Research Article

Subtidal reef fish and macrobenthic community structure at the temperate Juan Fernández Archipelago, Chile

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ABSTRACT. The Juan Fernández Archipelago (33º37'S, 78º51'W), an isolated group of islands 650 km west of continental Chile, has a high degree of endemism in its marine biota. Despite numerous scientific expeditions to these islands that have identified this high endemism, few studies have attempted to identify patterns of community structure in subtidal habitats. Using visual census, we surveyed fish and habitat associations at five sites located at two of the three islands of the archipelago. Given the isolation of the archipelago we asked: What is the composition of the reef fish fauna at these isolated islands? What habitats dominate subtidal environments? What influences the abundances of reef fishes? Our analysis confirms that fish communities at the archipielago are dominated by endemic species. The ichthyofauna is comprised of a mixture of subtropical and temperate taxa, with greater similarity to western than eastern South Pacific fauna. We identified different fish assemblages at wave-exposed and wave-sheltered sites. Brown and red macroalgae were correlated with the abundances of some reef fishes. Four broad trophic categories of reef fishes were present at the archipelago, with invertebrate consumers dominating abundance. To our knowledge, this is the first attempt to quantify patterns of community structure in subtidal environments at the Juan Fernández Archipelago.

Keywords: rocky reefs, fish assemblages, distribution, oceanic islands, Juan Fernández Archipelago, Chile.

Estructura comunitaria del macrobentos y peces costeros submareales del archipiélago Juan Fernández, Chile

RESUMEN. El archipiélago Juan Fernández (33º37'S, 78º51'W), es un grupo de islas situadas a 650 km al oeste de Chile continental, con alto grado de endemismo en su biota marina. A pesar de numerosas expediciones científicas a estas islas que han identificado este alto endemismo, pocos estudios han tratado de identificar los patrones de estructura de la comunidad en hábitats submareales. Mediante censos visuales, se registraron los peces y su asociación con el hábitat en cinco sitios de estudio, en dos de las tres islas del archipiélago. Dado el aislamiento del archipiélago nos preguntamos: ¿Cuál es la composición de la fauna de peces de arrecife en estas aisladas islas? ¿Qué hábitats dominan los ambientes submareales? ¿Qué influye en la abundancia de peces de arrecife? Los análisis realizados sugieren que la comunidad de peces en el archipiélago está dominada por especies endémicas. La ictiofauna se compone de una mezcla de taxa de origen subtropical y templado, con una mayor similitud a las especies del Pacífico occidental que a las del Pacífico suroriental. Se identificaron diferentes ensambles de peces en sitios expuestos y protegidos. Las macroalgas pardas y rojas limitaron la abundancia de algunos peces de arrecife. Cuatro categorías tróficas de peces de arrecife, estuvieron presentes en el archipiélago, siendo los invertívoros los consumidores dominantes. Hasta donde se sabe, este es el primer intento en identificar los patrones de la estructura comunitaria en ambientes submareales en el archipiélago de Juan Fernández.

Palabras clave: arrecifes rocosos, ensamble de peces, distribución, islas oceanicas, Archipiélago Juan Fernández, Chile.

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INTRODUCTION

The decline of marine resources has stimulated the implementation of marine protected areas (MPAs) worldwide (Lubchenco *et al.,* 2003). To maximize the benefits of MPAs and optimize the implementation processes, information on patterns of habitat distribution, species diversity, and abundance are needed (Bellwood *et al.,* 2004; Dalleau *et al.,* 2010). Consequently, conservation planning has primarily focused on representativeness, rarity, and endemism of species (Roberts *et al.,* 2003).

Isolated faunas have been essential for the progress and development of biogeographic and evolutionary theory, due to the relationship between biodiversity, degree of isolation, and endemism (Darwin, 1859; MacArthur & Wilson, 1967; Robertson, 2001). Isolated and endemic faunas offer good opportunities for testing divergent hypotheses such as whether recruitment is independent of reproduction (Sale, 1980) or if there is local replenishment of populations driven by physical (*i.e.,* suitable habitat) (Wolanski & Hamner, 1988) and behavioural (Lecchini *et al.,* 2005) mechanisms.

The Juan Fernández Archipelago (33º37´S, 78º51'W) is a group of three geologically young islands (Robinson Crusoe, Santa Clara, and Alejandro Selkirk), with an estimated age of six million years. These islands are located 650 km west of continental Chile (Stuessy *et al.,* 1984; Haase *et al.,* 2000). Intrigued by the isolation of these islands, Molina (1782) first recorded the fish fauna at Robinson Crusoe, and Mann (1954) first discovered possible relationships of fauna at this islands with other geographic areas. The Juan Fernández Archipelago, Easter, Salas y Gomez, and Desventuradas Islands share more similarities among each another than with continental Chile, despite the shorter geographical distance to Chile (Mann, 1954). According to Briggs (1995), the Indo-Pacific region also includes Easter Island and the Desventuradas Islands, located 750 km north of Juan Fernández. Pequeño & Lamilla (2000) identified clear zoogeographic affinities among the Desventuradas Islands and western geographic areas. Juan Fernández and the Desventuradas Islands share more than 65% of their fish species. Pequeño & Saéz (2000) suggest that for fishes, the region of the west Indo-Pacific could be extended to the Juan Fernández Archipelago.

According to island biogeographic models, immigration to remote islands is slow, and components of the biota result from evolutionary changes; speciation thus increases with isolation and area of the island (MacArthur & Wilson, 1963). As for many isolated islands, the Juan Fernández Archipelago is volcanic in origin, and possesses a high degree of endemism in reef fish species (Dyer & Westneat, 2010). Marine populations are often organized by processes at both large (*e.g.,* recruitment) and small spatial scales (*e.g.,* availability of suitable habitats) (Levin, 1992). The Juan Fernández Archipelago offers the chance to test the influence of local-scale phenomena on subtidal community structure, which has not yet been addressed for these islands. Therefore, we aim to describe a) how assemblages of reef fishes are composed (*i.e.,* what proportion of the fauna is endemic), b) how sessile benthic assemblages are organized, c) if abundances of fish species are correlated with particular substratum species, and more broadly d) how this fish fauna resembles that of other temperate regions.

MATERIALS AND METHODS

Study area

This study was conducted on the rocky reefs surrounding the Juan Fernández Archipelago, Chile (Fig. 1). The Robinson Crusoe and Santa Clara islands, have areas of 47.9 and 2.2 km^2 respectively, and are located closest to the continent. The third island; Alexander Selkirk (33º45'S, 80º45'W), 49 km^2 in area, is located 178 km east of Robinson Crusoe. Our research focused on Robinson Crusoe and Santa Clara islands, due to limited access to Alexander Selkirk island. We selected five study sites around Robinson Crusoe and one at Santa Clara islands, mainly limited by weather conditions at the time of the survey (Fig. 1). We hypothesised *a priori* that community structures would differ based on spatial separation, subtidal habitat, and wave exposure. Our sampling was conducted at three wave-protected and three wave-exposed sites (Fig. 1). In general, wave-protected sites occurred on the northeastern side of Robinson Crusoe Island, where the substratum is characterized by low bottom relief with small boulders, cobbles, and sand. Wave-exposed sites occured on the south-western and north-western sides of Islas Robinson Crusoe and Santa Clara respectively, and were characterized by high bottom relief, with vertical walls, large boulders, and caves.

Survey

All sampling was performed in austral spring (September 15-October 21) 2007. Subsurface water temperature was on average 13.5 ± 0.3ºC and underwater visibility was on average 14.6 ± 1.8 m among sites. At each study site, fish and habitat surveys were conducted between 3-18 m depth, and when possible, all habitat types present in a 40 m transect were quantified (*i.e.,* barrens, macroalgal-dominated bottoms, encrusting, and sessile fauna). The survey methodology for estimating fish abundance and richness
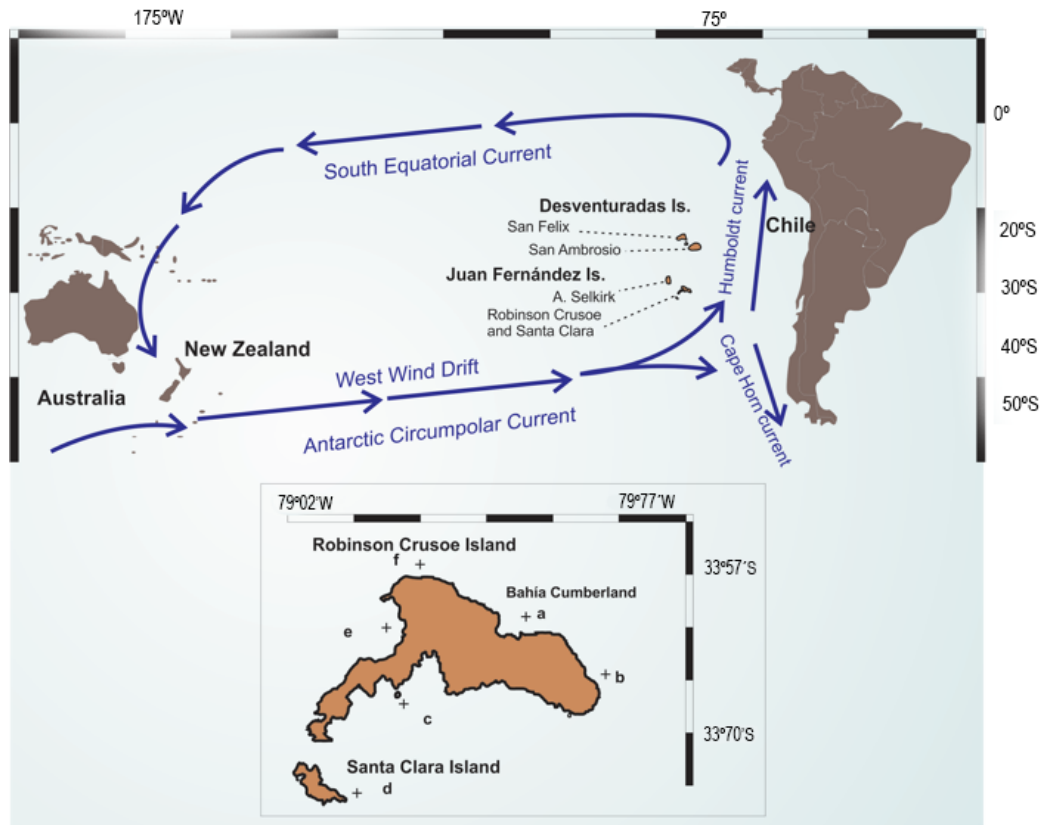
Figure 1. Map indicating the location of the study sites at Robinson Crusoe and Santa Clara islands of Juan Fernández Archipelago (not to scale) and currents in the region in relation to other isolated South Pacific islands. Study sites are: a) Bahía Cumberland, b) El Francés, c) Los Chamelos, d) Punta Freddy, e) Bahía Tres Puntas, and f) Sal si Puedes.

consisted of Underwater Visual Census (UVC) and underwater photography for species identification, while using SCUBA (following Ramírez *et al.,* 2013) to position transects perpendicular to the coastline. A total of 47 (mean = 7.6 per site) transects of 40 m length were used to survey fish around each island. Species identity and abundance of all fishes observed within 5 m of the transect line (2.5 m right and left of the transect) were recorded (total survey area 200 m^2). All fish surveys were conducted by two observers (APM and TDE) between 10:00 and 14:00 h. We compared the results for fish species richness density measured by the two observers using a Kruskal-Wallis rank sum test (Kruskal & Wallis, 1952). Because differences were small (Kruskal-Wallis, df = 1, H = 1.79, *P*-value = 0.182), we combined the data of the two observers.

Percent covers of sessile organisms were obtained using a random point contact (RPC) method. A 50x50 cm quadrat (0.25 m^2) divided into a matrix of 81 equi-spaced intersections was randomly placed at two positions every 10 m along the transect (see above), to record counts of sessile species to the lowest taxonomic level possible. A total of 10 quadrats per transect were surveyed. Unidentified items were collected, stored in buffered formalin (5%), and identified in the laboratory. A total of 22 (mean = 3.1) RPC transects were conducted for this study (10 quadrats per transect). The unbalanced number of transects for fish (47) and percent cover counts (22) was due to logistical constraints.

Trophic groups were generated after Halpern & Floeter (2008), and were based on published dietary information, unpublished data, and visual observations (see Ramírez *et al.,* 2013). Fishes were categorized into one of the following four trophic groups: 1) herbivores (browsers, macroalgal eaters, scrapers, territorial herbivores, and algal turf eaters), 2) planktivores, 3) macroinvertivores, and 4) piscivores.

Data analysis

Fish and sessile organism data were compiled into abundance by site matrices for fish and sessile organisms to calculate similarity among sites. We conducted non-metric, one-way pairwise Analysis of Similarity Among groups (ANOSIM; Clarke & Warwick, 1994) and a similarity percentages analysis

(SIMPER) to identify species that contributed most to observed similarities (or differences) in fish assemblages, by site. Since SIMPER does not indicate statistical significance, we tested significance of the discriminating species using canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003). The *P*-values for site effects were obtained using 999 permutations of the observed data. To visualize differences and clustering of data among study sites, we used non-metric multidimensional scaling (MDS; Clarke, 1993). Because of the large number of fish transects, we used the centroids obtained from the principal coordinate analysis (following Terlizzi *et al.,* 2005). To assess how much of the variation in fish abundance and benthic cover was explained by depth, the relationship between multivariate species data and the factor "depth" was analysed using non-parametric multivariate regression with distance-based linear models "DISTLM" (McArdle & Anderson, 2001).

We performed a redundancy analysis (RDA) of the abundant species for each fish assemblage against major substratum species. We selected this constrained method due to our *a priori* hypothesis of the possible effects of substratum on abundances of reef fishes. To test for associations among fish abundances and substratum species, we performed the permutational analysis of variance (PERMANOVA) routine among sites (Legendre & Legendre, 1998). We used the Hellinger transformation of the fish and point-count data; this transformation makes the data amenable for the types of analyses performed here (see Legendre & Gallaher, 2001 for details). We used RDA to graphically display the differences of the most abundant species among the study sites, and report the contribution of each parameter. All analyses were conducted using the R package 'vegan' (http://www.r-project.org/).

RESULTS

Our fish surveys documented a total of 26 species, representing 23 genera, 18 families, 6 orders, and 1 class (Table 1). Of the 26 fish species observed, 16 were present in low abundance (less than 1 individual) (Table 1). 12% of observed fish species were endemic to the archipelago (Table 2). 85% of observed fish species also occur at the Desventuradas Islands (Table 2). Less than 25% of the surveyed fish species occur frequently within the Pacific region (Table 2). Species present at other geographic areas included: *Seriola lalandi*, *Caprodon longimanus*, *Trachurus murphyi*, *Mola mola*. Only 19.2% of the fish species we observed are also common in continental Chile, Australia or New Zealand. A slightly higher proportion (~30%) of species are shared with Easter Island (Table 2).

Labridae (wrasses) comprised nearly 50% of the total abundance of the reef fish assemblage (Fig. 2). The next most abundant family of fishes was Kyphosidae (accounting for 18% of total abundance), followed by Carangidae and Serranidae, each comprised 10% of the total abundance. Blennioid fishes accounted for less than 4% of total abundance (Fig. 2). The most abundant and frequently observed species were: *Pseudolabrus gayi* and *Malapterus reticulatus* (Labridae), followed by *Scorpis chilensis*, *Pseudocaranx chilensis*, and the serranids *Caprodon longimanus* and *Hypoplectrodes semicinctum* (Table 1).

Sites differed in total fish species abundance and richness. Variation in reef fish assemblages was globally significant among sites (ANOSIM, R = 0.25, *P*-value = 0.001). This pattern was further confirmed by the CAP analysis (df = 5, F = 2.39, *P*-value = 0.005). The nMDS plot identified three main clusters: 1) Bahía Cumberland and Sal si Puedes (which are nearly identical), 2) wave-exposed sites Los Chamelos and Bahía Tres Puntas, and 3) El Francés and Punta Freedy, which do not form a tight cluster (Fig. 3a). Several fish species were identified by the SIMPER analysis as contributing to these differences among sites. The wrasses *Malapterus reticulatus* and *Pseudolabrus gayi* contributed to more than 60% of similarity among sites. The serranid *Hypoplectrodes semicintum*, and the wrasses (*M. reticulatus* and *P. gayi*), contributed to more than 70% of the numerical abundance for the assemblage at Bahía Cumberland, El Francés, and Sal si Puedes. According to the SIMPER analysis, these discriminating species contributed more than 50% of similarities. Other species such as *Caprodon longimanus*, *Scartichthys variolatus*, and *Scorpis chilensis* were also abundant at Los Chamelos, Punta Freddy, and Bahía Tres Puntas respectively, and their contribution to the similarities were approximately 30%. The random point contact counts revealed differences in benthic invertebrates and algae species abundances among sampling sites (ANOSIM, R = 0.50, *P*-value = 0.001), confirmed by CAP analysis (CAP, df = 5, F = 4.26, *P*-value = 0.005). With the exception of Bahía Tres Puntas, which shared similarities in abundances of substratum species with all other sites, two clusters were observed. One cluster is composed of the wave-exposed sites (on the right side of the biplots), while the other is composed of the wave-protected sites (left side of the biplots) (Fig. 3). The wave sheleterd sites; Bahía Cumberland and El Francés, clustered together (Fig. 3b). Generally, macroalgae dominated the substratum at all sampled depths at our wave-protected sites. Species such as *Dictyota* spp. dominated benthic cover at Bahía Cumberland, El Francés, Bahía Tres Puntas, and Sal si Puedes (Fig. 4). Rhodophyta (turfing red algae),

Table 1. Mean (±SD) abundance per 200 m^2 and trophic category of all the species recorded at the six sites at Juan Fernández. N: number transects (40 m transects covering an area of 200 m^2) sampled per site.

Family	Species	Trophic category	Bahía Cumberland N=8	El Francés N=8	Los Chamelos N=3	Punta Freddy N=10	Bahía Tres Puntas N=9	Sal si Puedes N=8
Molidae	Mola mola	Invertivore	-	-	-	0.1 ± 0.3	-	-
Paralichtyidae	Paralichthys fernandezianus	Invertivore	-	-	-	0.1 ± 0.3	-	0.1 ± 0.4
Chaetodontidae	Amphichaetodon melbae	Omnivore	0.4 ± 1.1	0.1 ± 0.35	-	1.2 ± 1.9	0.3 ± 0.5	1.3 ± 1.5
Callanthiidae	Callanthias platei	Invertivore	-	0.1 ± 0.35	2.7 ± 4.6	-	-	-
Serranidae	Caprodon longimanus	Planktivore	29.9 ± 64.9	73.9 ± 119.09	153.0 ± 66.8	14.0 ± 35.0	32.0 ± 38.4	27.9 ± 58.0
	Hypoplectrodes semicinctum	Invertivore	17.1 ± 8.0	14.4 ± 6.30	3.3 ± 1.5	9.6 ± 9.8	13.4 ± 10.4	12.9 ± 5.0
Chironemidae	Chironemus bicornis	Invertivore	0.1 ± 0.4	0.9 ± 1.24	-	-	0.25 ± 0.7	-
	Chironemus delfini	Invertivore	-	0.4 ± 0.74	-	-	0.1 ± 0.4	-
Kyphosidae	Girella albostriata	Omnivore	-	3.1 ± 3.48	7.0 ± 9.5	2.4 ± 1.9	4.4 ± 6.0	4.1 ± 9.0
	Scorpis chilensis	Omnivore	45.7 ± 30.3	80.3 ± 45.27	20.0 ± 23.3	57.7 ± 56.2	123.6 ± 49.1	65.9 ± 54.2
Labridae	Malapterus reticulatus	Invertivore	54.4 ± 3.2	95.0 ± 20.63	55.3 ± 21.1	88.2 ± 34.2	77.4 ± 33.8	77.4 ± 23.7
	Pseudolabrus gayi	Invertivore	141.9 ± 81.1	84.5 ± 46.48	90.0 ± 41.9	115.6 ± 46.8	136.8 ± 46.0	77.9 ± 34.5
Cheilodactylidae	Nemadactylus gayi	Invertivore	6.7 ± 13.6	5.4 ± 5.70	9.0 ± 14.7	0.2 ± 0.6	0.5 ± 0.9	3.7 ± 7.4
Pinguipedidae	Parapercis dockinsi	Invertivore	6.4 ± 9.7	0.8 ± 1.48	-	-	-	0.9 ± 1.5
Gobiidae	Paratrimma nigrimenta	Invertivore	-	-	-	1.1 ± 3.5	-	-
Carangidae	Pseudocaranx chilensis	Invertivore	5.7 ± 8.1	107.2 ± 81.92	16.7 ± 8.9	6.2 ± 11.6	44.5 ± 69.0	62.8 ± 56.5
	Seriola lalandi	Invertivore	-	0.1 ± 0.35	1.0 ± 1.7	0.1 ± 0.3	0.1 ± 0.4	3.5 ± 9.5
	Trachurus murphyi	Invertivore	-	33.9 ± 52.94	9.0 ± 15.6	-	0.1 ± 0.4	0.3 ± 0.7
Blenniidae	Scartichthys variolatus	Herbivore	6.9 ± 5.1	11.6 ± 5.39	1.7 ± 2.1	29.0 ± 22.1	13.3 ± 5.5	12.5 ± 7.2
	Scartichthys viridis	Herbivore	-	-	-	-	0.9 ± 1.8	-
Sciaenidae	Umbrina reedi	Omnivore	-	-	-	-	-	0.1 ± 0.4
Scorpaenidae	Scorpaena fernandeziana	Invertivore	0.3 ± 0.5	0.3 ± 0.46	0.3 ± 0.6	2.0 ± 5.6	-	0.3 ± 0.5
	Scorpaena thomsoni	Invertivore	0.1 ± 0.4	-	-	1.4 ± 1.6	0.3 ± 0.5	-
Moridae	Lotella fernandeziana	Invertivore	0.1 ± 0.4	4.1 ± 7.35	0.3 ± 0.6	-	1.8 ± 4.2	1.0 ± 1.8
Trachichthyidae	Paratrachichthys fernandezianus	Invertivore	0.5 ± 0.8	1.5 ± 2.13	-	-	0.4 ± 1.1	6.0 ± 10.5
Muraenidae	Gymnothorax porphyreus	Invertivore	0.3 ± 0.5	0.5 ± 0.53	2.0 ± 1.0	5.7 ± 5.1	0.1 ± 0.4	0.3 ± 0.7
Total Abundance (n)			316.5 ± 103.5	518.5 ± 140.0	371.6 ± 122.2	335.2 ± 78.7	450.4 ± 123.4	358.6 ± 109.3
Total Richness (S)			8.4 ± 2.5	12.0 ± 1.1	10.7 ± 2.1	9.5 ± 1.4	9.6 ± 1.7	9.9 ± 1.9

Table 2. Occurrences of subtidal fish species at Juan Fernández in relation to other regions of the South Pacific. Easter Island encompasses Salas y Gómez Island; New Zealand includes the Kermadec Islands, and South Pacific region includes Galápagos Islands. PE: Perú, LH: Lord Howe. Adapted from (Pequeño & Sáez, 2000).

	Endemic	Desventuradas	Easter Island	Chile	New Zealand	Australia	South-Pacific
Mola mola		+	+	+	+	+	+
Paralichthys fernandezianus		+					
Amphichaetodon melbae		+	+				
Callanthias platei		+					
Caprodon longimanus		+	+		+	+	+
Hypoplectrodes semicinctum		+	+				
Chironemus bicornis		+					
Chironemus delfini	+						
Girella albostriata		+					
Scorpis chilensis		+					
Malapterus reticulatus		+					
Pseudolabrus gayi		+					
Nemadactylus gayi		+					
Parapercis dockinsi	+						
Paratrimma nigrimenta	+						
Pseudocaranx chilensis		+					
Seriola lalandi		+	+	+	+	+	+
Trachurus murphyi		+	+	+	+	+	+
Scartichthys variolatus		+					
Scartichthys viridis				+			PE
Umbrina reedi		+					
Scorpaena fernandeziana		+					
Scorpaena thomsoni		+					
Lotella fernandeziana		+					
Paratrachichthys fernandezianus		+					
Gymnothorax porphyreus		+	+	+	+	+	PE, LH
Total (%)	12	85	27	23.1	19.2	19.2	23,1

were also abundant at shallow depths (4-8 m) at these sites (Fig. 4). Benthic cover of sessile fauna was high at wave-exposed sites, and at greater depths (10-22 m) at wave-protected sites. Cnidarians (*e.g.*, *Parazoanthus juanfernandezi* and *Corynactis* spp.) and barnacles (*e.g.*, *Austromegabalanus psittacus* and *Balanus psittacus*) dominated the subtratum at los Chamelos and Punta Freddy (Fig. 4). Vermetid molluscs (*Serpulorbis* sp.) were abundant on benthic substrata at El Francés, Punta Freedy, Bahía Tres Puntas, and Sal si Puedes (Fig. 4). Differences among sites are displayed in the multivariate biplots (Fig. 3). According to SIMPER analysis, species responsible for the cluster in the wave-protected sites were *Padina* spp., *Colpomenia* spp., and *Dictyota* spp., collectively contributing to more than 80% of the similarity. The vermetid, *Serpulorbis* sp. and cnidarians contributed to similarities of more than 50% among wave-exposed sites.

Depth explained a small amount of observed patterns in fish, benthic substratum species, and overall reef community structure. Only 9% of the total variation in reef fish abundance was explained by depth (DISTLM, F = 6.63, *P*-value = 0.001). Depth explained 15% of variation in substratum species (DISTLM, F = 11.76, *P*-value = 0.001) and 11% of the total variation in reef communities (*i.e.*, fishes and benthic species combined; DISTLM, F = 8.24, *P*-value = 0.001), indicating that depth alone is not sufficient to explain observed variation.

Among sites, different subsets of fish species were associated with different subsets of substratum species. Redundancy analysis (RDA) and permutation tests revealed associations between substratum species and fish species in our study sites at the Juan Fernández Archipelago (pseudo F = 1.93; *P*-value = 0.035). For example, when present, brown macroalgae such as *Dictyota* spp. and a cluster of red algal species such as crustose coralline algae and turfing algae, contributed to observed associations with reef fishes (*Dictyota* spp.; pseudo F = 1.71, *P*-value = 0.04 and Rhodophyta; pseudo
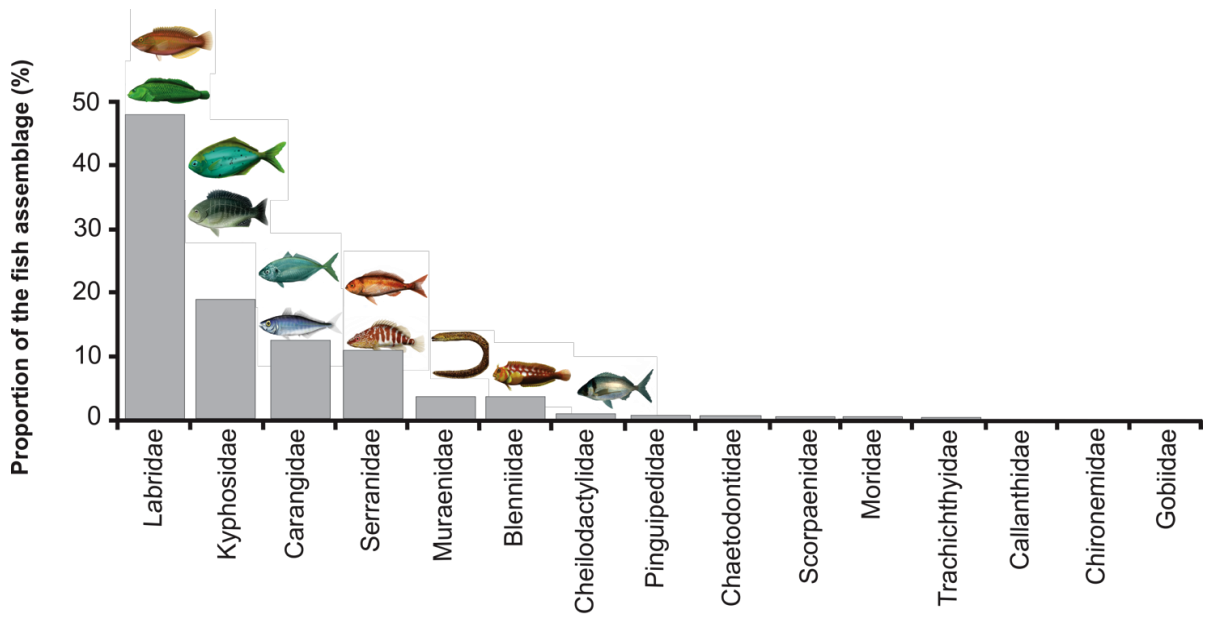
Figure 2. Percent contribution by abundance of observed fish species summed to family level and pooled across all sites.
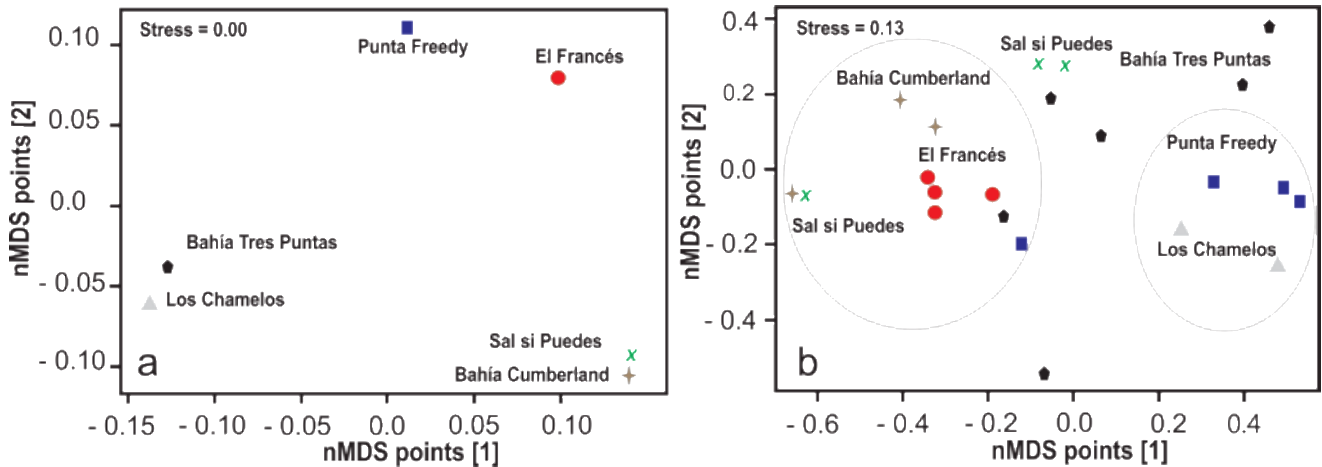

Figure 3. Unconstrained nMDS ordination plot of a) centroids of fish assemblages per site (refer to methods for details), and b) cover of substratum species by transect per site.

F = 2.09, *P*-value = 0.02). Substratum explained 82, 41, 100, 43, 48, and 99% of the variation in total fish abundance at Bahía Cumberland, El Francés, Los Chamelos, Punta Freedy, Bahía Tres Puntas, and Sal si Puedes, respectively. Graphically, macroalgae were grouped in the first two quadrants of the biplot, whereas encrusting and sessile fauna were found in the lower quadrants (Fig. 5). Similarly, the fish assemblage of the most abundant species among sites were dispersed over the biplot, suggesting differential substratum associations (Fig. 5). *Nemadactylus gayi* and *Trachurus murphyi* did not show a particular association with any substatum variable. A weak association was evident

between *Pseudolabrus gayi* and cirripedians (Fig. 5). *Scartichthys variolatus* was more associated with red and green algae, as was *Scorpis chilensis*, whereas *Malapterus reticulatus* was associated with red algae (Fig. 5). Brown macroalgae occurred in the right upper corner of the biplot and fishes such as *Hypoplectrodes semicinctum* and *Psudocaranx chilensis* were associated with *Padina* spp. and *Dictyota* spp. (Fig. 5). In the lower quadrants of the biplots, *Gymnothorax porphyreus* was associated with sponges while *Girella albostriata* was more associated with cnidarians. *Caprodon longimanus* showed a tendency for association with vermetid molluscs (Fig. 5).
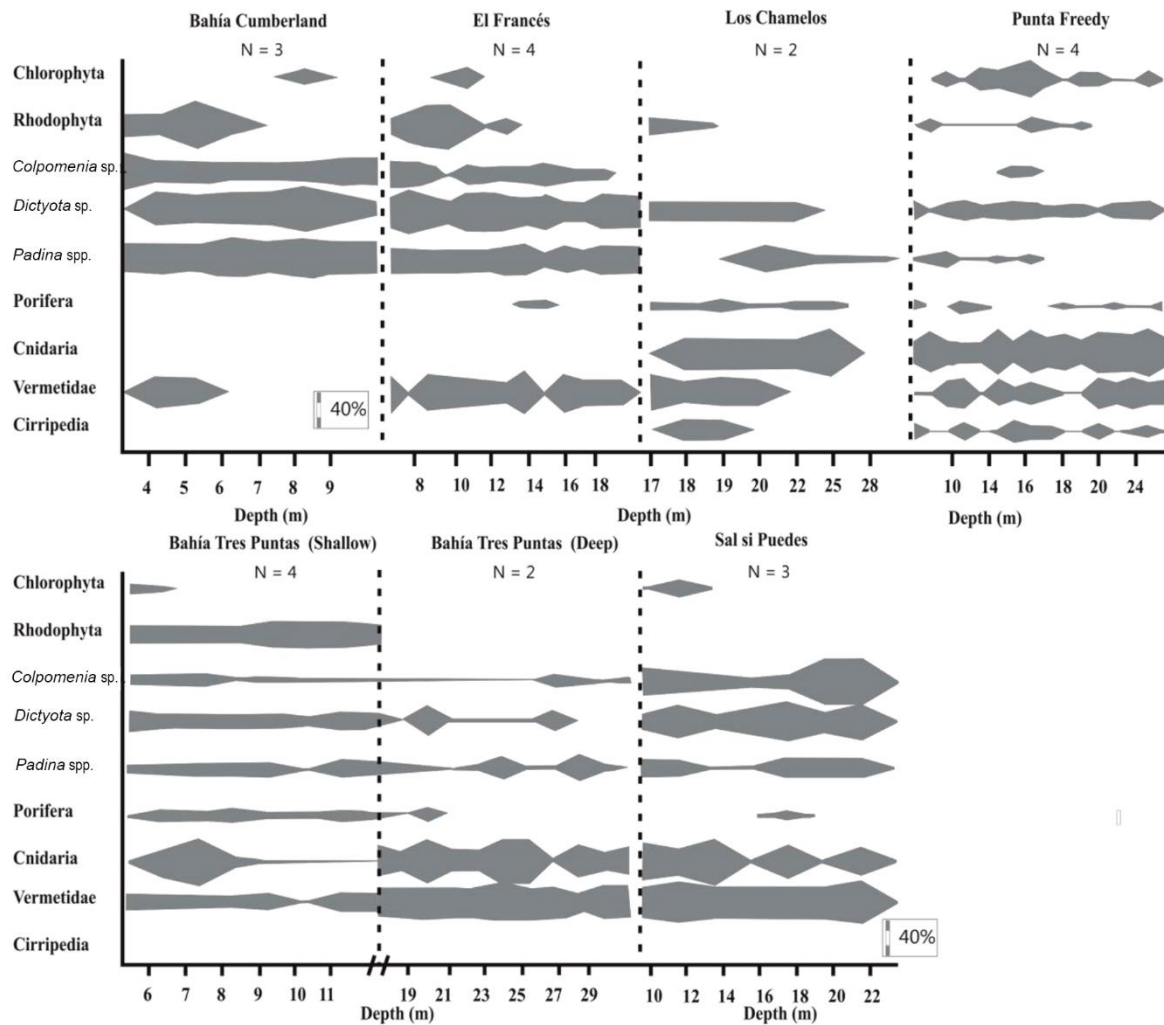
Figure 4. Kite diagrams of showing depth zonation of benthic sessile taxa at the six study sites. Scale bar represents 40% of cover in 0.25 m². Number of transects (N) are given per site.

A total of four trophic groups were present at the study sites. The invertivore group was numerous in terms of numbers of species, with a mean of 13.3 ± 1.8 individuals per site, following by omnivores, (mean of 2.8 ± 0.7), herbivores (1.2 ± 0.4), and planktivores representative (Table 1). The serranid, *Caprodon longimanus,* drives the planktivores as the most abundant trophic group but its distribution within the island is very limited. Omnivores were the trophic group with second highest number of individuals among study sites (mean of 29 ± 2.5), followed by invertivores (mean of 22.1 ± 3.4), and herbivores (mean of 11.5 ± 9.4) (Table 1).

DISCUSSION

Reef fish assemblages at Juan Fernández are dominated by a few species, most of which are endemic to the biogeographic province of the Juan Fernández and Desventuradas archipelagos (see Dyer & Westneat, 2010). Within Juan Fernández, the substratum is dominated by foliose brown and red macroalgae at protected sites; while at exposed sites, sessile species (*i.e.,* cnidarians, vermetids, barnacles) structure the substratum. These habitats explained the composition of fishes at our study sites, principally driven by differences in the composition of substratum species and architectural complexity, rather than changes in abiotic factors such as depth. With the exception of the planktivore *Caprodon longimanus*, most reef fishes from Juan Fernández are characterized as benthic invertebrate eaters, while omnivores are also important in number of species as well as numerical abundance.

The reef fish fauna in Juan Fernández more closely resembles regions from the southern and western Pacific such as New Zealand and Australia, than continental Chile. Labrids (two species) and kyphosids
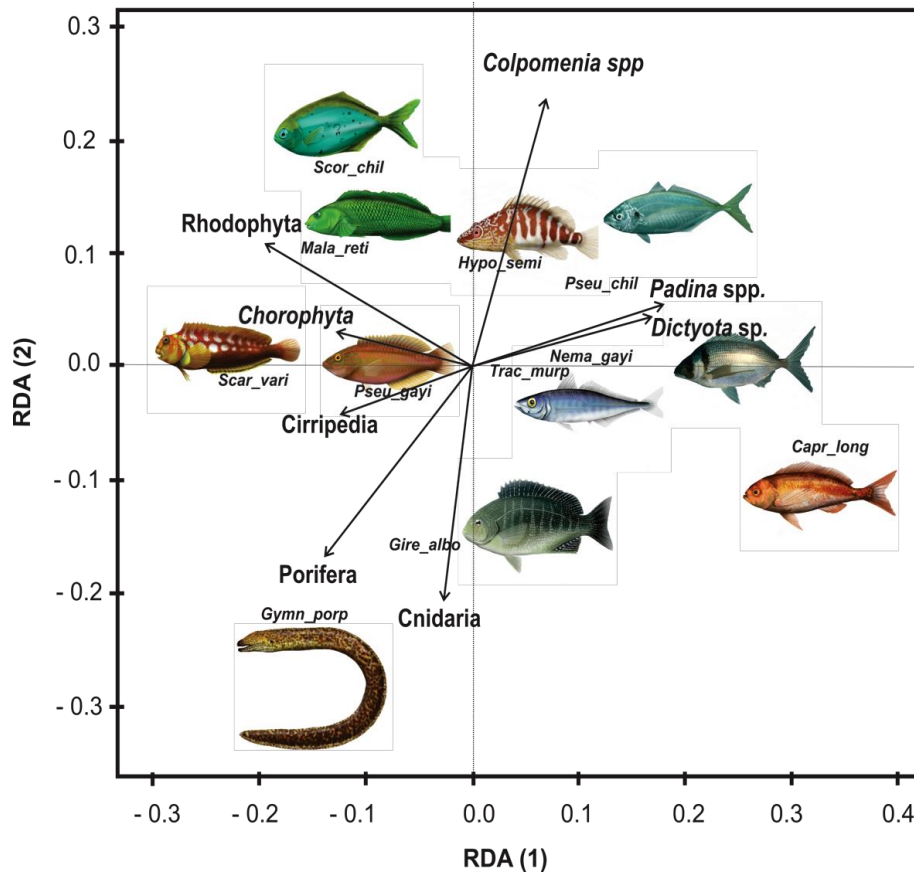
Figure 5. Redundancy Analysis (RDA) ordination plots of the most abundant fish species at sampled sites. Vectors represent benthic substratum species cover and centroids of fish species abundance. The lengths of vectors represent the variability and association for each fish species. Fish species names were formed using the first four letters of their genus and species.

(two species) composed more than 70% of fish species abundance at the Juan Fernández Archipelago. In northern (~18-30ºS) Chile (only 650 km east of our study sites), pomacentrids, haemulids, and cheilodactylids dominate the fish assemblages (Angel & Ojeda, 2001; Pérez-Matus *et al.,* 2007), and similar families dominate the Peruvian coasts (~12ºS) (Gárate & Pacheco, 2004), while nototothenids dominate the southern Chilean (~50ºS) fish faunas (Moreno & Jara, 1984). At the Galápagos Archipelago (Jennings *et al.,* 1994), three western Pacific temperate families (Pomacentridae, Labridae, and Serranidae) dominate the assemblages, although biogeographical differences occur within the archipelago (Edgar *et al.,* 2004).

In western temperate Pacific regions such as western Australia, three families dominate the fish assemblages (Labridae, Kyphosidae, and Carangidae) (Tuya *et al.,* 2011), similar to the Juan Fernández Archipelago. Similar conditions of the proportion of fish assemblages occur at the Poor Knights Islands (North Island of New Zealand), where the most

important families in terms of numerical abundance are: Pomacentridae (three species), Tripterygidae (eight species), and Labridae (Francis, 2001) followed by Kyphosidae and Carangidae with two species each (Taylor *et al.,* 2011). At the Kermadec Islands (31º21′S, 178º48′W-29º15′S, 177º55′W), kyphosids, pomacentrids, and labrids dominate the assemblage, and these islands are known for their components of both subtropical and temperate faunas (Schiel *et al.,* 1986; Francis *et al.,* 1987; Francis, 1996; Eddy, 2011). Four families are found in similar proportions in the northern New Zealand fish assemblages; Carangidae and Labridae with three species, accounting for more than 40% of the composition of the fish assemblages abundance, followed by Kyphosidae, Triplefins (six species), and Mullidae (one species), which altogether account for 20% of reef fish abundance (Anderson & Millar, 2004; Williams *et al.,* 2008). The fish fauna in the south of New Zealand, is more dominated by wrasses, particularly *Notolabrus celidotus*. In the south of New Zealand's North Island, similarly to Juan

Fernández, wrasses (three species) dominate the assemblage, accounting for more than 45% of the total abundance, followed by Serranidae (two species), Odacidae (one species), and Tripterigiidae (seven species) (Choat & Ayling, 1987; Francis, 1996; Anderson & Millar, 2004; Williams *et al.,* 2008).

The arrival of eggs and larvae or juveniles at Juan Fernández Archipelago via rafting, surface currents or other possible mechanisms of transport from distant areas deserves further research. For example, Burridge *et al.* (2006) identified a possible route of colonization via seamounts. These seamounts might connect western faunas, and this can be illustrated by the network of seamounts in the South Pacific. Rojas & Pequeño (1998) put forward an explanation for the distribution and colonization of serranids (*e.g., H. semicinctum, C. longimanus*) in the Juan Fernández Archipelago, arguing that dispersal capabilities depend on the abilities of larvae to use water masses. Some species use the Equatorial Counter Current (ECC) and the Equatorial submerged current (ESC) that drift from west to east, to colonize tropical areas (Clarke, 1995). The importance of currents and water masses is that the chemical, physical, and thermal conditions are stable, favouring the transport of larvae, and thus facilitating colonization from western Indo-Pacific regions to southeastern Pacific areas, such as the Juan Fernández Archipelago (Briggs, 1961; Clarke, 1995; Rojas & Pequeño, 1998).

The most abundant fish species in this study were either species endemic to Juan Fernández or shared with Desventuradas Islands. Presence-absence data reported more endemic species than our surveys (see Pequeño & Sáez, 2000). Presence-absence data may be problematic for ecological studies, as they assign equal weights to all species (Francis *et al.,* 1987; De Martini & Friedlander, 2004). The higher abundance of endemic species in the study suggests self-replenishment (see Swearer *et al.,* 2002, for a review) within these archipelagos. Endemism is frequent across the Eastern Pacific Islands and Central Atlantic (Robertson, 2001; De Martini & Friedlander, 2004). Life history characteristics may differ among endemic and non-endemic species. De Martini & Friedlander (2004) found that for endemic pomacentrids, larval duration was considerably shorter than for non-endemic species, though this is countered by studies of wrasses (Cowen & Sponaugle, 1997). However according to Victor & Wellington (2000), larval duration is not often correlated with species' geographic range. Life history characteristics and adaptations that may facilitate self-recruitment include developmental modes that reduce passive dispersal and improve active control over dispersal during larval stages, increased

reproductive capacity (larger size, early maturation), and increased spawning synchrony and aggregation (Swearer *et al.,* 2002). A comparison between the early life history characteristics of endemic and non-endemic species at the Juan Fernández Islands warrants further research.

We detected important habitat associations for reef fishes at the Juan Fernández Archipelago. The influence of tropical faunas in the temperate islands is principally due to a coral reef component of the benthic substratum (*e.g.,* in Kermadec Islands, Gardner *et al.,* 2006). Although we did not find coral reefs in our surveys, components of tropical fish fauna were present (*e.g.,* Serranidae, Chaetodontidae). In the absence of corals and large brown macroalgae, other substratum species influence reef-associated fishes, especially *Dictyota* spp. This macroalgae has a widespread distribution in the Pacific Ocean and can be a dominant species in both tropical and temperate regions (Clerck *et al.,* 2006). The ability of *Dictyota* to deter herbivores (Clerck *et al.,* 2006) may explain the high abundance of this genus at our study sites. Additionally benthic algae may host numerous amphipods, isopods and gastropods, providing a trophic link to predatory fishes (Pérez-Matus *et al.,* 2007). As with many coastal reef fish assemblages, invertebrate consumers of this epifauna dominate the fish assemblage at Juan Fernández.

The other taxon that covered much of the substratum at Juan Fernández is vermetid molluscs. They form reefs and add structural complexity to subtidal environments. On temperate Mediterranean reefs, the fish fauna associated with vermetid molluscs is distinct from that associated with other substratum species (Consoli *et al.,* 2008), a pattern similar to our findings. Further manipulative studies are required to understand to what extent these habitats influence the distribution of fishes and other organisms, and what kinds of "services" (niche requirements) they provide for reef fishes.

To our knowledge, the present study is the first attempt to quantify patterns of reef fish and macrobenthic community structure in Juan Fernández Archipelago. This is of particular interest for the conservation and management of oceanic islands (Yáñez *et al.*, 2009). Despite recent advances towards sustainable fisheries (*e.g.*, crustacean fisheries) within Juan Fernández Archipelago (P. Manríquez *pers. comm.*), diverse fish are increasingly caught as bait for the lobster fishery (Arana & Ziller, 1985; Ernst, 2013) highlighting the need for broad, community-based resource management. Moreover, more information regarding the ecological role of seamounts in the

connectivity, dispersal and rates of recolonization and recovery of reef fish is needed.

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