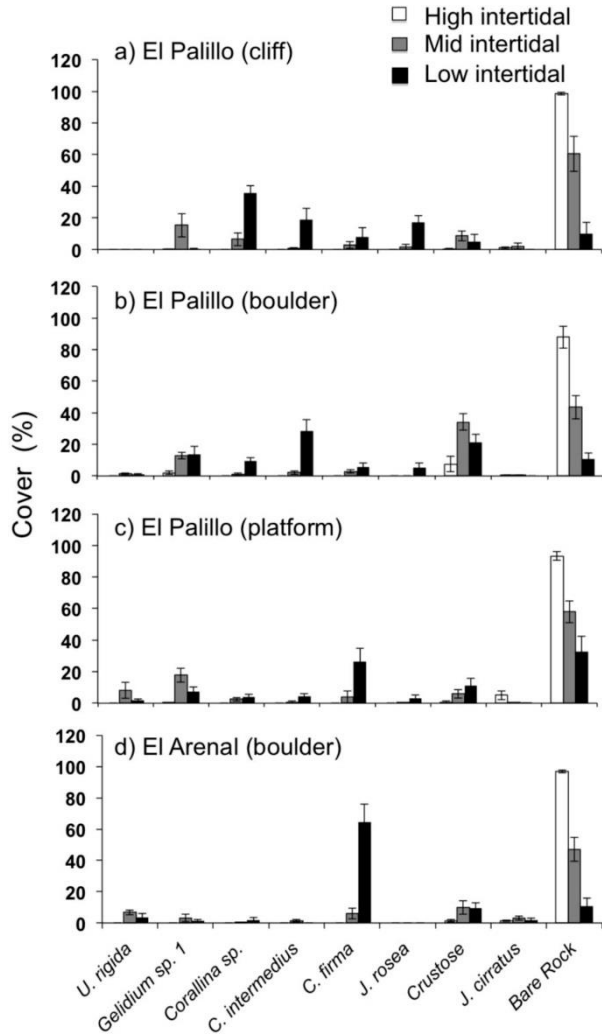
Figure 3. Abundance of the dominant sessile organisms (% cover m^{-2}) in the three rocky intertidal habitats of El Palillo (cliffs, boulders and platforms) and in El Arenal (only boulders).

Figure 4. Abundance of dominant mobile invertebrates (ind m^{-2}) in the three rocky intertidal habitats of El Palillo (cliffs, boulders and platforms) and in El Arenal (only boulders).

highest number of invertebrates (Tukey, $P = 0.01$) (Table 1). In terms of species composition (abundance and richness), there were significant differences between the three sites (PERMANOVA, df = 2, Pseudo$F = 6.8$, $P = 0.0001$). SIMPER analysis of subtidal macroinvertebrates showed that the species that contributed the most to these differences were the sea cucumber *H. platei* and the seastar *P. calcarata* (Table 1). The species that contributed the most to the differences among El Palillo and the other two sites, El Arenal and Tierras Blancas, was *P. calcarata*, with values close to 82%. Nonetheless, the sea cucumber, *H. platei*, explained 95% of the differences between El Arenal and Tierras Blancas. Additionally, a one-way ANOVA showed differences in the abundance of *H. platei* among the three sites (df = 2, $F = 10.76$, $P = 0.0006$),
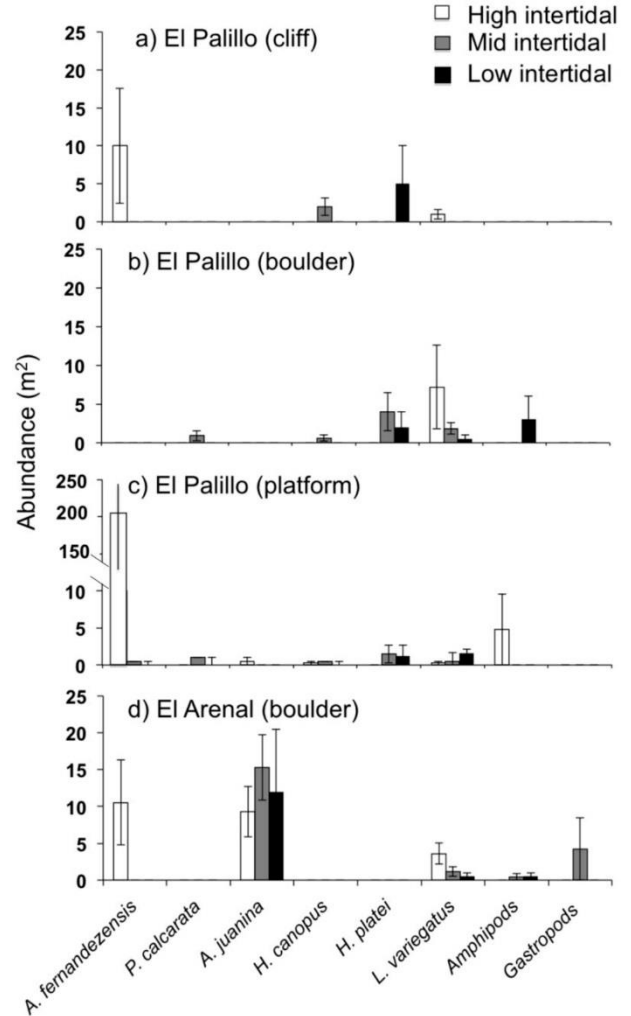
with significant differences only between El Palillo and Tierras Blancas (Tukey, $P = 0.00048$; Table 1).

In subtidal habitats, the average abundance of fish (ind 200 m^{-2}) registered in the transects was significantly higher at El Palillo than at El Arenal and Tierras Blancas (ANOVA, df = 2, $F = 4.9$, $P = 0.01$). There were also significant differences among sites in species composition (PERMANOVA; df = 2, Pseudo$F = 2.8$, $P = 0.003$). Based on SIMPER analysis, the fish species important in determining these differences, in order of importance, were: *Pseudolabrus gayi*, *Caprodon longimanus*, *Malapterus reticulatus*, *Pseudocaranx chilensis* and *Scorpis chilensis*. The two species that contributed to the differences between El Palillo and El Arenal and El Palillo and Tierras Blancas were *P. gayi* y *C. longimanus*, with 44% and 47%, respecti-

Table 1. List of the most abundant algae, invertebrate and fish species in subtidal habitats in El Palillo, El Arenal and Tierras Blancas.

Group	Species	Abundance		
		El Palillo	El Arenal	Tierras Blancas
Sessile organisms	*Distromium skottsbergii*	37 ± 1	17 ± 5	11 ± 2
(% cover)	*Litophyllum* sp.	19 ± 2	5 ± 1	7 ± 2
	Padina fernandeziana	14 ± 3	32 ± 5	13 ± 3
	Delesseriaceae	-	18 ± 3	15 ± 1
	Jania rosea	4 ± 2	21 ± 3	21 ± 7
	Vermetidae	25 ± 1	-	11 ± 2
Mobile invertebrates	*Centrostephanus rodgersii*	106 ± 47	8 ± 3	5 ± 2
(100 m^2)	*Holothuria (Mertensiothuria) platei*	41 ± 14	249 ± 64	442 ± 107
	Parvulastra calcarata	7 ± 1	188 ± 51	335 ± 80
	Astrotole platei	2 ± 0.8	1 ± 0.5	10 ± 2
Fishes	*Pseudolabrus gayi*	120 ± 21	79 ± 23	83 ± 16
(200 m^2)	*Malapterus reticulatus*	36 ± 6	51 ± 5	21 ± 7
	Scorpis chilensis	26 ± 5	32 ± 14	24 ± 9
	Pseudocaranx chilensis	5 ± 4	29 ± 20	-
	Scartichthys variolatus	10 ± 6	12 ± 2	9 ± 3
	Hypoplectrodes semicintum	18 ± 4	6 ± 2	5 ± 2

vely. Meanwhile, the species driving differences in fish composition between El Arenal and Tierras Blancas were *P. gayi* and *M. reticulatus* with 48%.

Functional groups

Given the low cover of algae in the high intertidal zone (2%), almost exclusively of crustose algae, this tidal level was not included in our analysis. The PERMANOVA revealed significant interaction between intertidal level and habitat in functional groups (df = 2, Pseudo$F$ = 3.7, P = 0.0004). SIMPER analysis revealed that the differences between the mid and low intertidal were driven by corticated (25%), crustose (25%), and articulated calcareous algae (21%). In the mid intertidal, all sites and habitat types were dominated by corticated algae (*C. intermedius*, *C. pusilla*, *Gelidium* sp.1, *Bostrychia intricata*; Fig. 5a and inset), which had approximately 20% cover. In the low intertidal at El Palillo, abundance of functional groups was evenly distributed among functional groups (Fig. 5b). However, differences among habitats were observed. SIMPER revealed differences between platforms and cliffs, due to articulated calcareous (33%), filamentous (22%) and corticated algae (21%). Crustose (32%), corticated (25%) and filamentous algae (21%) drove observed differences between platforms and boulders. Finally, crustose (33%), articulated calcareous (32%) and corticated algae (24%) generated the differences detected between cliffs and boulders. Articulated calcareous algae dominated cliffs (*Corallina* sp. and *J.*

rosea; Fig. 5b inset). Platforms were dominated by filamentous (*C. firma*, *Cladophora perpusilla*, *Polysiphonia* sp., *Pterosiphonia* sp.), corticated (*C. intermedius*, *C. pusilla*, *Gelidium* sp.1) and crustose algae. Boulders were dominated by corticated and crustose algae (Fig. 5b inset).

There were significant differences between El Palillo and El Arenal in functional groups (PERMANOVA, df = 1, Pseudo$F$ = 8.8, P < 0.01). SIMPER analysis showed that these differences were driven by crustose (32%), corticated (30%) and filamentous algae (25%). There was a clear dominance of crustose and corticated algae in the boulders at El Palillo, while dominance was distributed among various groups in the mid intertidal at El Arenal. However, there was a clear dominance of filamentous algae (>70%) in the low intertidal at El Arenal (Fig. 5).

In subtidal habitats, corticated foliose algae (*D. skottsbergii*, *D. kunthii*, *D. phlyctaenodes* and *P. fernandeziana*) had the highest distribution and abundance at all sites and always covered more than 35% of the substrate (Fig. 5c). They reached 46% cover in El Palillo (Fig. 5c). Articulated calcareous algae (*Corallina* sp. and *J. rosea*) had over 15% cover at El Arenal (Fig. 5c). There were significant differences between sites in subtidal algae (PERMANOVA, df = 2, Pseudo$F$ = 5, P = 0.001). Following the SIMPER analysis, the functional group that contributed most to these differences was corticated foliose algae with 24% between El Palillo and El Arenal, 31% between El
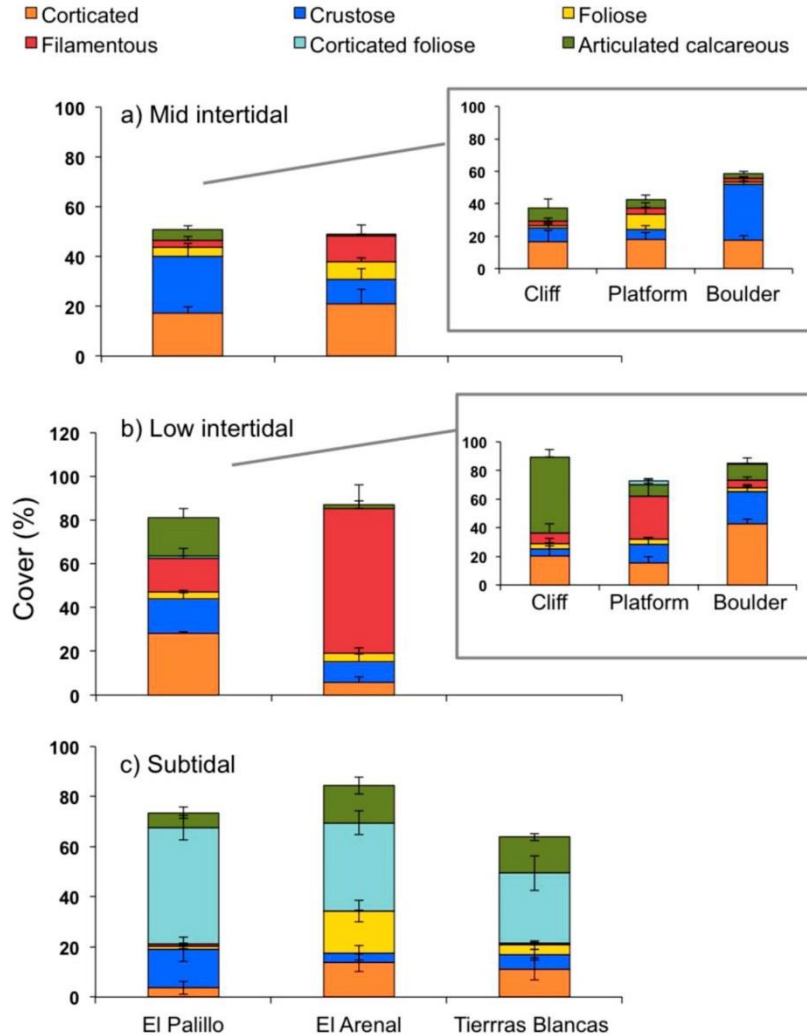
Figure 5. Average cover (± SE) of functional groups at the study sites in a) the mid intertidal zone, including different habitats at El Palillo (inset), b) the low intertidal, zone including different habitats at El Palillo (inset) and c) the subtidal zone.

Arenal and Tierras Blancas, and 37% between El Palillo and Tierras Blancas.

Trophic groups

Intertidal invertebrates were classified into three trophic groups: herbivores, carnivores and detritivores, with six, two and one species, respectively (Fig. 6a). As mentioned previously, mobile invertebrate abundance was low, but variable, at all intertidal levels. A great part of this variability was explained by the herbivore *A. fernandezensis*, which was only found in the high intertidal. Abundances for this species were excluded from the graphical representation to facilitate the interpretation of the data (*i.e.,* mean abundance *A. fernandezensis* (± SE); El Arenal: 4.54 ± 2.57; El Palillo cliff: 5 ± 3.87; El Palillo platform: 78.06 ±

31.09; El Palillo boulders: 0). There were significant differences in the trophic groups found at El Palillo and El Arenal (PERMANOVA: df = 2; Pseudo$F$ = 9.085; P < 0.05). SIMPER analysis showed that hervbivores was the group determining the difference between sites (64.8%). The mid and high intertidal zones of El Arenal were characterized by a high abundance of herbivores, principally *A. juanina* (Fig. 6a). No significant differences in abundance of trophic groups among habitats were detected in El Palillo (PERMANOVA, df = 2, Pseudo$F$ = 1.84, P = 0.07; Fig. 6a inset).

In the subtidal, five trophic groups of mobile macroinvertebrates were identified and represented as follows: five carnivores, four herbivores, two scavengers, one detritivore and one omnivore (Fig. 6b).
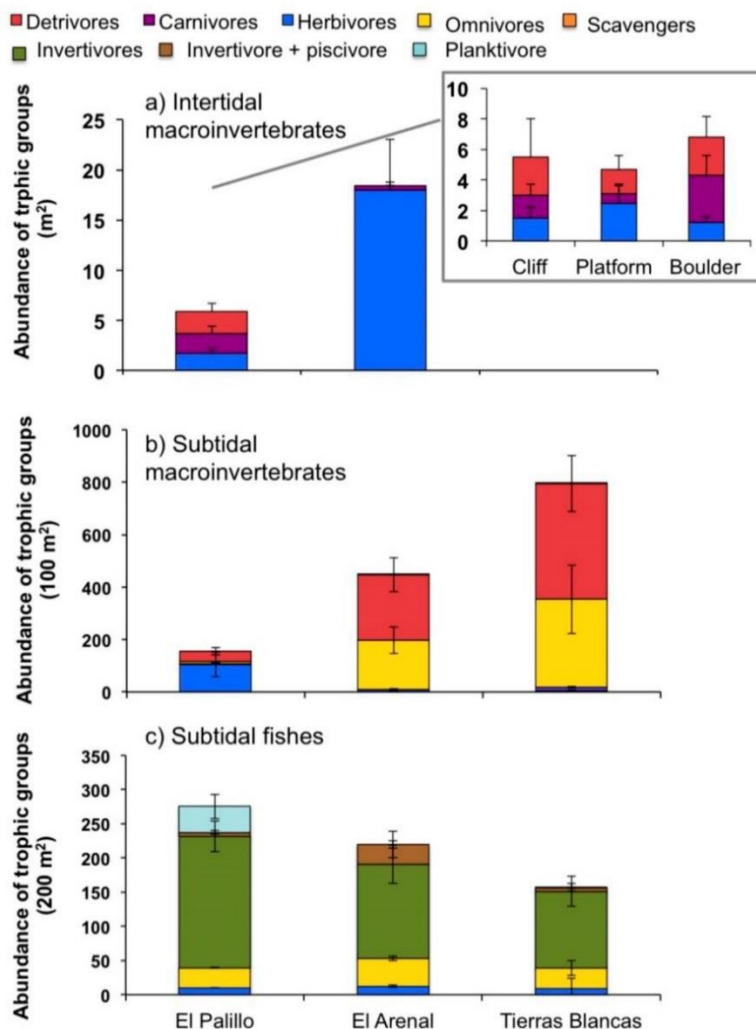
Figure 6. Average abundance (± SE) of trophic groups at the study sites of a) intertidal mobile macroinvertebrates, including different habitats at El Palillo (inset), b) subtidal mobile macroinvertebrates, and c) subtidal fishes.

The composition of the trophic groups was significantly different between sites (PERMANOVA; df = 2, Pseudo$F$ = 6.8, P < 0.01). SIMPER analysis showed that detritivores and omnivores were the groups that established these differences. Between El Palillo and El Arenal, omnivores contributed with 39% of the differences, while detritivores explained most of the differences (42%) between El Arenal and Tierras Blancas. Finally, omnivores contributed in 30% to the differences between El Palillo and Tierras Blancas.

Of the 24 fish species present in the subtidal, five trophic groups were identified: two planktivores, one herbivore, four omnivores, 11 invertivores and six piscivore/invertivores (species that consume both fish and invertebrates; Fig. 6c. The most important groups were invertivores, followed by omnivores. The composition of the trophic groups was significantly different among sites (PERMANOVA; df = 2, Pseudo$F$

= 2.5, P = 0.02). SIMPER analysis showed that the groups that established these differences were the invertivores, omnivores and planktivores. Invertivores and omnivores explained 61% of the differences between El Palillo and El Arenal. Omnivores were the most important in establishing differences between El Arenal and Tierras Blancas. Finally, invertivores and planktivores, particularly *C. longimanus*, contributed 25% of the differnces between El Palillo and Tierras Blancas. Planktivores were only present in El Palillo.

DISCUSSION

The first characterization of the inter- and subtidal coastal habitats of Robinson Crusoe Island show the following patterns: a) the dominant substrate varies among the three marine parks, b) a high level of endemism in the different taxonomic groups, c) both

species richness and abundance show typical patterns of zonation, increasing from the high intertidal towards the subtidal, though the study sites lack characteristic mussel beds in the mid intertidal and large brown macroalgal belts in the low intertidal, d) algal species richness and abundance were high, both in the intertidal and subtidal zones; however in intertidal habitats the dominant functional groups were corticated (*e.g.*, *C. intermedius*, *C. pusilla*, *Gelidium*, *B. intricata*), crustose and filamentous algae (*e.g.*, *C. firma*, *C. perpusilla*, *Polysiphonia* sp., *Pterosiphonia* sp.), while in the subtidal zone corticated foliose algae (*e.g.*, *D. skottsbergii*, *P. fernandeziana*) dominated the three study sites and the presence of rhodoliths beds in El Palillo (Macaya *et al.*, 2014), e) herbivorous invertebrates, particularly gastropods, dominated the intertidal, while the subtidal was dominated by detritivores, with *H. platei* as the most abundant, f) the highest fish abundance was recorded in subtidal habitats at El Palillo, followed by El Arenal and finally Tierras Blancas, while fish were very scarce in the intertidal zones, g) invertivore fishes, consumers of benthic invertebrates, dominated Robinson Crusoe's coastal habitats, which suggests a negative relationship between fish abundance and benthic invertebrate abundance, and h) the composition of sessile communities, mobile invertebrates and fish were clearly distinctive in the three proposed marine parks in Robinson Crusoe. The patterns observed in this first study, integrating inter- and subtidal communities, allow us to propose hypotheses relative to the main factors structuring these coastal communities.

The main substrata from the inter- and subtidal zones in the three marine parks show clear differences, which are accompanied by singularities in the groups of species present at each site suggesting that different communities are protected at each marine park. El Palillo represents diverse rocky substrates (boulders, platforms, cliffs) in the inter- and shallow subtidal habitat. Tierras Blancas represents a rocky coast with extensive subtidal areas covered by small cobbles and sand. Finally, El Arenal represents rocky and sandy habitats in both the inter- and shallow subtidal, though the area covered by these substrates is variable in time given the characteristic dynamics of their system (J. Chamorro-Solis, *pers. comm.*). The amount of sand fluctuates significantly over time, going from a sand covered beach to entirely exposed rock. This beach dynamic is an extremely important characteristic of El Arenal, the only sandy coastline in the archipelago. The dynamics of the sand could explain the complete absence of invertebrates in the soft sediment of intertidal areas. The amount of sand and its seasonality influences the number of females and young of a top predator in El Arenal: the Juan Fernández fur seal (J.

Chamorro-Solis, *pers. comm.*). The influence of soft sediments in structuring the coastal communities associated with this marine park requires further research. It is important to note that we sampled only during the summer, which may represent a unique physical and subsequent biological processes within the island.

The geographic location of the Juan Fernández Archipelago, isolated from the South American continent by the Humboldt Current System and far from other Oceanic Pacific islands, explains the high level of endemism in its marine communities, as well as the species richness observed. The high level of endemism observed across taxonomic groups is in agreement with previous reports of endemism for the area. On a global level, we found 15.6% endemism in subtidal and intertidal algae in Juan Fernández Archipelago (18.7% if we consider Juan Fernández and Desventuradas Islands), with the lowest levels among green algae and the highest level of endemism among brown algae (33%). These results are consistent with previous studies, which report low levels of endemism among green algae and the highest among the brown algae (30%; Ramírez & Osorio, 2000). There were important variations in the level of endemism within invertebrates. For instance, 25% of the mollusk species found were endemic to Juan Fernández Archipelago, while 33% of the crustaceans and 80% of the echinoderms observed were endemic to Juan Fernández and Desventuradas Islands. This level of endemism is similar to prior reports, which included deep-sea and seamount species (22% decapods, 66% mollusks, 89% polychaetes; Andrade, 1985; Retamal & Arana, 2000). Among fish, 9% endemism was recorded for coastal species in Juan Fernández. Additionally, 57% of the observed fish species were endemic to the Juan Fernández Archipelago and Desventuradas Islands biogeographic region (Sepúlveda, 1987; Pequeño & Sáez, 2000; Dyer & Westneat, 2010; Pérez-Matus *et al.*, 2014). These results highlight the high number of unique species found in this study (a total of 31 species of macroalgae, invertebrates and fish endemics to the Juan Fernández and Desventuradas Islands) that are currently protected only within the coastal marine parks recently created in the Juan Fernández Archipelago.

The geographic isolation and age of the islands (~4 Mya, see Stuessy *et al.*, 1984), in addition to other factors such as the absence of kelp forests, are possible causes of the low species richness in comparison to similar habitats on continental Chile and even other, equally isolated, Pacific islands. For the intertidal, this study reports site-specific richness lower than that registered in other isolated ecosystems like Easter Island (57 species: 21 algae and 36 invertebrates;

Gaymer *et al.*, 2011) or in continental Chile at similar latitude and using the same sampling method and season (56.4 species; average richness at Matanzas, Las Cruces, El Quisco, Quintay and Curaumilla in central Chile; Broitman *et al.*, 2011). Intertidal species richness was 29 and 36 in El Arenal and El Palillo, respectively. It is important to note that we sampled a higher diversity of habitat types at El Palillo, which may explain the higher species richness. In fact, we only sampled rocky platforms at El Palillo, the habitat with highest species richness (33 species). Although other studies reported higher species richness for rocky platforms at El Palillo (75 species: 47 benthic macroalgae and 28 invertebrates; Ramírez & Osorio, 2000), the methodology is not comparable between both studies. Our methodology only quantifies species occupying primary substrate (as in Broitman *et al.*, 2011; Gaymer *et al.*, 2011), thus, epiphytes were not quantified (15 species in Ramírez & Osorio, 2000). The species richness reported here is similar (cliffs) or higher (boulders) than that reported by Díaz *et al.* (2007), using a similar methodology. Site-specific species richness in subtidal zones is also lower in the Juan Fernández Archipelago than in other isolated areas (*e.g.*, Rapa Nui) or continental areas of similar latitudes. Among fish, for example, there is evidence of a longitudinal gradient of species richness that decreases towards the east Pacific (Briggs, 2007; Randall & Cea, 2011; Briggs & Bowen, 2011). This longitudinal gradient is, in part, explained by the availability of transitional habitats between land and sea (almost nonexistent at Robinson Crusoe) and isolation from the origin in the Indo Australian Area (IAA) triangle (Bellwood & Hughes, 2001; Briggs, 2007).

At all study sites, the high intertidal was characterized by the presence of the only endemic littorine species on the island, *A. fernandezensis* (Ramírez & Osorio, 2000; Díaz *et al.*, 2007*)*, and low algal abundance, a characteristic shared with other intertidal habitats at similar latitudes (Reid, 1986). However, the typical belt of barnacles in the high intertidal of rocky habitats was not observed on the platforms or cliffs studied. Although there were barnacles in the intertidal, the majority of the individuals were dead, showing low abundance (1.5% cover). Prior studies from the last decade show similar patterns of abundance pre- and post-tsunami (Díaz *et al.*, 2007), which contrasts with records from Ramírez & Osorio (2000), who reported levels of cover near 10%. The potential factors behind the large-scale mortality in barnacles in the last decade are unknown. The coast of the Desventuradas Islands have a belt of the barnacle, *Jehlius gilmorei*, in the high intertidal in addition to the typical zone of brown algae, primarily

the kelp *Eisenia cookerii,* in the low intertidal (National Geographic & Oceana, 2013). The coasts of Robinson Crusoe lack the algal kelp belts, but also the characteristic mussel bed in the mid intertidal, which are present in almost all temperate coasts in both hemispheres (Ramírez & Osorio, 2000; Broitman *et al.*, 2011), including islands with the same origin and age, such as the Desventuradas Islands (National Geographic & Oceana, 2013). On Easter Island, the belt of brown algae is primarily *Sargassum* (Gaymer *et al.,* 2011). Ramírez & Osorio (2000) explain these differences based on the geology of the rock, temperature and biogeographic factors. Given the available information, we are not able to propose new hypotheses.

Although in continental Chile there is a clear dominance of mussels and barnacles in rocky areas, there is also a rich fauna of mobile invertebrates (Broitman *et al.,* 2011). A distinctive characteristic of the rocky intertidal on Juan Fernández and Easter Island (Gaymer *et al.,* 2011) is the high abundance of algae. Nonetheless, on Easter Island the abundance of sessile invertebrates, such as barnacles (16% cover on average), and of mobile invertebrates, such as sea urchins and sea cucumbers, is high (Gaymer *et al.,* 2011). In contrast, one of the characteristics of the rocky intertidal of Robinson Crusoe was the low abundance of invertebrates. We recognize that the methodological approach may have underestimated the abundance of highly mobile species, such as *L. variegatus*. However, this is not an issue for sedentary species. The low abundances of invertebrates (*e.g.*, herbivores) may explain a community dominated by algae, which cannot be controlled by the low abundance of invertebrates. The subtidal habitats of Robinson Crusoe, Easter Island and continental Chile are similar with regards to the dominance of brown and crustose algae (Palma & Ojeda, 2002; Gaymer *et al.*, 2011; Ramírez *et al.*, 2013). Species from the Order *Dictyotales* are the most abundant on both islands, but the sea floor of Robinson Crusoe differs from that of Easter Island in that it is made up of rocky reefs with high abundances of sessile invertebrates (*e.g.*, Vermetida, Cnidaria) and rhodoliths beds (Macaya *et al.*, 2014). On the other hand, around Easter Island the substrate is also primarily reefs but they are principally coral (*Pocillopora* sp. and *Porites lobata*; Gaymer *et al.*, 2011; Wieters *et al.*, 2014). The subtidal habitats of continental Chile are dominated by brown algae, primarily from the Order Laminariales, which form extensive forests with an understory dominated by crustose algae (Palma & Ojeda, 2002; Pérez-Matus *et al.*, 2007).

The morphology, physiology and ecological adaptations of functional groups of algae can be related

to the level of disturbance, given that the least structured functional groups are the most abundant in disturbed habitats (Litter & Litter, 1984; Steneck & Dethier, 1994). In the different habitats of El Palillo and in the boulders at El Arenal we observed differences in patterns of abundance of the functional groups, which may be related to varying levels of disturbance. A high abundance of corticated algae and greater diversity of functional groups in the low intertidal characterize El Palillo. In contrast, the high abundance of filamentous algae in the low intertidal at El Arenal suggests a high level of disturbance, which could be due to the erosion (scour) related to the dynamics of the sand as well as intense wave exposure. Filamentous algae, such as *Chaetomorpha linum*, are opportunistic species (Litter & Litter, 1984) capable of rapidly repopulating open space created by physical perturbations (Murray & Litter, 1979; Litter *et al.*, 1983; Taylor *et al.*, 2011) which might be the case of high amount of ephemeral algae near El Palillo after the tsunami in 2010 (A. Pérez-Matus and E. Macaya, *pers. comm.*). Some studies have argued that in areas with sand deposition only opportunistic algae, or those that can tolerate this stressor (*e.g.*, some with a crustose phase within the life cycle), can settle (Litter *et al.*, 1983), while more complex species establish themselves in sheltered habitats (Litter *et al.*, 1983). The low intertidal, where the opportunistic filamentous alga *C. firma* dominates, could be disturbed by sand deposition, temperature and light. Higher wave exposure could favor the dominance of these algae, an effect that has also been described in the Desventuradas Islands where *C. firma* is very abundant in lava canals with intense water circulation (National Geographic & Oceana, 2013). Nonetheless, this wave exposure with high abundances of articulated calcareous algae contrasts with the predictions of Steneck & Dethier's (1994) model. On the other hand, Phillips *et al.* (1997) argued that the responses of different functional groups to disturbances caused by wave action are not predictable given the high variability of physiological responses within each group. Thus, the dominance of calcareous algae on the cliffs of El Palillo could be the result of a combination of wave exposure and reduced light exposure since calcareous algae are structurally complex, very resistant to physical damage and require less light than filamentous algae (Gattuso *et al.*, 2006).

The high abundance of the sea cucumber *H. platei*, recorded for the first time in subtidal habitats of Robinson Crusoe Island (*i.e.*, El Arenal and Tierras Blancas) may reflect the importance of the total organic matter content present in the surface sediments of the seafloor of the studied sites. As also recorded in other tropical and temperate species of deposit-feeding sea cucumbers, *H. platei* could be effectively feeding on sediments enriched with biodeposits from the fur seal colonies, which would support the higher biomass observed in those sites compared with lower abundances in sites farther away from such naturally-enriched habitats (*i.e.*, El Palillo; for examples see: Slater & Jeffs, 2010; Zamora & Jeffs, 2012; Navarro *et al.*, 2013). Additionally, given the high dynamic of soft sediments observed in El Arenal, it is also plausible that biodeposit deposition in this site is not constant or spatially uniform and depends on several factors such as the size and density of fur seals and their diet, as well as the erosion of biodeposits, which can vary seasonally depending on the hydrodynamic regime to which the fur seal colony is exposed. In spite of the important role of sea cucumbers as benthic nutrient recyclers (through their feeding activity), as well as their important economic importance, the ecology of the species and factors influencing their habitat selection remain largely unexplored.

Based on the abundances of different functional and trophic groups, in both the inter- and subtidal, in addition to a clear gradient in the abundance of mobile invertebrates (high in Tierras Blancas, intermediate in El Arenal, low in El Palillo) and fish (high in El Palillo, intermediate in El Arenal, low in Tierras Blancas), it is evident that the three marine parks represent distinct communities and, likely, different structuring processes (*e.g.*, sand dynamics). Additionally, the presence (and abundance) of a top predator, the Juan Fernández fur seal, *A. philippi,* the only pinniped endemic to Chile, needs to be considered (Osman, 2008). Given that the pattern of abundance for invertebrates is negatively correlated with the pattern in fish abundance, which is in turn negatively correlated to fur seal abundances (CONAF), it is possible to hypothesize about a potential trophic cascade that warrants further consideration. Although knowledge about the dynamics and population connectivity of coastal communities in the Juan Fernández Archipelago is scarce, the patterns reported here, in addition to the widespread endemism across functional and trophic groups, allows us to conclude that the established conservation measures cover distinct types of habitats and communities.

REFERENCES

Allison, G.W., J. Lubchenco & M.H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl., 8(1): S79-S92.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol., 26: 32-46.

Andrade, H. 1985. Crustáceos decápodos marinos del archipiélago de Juan Fernández. In: P. Arana (ed.). Investigaciones marinas en el Archipiélago Juan Fernández. Universidad Católica de Valparaíso, Valparaíso, pp. 109-116.

Bellwood, D.R. & T.P. Hughes. 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science, 292(5521): 1532-1535.

Briggs, J.C. 2007. Marine longitudinal biodiversity: causes and conservation. Divers. Distrib., 13: 544-555.

Briggs, J.C. & B.W. Bowen. 2011. A realignment of marine biogeographic provinces with particular reference to fish distributions. J. Biogeogr., 39(1): 12-30.

Broitman, B.R., S.A. Navarrete, F. Smith & D.G. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Mar. Ecol. Prog. Ser., 224: 21-34.

Broitman, B.R., F. Véliz, T. Manzur, E.A. Wieters, G.R. Finke, P.A. Fornes, N. Valdivia & S.A. Navarrete. 2011. Geographic variation in diversity of wave exposed rocky intertidal communities along central Chile. Rev. Chil. Hist. Nat., 84: 143-154.

Comisión Nacional del Medio Ambiente (CONAMA). 2005. Plan de acción de país para la implementación de la estrategia nacional de biodiversidad 2004-2015. Comisión Nacional del Medio Ambiente, Santiago, 139 pp.

Crawley, M.J. 2007. The R book. John Wiley & Sons, Chichester, 1076 pp.

Díaz, P., A.M. Vega, A.M. Mora, M. Aldana & J.M. Pulgar. 2007. Distribución y abundancia de macroalgas y macroinvertebrados de dos ambientes intermareales de la Isla Robinson Crusoe, Archipiélago Juan Fernández, Chile. XXVIII Congreso de Ciencias del Mar. Universidad Andrés Bello y Sociedad Chilena de Ciencias del Mar, Viña del Mar, 77 pp.

Donald, M.K., M. Kennedy & H.G. Spencer. 2005. The phylogeny and taxonomy of austral monodontine topshell (Mollusca: Gastropoda: Trochidae), inferred from DNA sequences. Mol. Phylogenet. Evol., 37: 474-483.

Dyer, B. & M. Westneat. 2010. Taxonomy and biogeography of the coastal fishes of Juan Fernandez Archipelago and Desventuradas Islands, Chile. Rev. Biol. Mar. Oceanogr., 45: 1-29.

Etcheverry, H. 1960. Algas marinas de las islas oceánicas chilenas. Rev. Biol. Mar., 10: 83-132.

Fernández, M. & J.C. Castilla. 2005. Marine conservation in Chile: historical perspective, lessons, and challenges. Conserv. Biol., 19: 1752-1761.

Froese, R. & D. Pauly. 2014. FishBase world wide web electronic publication. [http://www.fishbase.org]. Reviewed: 10 July 2014.

Gattuso, J.P., B. Gentili, C.M. Duarte, J.A. Kleypas, J.J. Middelburg & D. Antoine. 2006. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. Biogeosciences, 3: 489-513.

Gaymer, C., P.F. Cárcamo, A.M. Friedlander, A.T. Palma, I.A. Bodin, A. Muñoz, M. García, E. Sorensen, I. Petit, L. Zañartu, B. Rapu, C. Gutierrez & A. Hoffens. 2011. Implementación de una Reserva Marina en la bahía de Hanga Roa: estudio de línea base. Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, 142 pp.

Guarderas, A.P., S.D. Hacker & J. Lubchenco. 2008. Current status of marine protected areas in Latin American and the Caribbean. Conserv. Biol., 22: 1630-1640.

Häussermann, V. & G. Försterra. 2009. Marine benthic fauna of Chilean Patagonia. Nature in Focus, Santiago, 1000 pp.

Lester, S.E., B.S. Halpern, K. Grorud-Colvert, J. Lubchenco, B.I. Ruttenberg, S.D. Gaines, S. Airamé & R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser., 384: 33-46.

Levring, T. 1941. Die Meeresalgen der Juan Fernández Islands. In: C. Skottsberg (ed.). The natural history of Juan Fernández and Eastern Island. Almqvist & Wiksells Boktrycker, Uppsala, Vol. 2, Part 5, 22: 601-670.

Litter, M.M. & D.S. Litter. 1984. Relationships between macroalgal functional groups and substrata stability in a subtropical rocky intertidal system. J. Exp. Mar. Biol. Ecol., 74: 13-34.

Litter, M.M., D.R. Martz & D.S. Litter. 1983. Effects of recruitment sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Mar. Ecol. Prog. Ser., 11: 129-139.

Macaya, E.C., R. Riosmena-Rodríguez, R.R. Melzer, R. Meyer, G. Försterra & V. Häussermann. 2014. Rhodolith beds in the South-East Pacific. Mar. Biodivers. (In press).

Murray, S.N. & M.M. Litter. 1979. Experimental studies of the recovery of populations of rocky intertidal macro-organisms following mechanical disturbance, Science Applications, La Jolla. Tech. Rept. II-2.0 to the BLM Contract AA550-CT7-44, 171 pp.

National Geographic & Oceana. 2013. Islas Desventuradas: biodiversidad marina y propuesta de conservación. Informe de la expedición "Pristine Seas". Oceana, Santiago, 62 pp.

Navarro, P.G., S. García-Sanz, J.M. Barrio & F. Tuya. 2013. Feeding and movement patterns of the sea cucumber *Holothuria sanctori*. Mar. Biol., 160: 2957-2966.

Ojeda, F. & S. Avilés. 1987. Peces oceánicos chilenos. In: J.C. Castilla (ed.). Islas oceanicas chilenas: conocimiento cientifico y necesidades de investigaciones. Ediciones Universidad Católica de Chile, Santiago, Santiago, pp. 247-270.

Osman, L.P. 2008. Population status, distribution and foraging ecology of *Arctocephalus philippii* (Peters, 1866) at Juan Fernández Archipelago. Ph.D. Dissertation, Universidad Austral de Chile, Valdivia, 106 pp.

Palma, A.T. & F.P. Ojeda. 2002. Abundance, distribution and feeding patterns of a temperate reef fish in subtidal environments of the Chilean coast: the importance of understory algal turf. Rev. Chil. Hist. Nat., 75: 189-200.

Pequeño, G. & J. Lamilla. 2000. The littoral fish assemblage of the Desventuradas Islands (Chile), has zoogeographical affinities with the western Pacific. Global Ecol. Biogeogr., 9: 431-437.

Pequeño, G. & S. Sáez. 2000. Los peces litorales del archipiélago de Juan Fernández (Chile): endemismo y relaciones ictiogeográficas. Invest. Mar., Valparaíso, 28: 27-37.

Pérez-Matus, A., L.A. Ferry-Graham, A. Cea & J.A. Vásquez. 2007. Community structure of temperate reef fishes in kelp dominated subtidal habitats of northern Chile. Mar. Fresh. Res., 58: 1069-1085.

Pérez-Matus, A., F. Ramírez, T.D. Eddy & R. Cole. 2014. Subtidal reef fish and macrobenthic community structure at the temperate Juan Fernández Archi-pelago, Chile. Lat. Am. J. Aquat. Res., 42(4): 814-826.

Phillips, J.C., G.A. Kendric & P.S. Lavery. 1997. A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. Mar. Ecol. Prog. Ser., 153: 125-138.

Pompa, S., P.R. Ehrlichb & G. Ceballosa. 2011. Global distribution and conservation of marine mammals. Proc. Nat. Acad. Sci. USA, 108(33): 13600-13605.

Ramírez, M.E. & C. Osorio. 2000. Patrones de distribución de macroalgas y macroinvertebrados intermareales de la isla Robinson Crusoe, archipiélago de Juan Fernández, Chile. Invest. Mar, Valparaíso, 28: 1-13.

Ramírez, F., A. Pérez-Matus, T.D. Eddy & M.F. Landaeta. 2013. Trophic ecology of abundant reef fish in a remote oceanic island: coupling diet and feeding morphology at the Juan Fernandez Archipelago, Chile. J. Mar. Biol. Assoc. U.K., 93: 1457-1469.

Randall, J. & A. Cea. 2010. Shore fishes of Easter Island. University of Hawai Press, Honolulu, 176 pp.

Reid, D. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region. British Museum (Natural History), London, 228 pp.

Retamal, M. & P. Arana. 2000. Descripción y distribución de cinco crustáceos decápodos recolectados en aguas profundas en torno a las islas Robinson Crusoe y Santa Clara (Archipiélago Juan Fernández, Chile). Invest. Mar., Valparaíso, 28: 149-163.

Rozbaczylo, N. & J.C. Castilla. 1987. Invertebrados marinos del Archipiélago de Juan Fernández. In: J.C. Castilla (ed.). Islas oceánicas chilenas: conocimiento científico y necesidades de investigaciones. Ediciones Universidad Católica de Chile, Santiago, pp. 167-189.

Santelices, B. 1987. Flora marina bentónica de las Islas Oceánicas Chilenas. In: J.C. Castilla (ed.). Islas oceánicas chilenas: conocimiento científico y necesidades de investigaciones. Ediciones Univer-sidad Católica de Chile, Santiago, pp. 101-126.

Sepúlveda, J. 1987. Peces de las islas oceánicas chilenas. In: J.C. Castilla (ed.). Islas Oceanicas Chilenas: conocimiento cientifico y necesidades de investigaciones. Ediciones Universidad Católica de Chile, Santiago, pp. 225-245.

Sierralta, L., R. Serrano, J. Rovira & C. Cortés 2011 Las Áreas Protegidas de Chile: antecedentes, institucionalidad, estadísticas y desafíos. ministerio de medio ambiente, Santiago, 35 pp.

Slater, M.J. & A.G. Jeffs. 2010. Do benthic sediment characteristics explain the distribution of juveniles of the deposit-feeding sea cucumber *Australostichopus mollis*? J. Sea Res., 64(3): 241-249.

Steneck, R.S. & M.N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos, 69: 476-498.

Stuessy, T.F., K.A. Foland, J.F. Sutter, R.W. Sanders & M. Silva. 1984. Botanical and geological significance

of potassium-argon dates from the Juan Fernández Islands. Science, 225(4657): 49-51.

Taylor, R.B., M.A. Morrison & N.T. Shears. 2011. Establishing baselines for recovery in a marine reserve (Poor Knights Islands, New Zealand) using local ecological knowledge. Biol. Conserv., 144(12): 3038-3046.

Tognelli, M.F., M. Fernández & P. Marquet. 2009. Assessing the performance of the exiting and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol. Conserv., 142(12): 3147-3153.

Vega, M.A., F.J. Rocha & C. Osorio. 2007. Resultados preliminares sobre un estudio de los octópodos del Archipiélago Juan Fernández. Cienc. Tecnol. Mar, 30(2): 63-73.

Waldron, A., A.O. Mooers, D.C. Miller, N. Nibbelink, D. Redding, T.S. Kuhn, J.T. Roberts & J.L. Gittleman. 2013. Targeting global conservation funding to limit immediate biodiversity declines. Proc. Nat. Acad. Sci. USA, 110(29): 12144-12148.

Wieters, E.A., A. Medrano & A. Pérez-Matus. 2014. Functional community structure of shallow hard bottom communities at Easter Island, (Rapa Nui). Lat. Am. J. Aquat. Res., 42(4): 827-844.

Willan, R.C., H.G. Spencer, R.G. Creese & S. de C. Cook. 2010. Class Gastropoda. In: S. de C. Cook (ed.). New Zealand coastal marine invertebrates. Canterbury University Press, Christchurch, Vol. 1, 316 pp.

Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy & C. Folke. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787-790.

Zamora, L.N. & A.G. Jeffs. 2012. The ability of the deposit-feeding sea cucumber *Australostichopus mollis* to use natural variation in the biodeposits beneath mussel farms. Aquaculture, 326-329: 116-122.

Appendix 1. List of species and trophic/functional groups found in the study sites. Endemic species of the Juan Fernández Archipelago (JF) and endemic species of the Juan Fernández and Desventuradas Islands (D) are indicated. Asterisk (*) indicated species found in Easter Island.

Group	Taxonomic Group	Species	Functional/Trophic Groups	Presence in the study sites				
				Endemic JF	Endemic JF-D	El Palillo	El Arenal	Tierras Blancas
Algae	Chlorophyta	Chaetomorpha firma	Filamentous			X	X	X
		Cladophora perpusilla	Filamentous			X	X	
		Cladophora sp.	Filamentous				X	
		Codium cerebriforme	Corticated	X		X	X	
		Codium fernandezianum	Corticated	X		X	X	X
		Ulva rigida	Foliose			X	X	
		Ulva sp. 1	Foliose			X	X	X
		Ulva sp. 2	Foliose			X	X	
	Phaeophyceae	Colpomenia sinuosa (*)	Foliose			X	X	X
		Dictyota kunthii	Corticated foliose			X	X	X
		Dictyota phlyctaenodes	Corticated foliose		X	X	X	X
		Distromium skottsbergii	Corticated foliose			X	X	X
		Padina fernandeziana	Corticated foliose	X		X	X	X
		Scytothamnus australis	Corticated			X	X	
	Rhodophyta	Ahnfeltiopsis sp.	Corticated				X	
		Bostrychia intricata	Corticated			X	X	
		Centroceras clavulatum (*)	Corticated			X	X	
		Chondracanthus intermedius	Corticated			X	X	
		Chondriella pusilla	Corticated	X			X	
		Corallina sp.	Articulated calcareous			X	X	
		Delesseriaceae	Corticated			X	X	X
		Gelidium sp.	Corticated			X	X	
		Gelidium sp.1	Corticated			X	X	
		Gelidium sp.2	Corticated			X	X	
		Gigartinaceae	Corticated			X	X	
		Jania rosea	Articulated calcareous			X	X	
		Hymenena decumbens	Foliose			X	X	X
		Liagora brachyclada	Corticated	X		X	X	
		Litophyllum sp.	Crustose			X	X	X
		Polysiphonia sp.	Filamentous			X	X	
		Pterosiphonia sp.	Filamentous			X		
		Crustose	Crustose			X	X	
Invertebrates	Crustacea	Acantharctus delfini	Scavenger		X			
		Amphipoda sp.	Herbivore			X		
		Guinusia chabrus	Scavenger					X
		Jasus frontalis	Carnivore		X	X		X
		Jehlius cirratus	Herbivore			X	X	X

Continuation

Group	Taxonomic Group	Species	Functional/Trophic Groups	Endemic JF	Endemic JF-D	El Palillo	El Arenal	Tierras Blancas
				Presence in the study sites				
	Mollusca	*Leptograpsus variegatus*	Herbivore			X	X	
		Acmaea juanina	Herbivore	X		X	X	
		Aplysia parvula	Herbivore			X		
		Austrolittorina fernandezensis	Herbivore	X		X	X	X
		Concholepas concholepas	Carnivore					X
		Diloma nigerrima	Herbivore			X	X	
		Cellana sp.	Herbivore			X	X	
		Unknow Nudibranch	Carnivore			X		
		Octopus sp.	Carnivore			X	X	X
		Plaxiphora fernandezi	Herbivore	X		X	X	
		Vermetidae sp.	-			X	X	X
		Unknown gasteropod	-			X	X	
	Echinodermata	*Astrostole platei*	Carnivore		X	X	X	X
		Centrostephanus rodgersii	Herbivore			X	X	X
		Heliaster canopus	Carnivore		X	X		
		Holothuria (Mertensiothuria) platei	Detritivore		X	X		
		Parvulastra calcarata	Carnivore	X		X	X	X
	Polychaeta	*Polychaeta sp.*	-			X	X	X
	Porifera	*Porifera indet.*	-			X	X	X
		Parazoanthus sp.	-			X		
	Cnidaria	*Phymactis sp.*	-			X	X	
Fishes	Actinopterygii	*Callanthias platei*	Invertivore		X	X		
		Caprodon longimanus	Planktivore			X	X	X
		Chironemus bicornis	Invertivore		X	X	X	X
		Chironemus delfini	Invertivore	X		X	X	X
		Girella albostriata	Omnivore		X	X	X	X
		*Gymnotorax pophyreus**	Invertivore + Piscivore			X	X	X
		Hypoplectrodes semicinctum	Invertivore			X	X	X
		Lotella fernandeziana	Invertivore + Piscivore		X	X	X	X
		Malapterus reticulatus	Invertivore		X	X	X	X
		Mola mola	Invertivore + Piscivore			X	X	
		Nemadactylus gayi	Invertivore		X	X	X	X
		Odontesthes gracilis	Planktivore	X		X		
		Paralichthys fernandezianus	Invertivore + Piscivore		X	X		
		Parapercis dockinsi	Invertivore	X		X	X	X
		Paratrachichthys fernandezianus	Invertivore		X	X	X	X
		Pseudocaranx chilensis	Invertivore + Piscivore		X	X	X	X
		Pseudolabrus gayi	Invertivore		X	X	X	X
		Scartichthys variolatus	Herbivore		X	X	X	X
		Scorpaena fernandeziana	Invertibore		X	X	X	X
		Scorpis chilensis	Omnivore			X	X	X
		Seriola lalandi	Invertivore + Piscivore		X	X	X	X