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1 **Biogeographic patterns in the cartilaginous fauna (Pisces: Elasmobranchii and**  
2 **Holocephali) in the southeast Pacific Ocean**

3

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9

10 **Running title:** Biogeographic patterns of Chilean cartilaginous fishes

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14

15 **Abstract**

16 The abundance and species richness of the cartilaginous fish community of the  
17 continental shelf and slope off central Chile is described, based on fishery-independent trawl  
18 tows made in 2006 and 2007. A total of 194,705 specimens comprising 20 species (9 sharks,  
19 10 skates, 1 chimaera) were caught at depths of 100 – 500 m along a 1,000 km transect  
20 between 29.5° S and 39° S. Sample site locations were grouped to represent eight  
21 geographical zones within this latitudinal range. Species richness fluctuated from 1 to 6  
22 species per zone. There was no significant latitudinal trend for sharks, but skates showed an  
23 increased species richness with increasing latitude. Standardised catch per unit effort  
24 increased with increasing depth for sharks, but not for skates, but the observed trend for  
25 increasing CPUE with latitude was not significant for either sharks or skates. A change in  
26 community composition occurred along the depth gradient with the skates, *Psammobatis*  
27 *rudis*, *Zearaja chilensis* and *Dipturus trachyderma* dominating communities between 100 and  
28 300 m, but small-sized, deep-water dogfishes, such as *Centroscyllium* spp. dominated the  
29 catch between 300 and 500 m. Cluster and ordination analysis identified one widespread  
30 assemblage, grouping 58% of sites, and three shallow-water assemblages. Assemblages with  
31 low diversity (coldspots) coincided with highly productive fishing grounds for demersal  
32 crustaceans and bony fishes. The community distribution suggested that the differences  
33 between assemblages may be due to compensatory changes in mesopredator species  
34 abundance, as a consequence of continuous and unselective species removal. Distribution  
35 patterns and the quantitative assessment of sharks, skates and chimaeras presented here  
36 complement extant biogeographic knowledge and further the understanding of deep-water  
37 ecosystem dynamics in relation to fishing activity in the south-east Pacific Ocean.

38

## 39 **Introduction**

40

41 Cartilaginous fishes have an important role as top predators and have complex  
42 distribution patterns (Wetherbee & Cortés, 2004), affecting the structure and function of  
43 marine communities through interactions with other trophic links in food webs to which they  
44 belong (Ferretti et al., 2010). Spatial distribution patterns of marine fishes in the south-east  
45 Pacific Ocean are poorly understood, and most studies of demersal communities have focused  
46 on the ecology of continental shelf fauna at depths of between 20 and 150 m (Brattström &  
47 Johanssen, 1983; Ojeda, 1983; Carrasco, 1997; Ojeda, Labra & Muñoz, 2000; Camus, 2001;  
48 Sellanes, 2007). Descriptions of geographical patterns of marine fishes have been restricted to  
49 littoral species (Mann, 1954; Pequeño, Rucabado & Lloris, 1990), and based on regional  
50 inventories (Ojeda, Labra & Muñoz, 2000). A general lack of quantification of species'  
51 abundance limits our understanding of the functional biodiversity of the continental shelf of  
52 Chile (Pequeño, 1989; Bustamante, Vargas-Caro & Bennett, *in press*).

53 Chile has a cartilaginous fish fauna that is relatively rich when compared with warm-  
54 temperate countries in South America (Bustamante, Vargas-Caro & Bennett, *in press*), but  
55 poor in the global context despite having one of the largest maritime territories in the world  
56 (Cubillos, 2005). Species checklists and biological observations constitute the first approaches  
57 in the study of the cartilaginous fish fauna in the Chilean marine ecosystem and there are a  
58 number of studies that have reported on elasmobranch species around the central and southern  
59 continental shelf, from both dependent and independent fishery surveys (Meléndez &  
60 Meneses, 1989; Pequeño, 1989; Pequeño, Rucabado & Lloris, 1990; Pequeño & Lamilla,  
61 1993). In northern Chile, bycatch analysis of the crustacean trawl fishery has contributed to  
62 knowledge of the continental slope ecosystem through the description of biological diversity,  
63 composition and structure of the demersal fish fauna over a wide depth range (Sielfeld &

64 Vargas, 1999; Acuña et al., 2005; Menares & Sepúlveda, 2005). While fishery-dependent  
65 studies a description of diversity and species assemblages of cartilaginous fishes, using catch  
66 per unit effort (CPUE) as a proxy for abundance (Acuña et al., 2005), they generally lack the  
67 ability to adequately identify or provide quantitative information on species richness,  
68 abundance hotspots and conspecific assemblages that are required for a better understanding  
69 of marine ecosystem interrelationships (Kyne & Simpfendorfer, 2007).

70 The aim of the present study is to analyse abundance and species richness of  
71 cartilaginous fishes of the continental shelf and slope in Chile to identify patterns in the  
72 geographical and bathymetric distribution of sharks, skates and chimaeras in the south-east  
73 Pacific Ocean to complement existing biogeographic models, and improve the understanding  
74 of deep-water ecosystem dynamics in the context of fishing activities.

## 77 **Material and Methods**

78  
79 Data were collected through direct observation of total catch on fishery-independent  
80 surveys made along the Chilean continental slope and shelf as part of a broader project to  
81 assess the biological and oceanographical characteristics of the Chilean seafloor (Melo et al.,  
82 2007). Surveys were carried out on-board two fishing vessels, PAM “Crusoe I” and PAM  
83 “Lonquimay”, equipped as oceanographic research platforms. Fishing gear comprised a 3 mm  
84 diameter polyamide nylon bottom trawl, 50 mm stretch-measure diamond-mesh in the tunnel  
85 and cod-end. The trawl had a 24 m headrope, a 28 m footrope, and a stretched circumference  
86 of 34 m with an average net opening during tows of 11 m. Tows lasted 18 – 53 min at a speed  
87 of 3.7 km h<sup>-1</sup> which resulted in an average swept area of 12.2 – 35.9 km<sup>2</sup>. Geometric  
88 construction of fishing gear and tow speed were used to calculate CPUE which was

89 standardised as individuals per hour and square kilometre ( $\text{ind km}^{-2} \text{h}^{-1}$ ). For each species,  
90 CPUE data were calculated separately and log-transformed ( $\text{Log CPUE}+1$ ) in order to assess  
91 the departure of original data from normality. Geographic coordinates and depth of each trawl  
92 were recorded for each tow.

93 A total of 128 tows were made in eight regions, numbered from north to south as  
94 zones 1 to 8, that span approximately 1,000 km between the latitudes  $29.5^\circ \text{ S}$  and  $39^\circ \text{ S}$ .  
95 Survey data were collected from four depth strata (100 – 199 m, 200 – 299 m, 300 – 399 m  
96 and 400 – 499 m) for each of four pseudoreplica sites in each zone (Fig. 1). Zones 1, 2, 4 and  
97 5 were sampled in July/August 2006, zones 6, 7 and 8 in November/December 2006, and  
98 zone 3 was sampled twice, in July 2006 and again in March 2007.

99 This study was carried out in accordance with the “standards for the use of animals in  
100 research” approved by the Animal Care and Ethics Committee of the Universidad Austral de  
101 Chile (UACH/FIP 2005-61). Capture of fishes during this study was permitted through  
102 Fisheries Undersecretariat Research Permit Number 1959-06, 2931-06 and 181-07 issued by  
103 Ministry of Economy, Development and Tourism.

104

### 105 *Community definition*

106 All cartilaginous fishes captured during surveys were counted and identified to species  
107 level. Some individuals were landed frozen to validate on-board identification using  
108 diagnostic features described in literature (Compagno, 1984a; Compagno, 1984b; Lamilla &  
109 Sáez, 2003; Lamilla & Bustamante, 2005; Ebert, Fowler & Compagno, 2013). Species  
110 diversity was described using the number of species per sampling site; and compared using  
111 the Shannon diversity index ( $H$  according to Spellerberg & Fedor, 2003) by depth and zone.

112 Species richness ( $S$ ) was calculated per depth stratum in each zone, and is defined as  
113 the number of species within a specific number of individuals sampled (Kempton, 1979).

114 Relative frequency of occurrence ( $F_O$ ) expressed as percentage, was determined for each  
115 species to explore the variability of species' occurrence along the bathymetric and latitudinal  
116 gradients. Three categories of  $F_O$  were determined for each depth stratum and zone according  
117 to Solervicens (1973): Regular species, where  $F_O = >50\%$ ; Accessory species, where  $F_O = 25$   
118  $- 49\%$  and; Incidental species, where  $F_O = 10 - 24\%$ . Latitudinal and bathymetric gradients of  
119 species diversity of the major taxonomic groups (sharks and skates) were compared using  
120 analysis of covariance (ANCOVA) with significance accepted at  $P < 0.05$ .

121

### 122 *Community structure*

123 Faunal assemblages and geographic patterns of cartilaginous fishes were determined  
124 through a global similarity matrix. Species composition and abundance in each tow were  
125 considered for the entire study area with CPUE values fourth-root transformed to balance  
126 outliers (rare and abundant species). Sampling sites were sorted by an agglomerative  
127 hierarchical cluster and through non-dimensional metric scaling (nMDS) considering the  
128 global similarity matrix (Clarke, 1993; Clarke & Warwick, 1994). Log-transformed CPUE  
129 values were used for hierarchical agglomerative clustering with group-averaging linking,  
130 based on the Bray–Curtis similarity measure to delineate groupings with a distinct community  
131 structure. A one-way ANOSIM was used to establish possible differences between sampling  
132 site groups. Additionally, a SIMPER analysis was used to determine the contribution of each  
133 species to the average Bray-Curtis dissimilarity between groups. All indices and statistical  
134 procedures were made using software PRIMER v.6.0 (Plymouth Marine Lab, Plymouth, UK).

135

### 136 **Results**

137

138 The total catch from 76 sites was 194,705 cartilaginous fishes, of which 2,725  
139 individuals were landed and examined, and the presence of 20 species: nine sharks, ten skates  
140 and one chimaera was confirmed (Table 1). Note, that for the purpose of the current study the  
141 term 'skate' includes the rays *Rajella sadowsky* and *Torpedo tremens*. In 40.6% of tows there  
142 was no catch of cartilaginous fishes and were thus excluded from the remaining analysis.  
143 Bathymetrically, the shallowest depth stratum (100 – 199 m) and latitudinally, the  
144 northernmost zone (zone 1) yielded the lowest percentage occurrence with of cartilaginous  
145 fishes caught in 3.13% and 37.5% of tows respectively (Table 2). The greatest number of  
146 species caught per family was five, in the family Arhynchobatidae, followed by the families  
147 Rajidae (four species), Etmopteridae and Scyliorhinidae (both three species). The  
148 Hexanchidae, Somniosidae, Centrophoridae, Torpedinidae and Chimaeridae were each  
149 represented by a single species (Table 1).

#### 151 *Community definition*

152 Species richness fluctuated between one and six species per site with no significant  
153 differences between sharks and skates in slopes of the regression (ANCOVA;  $F = 0.826$ ;  $df =$   
154  $1, 117$ ;  $P = 0.365$ ; Fig. 2), but there were significant differences in the intercepts (ANCOVA;  
155  $F = 24.972$ ;  $df = 1, 117$ ;  $P > 0.001$ ). There was no significant relationship between species  
156 richness and latitude for sharks, but species richness for skates increased with increasing  
157 latitude (Fig. 2A, C). Chimaeras were absent in the catch from zones 6 and 8, but occurred in  
158 the other six zones (Fig. 2E). Species richness increased significantly with depth for sharks,  
159 but not for skates (Fig. 2B, D). The slopes and intercepts of the regressions were significantly  
160 different (ANCOVA,  $F = 17.06$ ;  $df = 1, 117$ ;  $P > 0.001$  and  $F = 13.954$ ;  $df = 1, 117$ ;  $P >$   
161  $0.001$ , respectively). Chimaeras were restricted to 430 – 480 m within the deepest depth



162 stratum, and were observed off most of the central coast of Chile, between approximately  
163 29.5° and 37.5° S (Fig 2E, F).

164 The CPUE per site ranged widely, from 5.5 – 2,785 ind km<sup>-2</sup> h<sup>-1</sup> among individual sites  
165 and 728 – 7,942 ind km<sup>-2</sup> h<sup>-1</sup> among zones (Table 3). Log-transformed CPUE increased with  
166 latitude for both sharks and skates, although the slopes of the regressions were not significant  
167 (Fig. 3A, C). Based on latitude, ANCOVA did not reveal significant differences in slope (F =  
168 0.412; df = 1, 117; *P* = 0.523), but did in elevation between sharks and skates (F = 43.942; df  
169 = 1, 117; *P* > 0.001). There was a significant effect of depth on the CPUE for sharks, but not  
170 for skates (Fig 3B, D), and there was a significant difference between the slopes and  
171 elevations of the regressions (ANCOVA; F = 19.59; df = 1, 117; *P* > 0.001; F = 31.12; df = 1,  
172 117; *P* > 0.001, respectively). For chimeras, the CPUE was generally low across the species'  
173 latitudinal range (Fig. 3E).

174 Diversity index (*H*) was not influenced by latitude for sharks, but increased  
175 significantly for skates (Fig. 4; ANCOVA; F = 5.056; df = 1, 117; *P* = 0.263) and the  
176 intercepts were significantly different (ANCOVA; F = 15.92; df = 1, 117; *P* > 0.0001). Values  
177 of *H* for sharks averaged approximately 0.6 across the eight zones, but showed high  
178 variability among sites in each zone (Fig 4A). For skates, there were zero-values for *H* in all  
179 zones, particularly zone 1, but values of up to approximately 1.1 also occurred at sites in the  
180 central and southern zones (Fig. 4C). Significant differences were observed in the slopes and  
181 intercepts of the regression between sharks and skates based on depth (ANCOVA; F = 15.35;  
182 df = 1, 117; *P* > 0.001 and F = 8.40; df = 1, 117; *P* > 0.001). Diversity index for sharks was  
183 markedly higher in waters over about 325 m deep, and was almost absent in shallowed depth  
184 strata (Fig. 4B). Skate diversity varied considerably within most depth strata and, overall,  
185 showed no significant trend with depth (Fig. 4D).

186 Three incidental species (*Bathyraja multispinis*, *Dipturus trachyderma*, *Torpedo*  
187 *tremens*) and two regular species (*Psammobatis rudis*, *Zearaja chilensis*), represent the  
188 community at 200 – 299 m depth. *Hexanchus griseus* and *T. tremens* are regular species,  
189 along with six accessory species in the 300 – 399 m depth stratum. *Hexanchus griseus* was  
190 restricted to this stratum, whereas *T. tremens* was also captured at shallower depths.  
191 *Centroscymnus macracanthus*, *Apristurus nasutus*, *Bathyraja peruana*, *Bathyraja*  
192 *albomaculata*, *Rajella sadowskii* and *Hydrolagus macrophthalmus* were only found in the  
193 deepest stratum (400 – 499 m), whereas there were nine other regular species that were also  
194 represented in shallower strata (Table 5).

195 A taxonomic change in community composition occurred along the depth gradient.  
196 Three skates, *Psammobatis rudis*, *Zearaja chilensis* and *Dipturus trachyderma* dominated  
197 communities between 100 and 300 m accounting for >80% of total cartilaginous fish CPUE,  
198 but as depth increased there was a major shift in community, as small-sized, deep-water  
199 dogfishes, such as *Centroscyllium* spp. came to dominate the catch (Fig. 3, Table 4). Other  
200 contributors to this species-complex change were relative reductions in *Bythalelurus*  
201 *canescens* and small-sized skates (i.e., *Psammobatis rudis* and *Gurgesiella furvescens*) (Table  
202 4, 5).

203

#### 204 *Community structure*

205 Agglomerative hierarchical cluster analysis (Fig. 5) revealed four major fish  
206 assemblages (I – IV) at similarity level of 40%, and one outlier. The ANOSIM showed that  
207 the four assemblages were significantly separated from each other ( $n = 76$ ,  $R_{\text{Global}} = 0.68$ ;  $P$   
208  $> 0.01$ ), with the outlier characterised by presence of one single species (*Bathyraja peruana*)  
209 with the lowest total CPUE ( $8.6 \text{ ind km}^{-2} \text{ h}^{-1}$ ). Geographically, assemblage I grouped 11 sites  
210 located north of Coquimbo to Valparaíso (zones 1 – 3, Fig. 1) and between depths of 237 to

211 379 m, with an average of CPUE of 56.3 ind km<sup>-2</sup> h<sup>-1</sup> for 10 species (5 sharks and 5 skates).  
212 This community was dominated by *Centroscyllium nigrum* that comprised 34.3% of the  
213 CPUE, *Bythalelurus canescens* (22.2% CPUE) and *Psammobatis rudis* (11.5% CPUE) (Table  
214 5). Assemblage II included the largest number of sites (45), taxa (20) and specimens (average  
215 CPUE = 475 ind km<sup>-2</sup> h<sup>-1</sup>). Sites in this assemblage were scattered over the entire study area  
216 and occupied a depth range of 335 – 492 m. Prominent species in this assemblage were *C.*  
217 *granulatum* (37.6% CPUE), *C. nigrum* (28.5% CPUE), and *B. canescens* (15.9% CPUE)  
218 (Table 5). Assemblage III comprised 10 relatively shallow sites (149 – 262 m) in the most  
219 southerly zone offshore from Concepción, the second largest port in Chile. The skates *Z.*  
220 *chilensis* and *D. trachyderma* dominated this assemblage of 6 species with 83.3% of the  
221 assemblage CPUE (158 ind km<sup>-2</sup> h<sup>-1</sup>; Table 5). Assemblage IV grouped 10 relatively shallow  
222 sites (243 – 281 m) located south Valparaíso in zones 4, 5 and 6. This assemblage had the  
223 lowest diversity (5 species) and abundance (39.9 ind km<sup>-2</sup> h<sup>-1</sup>). Two species, *Psammobatis*  
224 *rudis* and *C. granulatum*, were the most abundant species accounting for 63.4% and 20.4% of  
225 CPUE respectively (Table 6).

226 Ordination analysis (nMDS) produced similar results to cluster analysis with four  
227 assemblages (Fig. 6). The outlier (3B.1) was a site off Valparaíso apparently separated from  
228 other sites due to the presence of a single species (*Bathyraja peruana*), observed in low  
229 abundance (8.5 ind km<sup>-2</sup> h<sup>-1</sup>). SIMPER analysis showed low average within-group similarity  
230 of 29.9 – 38.6% for all assemblages. Two main consolidating species, *P. rudis* and *D.*  
231 *trachyderma* were identified within each assemblage, and accounted for 100% within-group  
232 similarity in assemblage III; 59.4% in assemblage IV and >6% in assemblages I and II,  
233 respectively. Unlike within-group similarity, the dissimilarity levels between all four  
234 assemblages were high, ranging from 92.7 to 96.7%. *Psammobatis rudis*, *Bythalelurus*  
235 *canescens*, *Centroscyllium nigrum* and *Dipturus trachyderma*, accounted for 80.7% of total

236 (84.2%) dissimilarity between assemblages I and III. Nine species together contributed 92.9%  
237 towards total (96.7%) dissimilarity between assemblages I and II. Eight species were  
238 responsible for 91.9% (95.1%) and 90.5% (94.3%) of total dissimilarity in both, assemblages  
239 II and III and assemblages II and IV respectively. Finally, seven species contributed 92%  
240 towards total (93.4%) dissimilarity between assemblages II and III; while between  
241 assemblages III and IV, *Zearaja chilensis*, *Dipturus trachyderma*, *Psammobatis rudis* and  
242 *Centroscyllium granulatum* accounted for 91.9% of total (92.7%) dissimilarity.

## 244 Discussion

245  
246 Trawling has long been used to explore waters off the central-north and central-south  
247 coasts of Chile in order to identify regions where benthic crustaceans and teleost fishes of  
248 commercial interest occur in high abundance (Sielfeld & Vargas, 1996; Menares &  
249 Sepulveda, 2005). Currently, trawl-fishing effort is centred, but not restricted, on squat  
250 lobsters (*Cervimunida johni* and *Pleuroncodes monodon*), deep-water shrimps (*Heretocarpus*  
251 *reedi*), hakes (*Merluccius gayi* and *M. australis*) and Chilean horse mackerel (*Trachurus*  
252 *murphyi*). The abundance of these target species is estimated through regular trawl surveys to  
253 allow the fishing effort to be adjusted to achieve ‘maximum sustainable yield’. A useful by-  
254 product of such surveys has been the production of species checklists that have enriched  
255 knowledge of Chile’s national marine biodiversity (Pequeño, 2000; Acuña et al., 2005). These  
256 extensive fishery-dependent and independent surveys, that include cartilaginous fishes in the  
257 catch, are conducted annually in central Chilean waters (c. 21.5 – 38.5° S). For example,  
258 between 1994 and 2004, exploratory surveys for demersal crustaceans comprised 6,143 trawl  
259 hauls made at depths of 100 – 500 m (Acuña et al., 2005). Although 13 shark, 8 skate and 1  
260 chimaera species were caught, published data are limited to a simple indication of the

261 latitudinal range for each species (Acuña et al., 2005). The absence of quantitative data on the  
262 species' abundance, particularly in respect of fishing effort, location (latitude) and depth  
263 provides a challenge for management, whether for exploitation or for conservation. It is also  
264 of relevance to note that these fishery-dependent and independent surveys report on the  
265 diversity of animals from areas that are subject of continuous and often intense fishing  
266 activity which is implicated in a decline in species richness (Wolff & Aroca, 1995).

267         There has also been a number of fishing-independent studies, such as Ojeda (1983),  
268 who reported the presence of 2 shark and 3 skate species from 118 hauls made at depths of  
269 over 500 m on a trawl survey in austral Chile (52° S – 57° S). Further north, 133 hauls made  
270 between 31° S – 41°28' S at depths of 50 – 550 m produced 7 shark, 5 skate and 1 chimaera  
271 species (Menares & Sepúlveda, 2005). In central Chile, Meléndez & Meneses (1989) reported  
272 11 shark species from 173 hauls in exploration surveys using bottom trawl nets between 18° S  
273 – 38°30' S and at depths of 500 – 1260 m. In the most northerly survey, between 18° S and  
274 21° S, the same gear type used over a wider depth range (30 – 1050 m) resulted in 4 shark, 4  
275 skate and 1 chimaera species from 21 hauls (Sielfeld & Vargas, 1996). Each of these studies,  
276 however, also lacked quantification of the catch and are therefore of limited value, beyond  
277 providing information on the presence (or apparent absence) of species within a geographic  
278 region.

279

### 280 *Community definition*

281         The species richness observed in the current study (20 species), is higher than those  
282 found in surveys conducted previously in the region (Ojeda, 1983; Meléndez & Meneses,  
283 1989; Sielfeld & Vargas, 1996; Ojeda, Labra & Muñoz, 2000; Acuña & Villarroel, 2002;  
284 Acuña et al., 2005; Menares & Sepúlveda, 2005). Variation in the reported species richness of  
285 cartilaginous fishes within the region among years may reflect the different gear types used,

286 different effort, different depths sampled, and species misidentifications (Pequeño & Lamilla,  
287 1993; Lamilla et al., 2010). While the species richness reported here is similar to that reported  
288 by Acuña et al. (2005), the cartilaginous fish community appears to differ between the two  
289 studies. Direct comparisons are somewhat speculative as while our study provides  
290 quantification of the fauna in terms of CPUE and  $F_0$ ; the results of Acuña et al. (2005) are  
291 limited to whether a species was present, but in unreported abundance. Nevertheless, a couple  
292 of thematic differences are apparent with small, shallow-water skates (i.e., *Psammobatis*  
293 *scobina*, *Sympterygia lima*, *S. brevicaudata* and *Discopyge tschudii*) absent in our study,  
294 while deep-sea skates of the genera *Bathyraja* and *Rajella* were not caught in the earlier study  
295 (Fig. 7). These results suggest that, in comparison to our study, (a) shallower waters may have  
296 been sampled, and (b) the fishing effort in deeper waters was more limited in the study  
297 reported by Acuña et al. (2005). Taken together, these two studies indicate that at least 30  
298 cartilaginous fishes inhabit (or did inhabit) the continental shelf and slope off central Chile;  
299 although some species showed pronounced latitudinal variation in distribution (e.g. *Aculeola*  
300 *nigra*, *Centroscyllium nigrum*, *Gurgesilla furvescens*) while in some others, the latitudinal  
301 extension is not reported (i.e., *Bathyraja peruana*, *Sympterygia brevicaudata*, *S. lima*,  
302 *Discopyge tschudii*).

303 Species abundance was highly variable between zones with the lowest abundance in  
304 the north (zone 1). The abundance in the central and the most southern zones (2, 3, 4 and 8)  
305 was about double this value, in zones 5 and 7 it was four times as large and in zone 6 it was  
306 an order of magnitude greater. Interestingly, five species (e.g., *Hexanchus griseus*,  
307 *Centroscymnus macracanthus*, *Bathyraja brachyurops*, *B. multispinis*, *Rajella sadowskii*)  
308 were caught, mostly in low numbers, only within a single zone and within a single depth  
309 stratum. The pattern of occurrence suggests that the species are naturally uncommon or, more  
310 likely, that the trawl regime only sampled the upper end of their natural depth range (Fig. 7).

311 In contrast, two species (e.g., *Apristurus nasutus* and *Hydrolagus macrophthalmus*) showed a  
312 marked preference for a particular depth stratum but occurred in more than one zone. Others  
313 species showed an obvious latitudinal variation in abundance, for example, *Aculeola nigra*  
314 was common in the north (zones 1 – 4), rare in central zones (5 – 6) and absent in the southern  
315 zones (7 – 8); whereas, *Psammobatis rudis* and *Dipturus trachyderma* showed the opposite  
316 trend. Both *Centroscyllium* species (*C. granulatum* and *C. nigrum*) have a high abundance in  
317 central Chile and are less common in both north and south, and appear to become extremely  
318 abundant with increasing depth. Between 300 and 500 m, the diversity approximately further  
319 doubled and the abundance of most species increased. With the exception of two species  
320 (*Zearaja chilensis* and *Torpedo tremens*), all cartilaginous fishes were caught at depths below  
321 200 m and most increase their abundance with depth. This relative absence of cartilaginous  
322 fishes in shallow waters (100 – 199 m) was both unexpected and difficult to explain, and  
323 needs to be addressed in future studies.

324

### 325 *Community structure*

326 Species richness of cartilaginous fishes in the south-east Pacific has been described to  
327 increase towards lower latitudes following the same geographic pattern of other marine fishes  
328 (Meléndez & Meneses, 1989; Pequeño, Rucabado & Lloris, 1990; Rohde, 1992; Pequeño &  
329 Lamilla, 1993; Camus, 2001); although these observations are based on species inventories  
330 without reference to latitudinal or bathymetric ranges which obviously can have a marked  
331 influence on species distributions. Also, elasmobranch diversity in the Atlantic and Pacific  
332 oceans have been described to decrease with depth, especially below 1,000 m depth  
333 (Pakhomov et al., 2006; Priede et al., 2006). Our results provided evidence of an overall  
334 increase in species richness with increasing latitude and depth, in contrast to a decrease in  
335 diversity with increasing latitude demonstrated by littoral fishes (Ojeda, Labra & Muñoz,



336 2000), but similar to diversity gradients of benthic invertebrates and in the Northern  
337 Hemisphere described by Rex et al. (2000). In our study, the latitudinal and bathymetric  
338 stability of assemblage II (Fig. 5), is consistent with a “transition intermediate area” as  
339 described by Camus (2001), and suggests that differences between assemblages were due to  
340 compensatory changes in mesopredator abundance (Navia et al., 2011). There is a correlation  
341 between the location of assemblages I, III and IV and intensive trawl fishing areas (Wolff &  
342 Aroca, 1995; Escribano, Fernandez & Aranís, 2003; Acuña et al., 2005). Continuous and  
343 unselective removal of certain species by commercial fisheries may explain in part the  
344 variation of species abundance among assemblages.

345 At community level, the main assemblage (II) was distributed across the entire  
346 surveyed area comprising 58% of sites; and showed a high average dissimilarity to  
347 assemblages I, III and IV (96.7, 95.1 and 94.3% respectively). Differences were mainly due to  
348 the importance of small-sized sharks (*Bythalelurus canescens*, *Centroscyllium granulatum*  
349 and *C. nigrum*); although diversity of small-sized skates also contributed to overall  
350 dissimilarity. In our study assemblages I, III and IV represented ‘coldspots’ of diversity,  
351 similar to those found along the outer shelf in south-west Atlantic cartilaginous fish  
352 community (Lucifora et al. 2011). While those coldspots were simply defined as areas of low  
353 diversity, in the current study coldspots coincide with traditional fishing grounds. Commercial  
354 fisheries in Chile, in particular trawl-based activities, are likely to have a direct effect on  
355 cartilaginous fish community structure and distribution as have been previously documented  
356 for other marine fishes in central Chile (Arancibia & Neira, 2005).

357 Different levels of fishing pressure can generate multiple effects on the function of  
358 species and their interactions (Navia et al., 2011). High species richness and abundance  
359 represented in assemblage II, is consistent with a more stable community as high biodiversity  
360 has been linked to the stability of trophic networks through the complex interactions that arise



361 among its components (Navia et al., 2011). In contrast, when there is an external disturbance,  
362 in this case differential exposure to fishing pressure, the result may be a complete  
363 reorganisation of the community (Bascompte, Melián & Sala, 2005).

364 Considering the overall species composition without accounting rare species (defined  
365 in relation to low species abundance), such as *Echinorhinus cookei* and *Centroscymnus*  
366 *owstonii*; the absence of mid- to large-sized sharks is evident in our study (Fig. 7). Ferretti et  
367 al. (2010) described the ecological restructuring of demersal elasmobranch communities in  
368 fishing areas worldwide. Diversity and abundance of elasmobranchs erodes quickly as  
369 fisheries remove, unselectively, both small and large species despite the lower catchability of  
370 the latter. As large sharks disappear from the catch as fisheries develop, the community tends  
371 to become dominated by mesopredators. In the current study these mesopredators are  
372 predominantly small-sized sharks, that are more fecund and more resilient to fishing pressures  
373 than other elasmobranchs. Examples of similar community restructuring have been  
374 documented for trawl fishing areas in the Atlantic (Ellis et al., 2005), Gulf of Mexico  
375 (Shepherd & Myers, 2005), the Mediterranean Sea (Ferretti et al., 2008) and Australian waters  
376 (Graham, Andrew & Hodgson, 2001); although its extension to similar trawl fisheries  
377 elsewhere has not been properly evaluated due to a lack of temporal and seasonal catch-  
378 composition data for elasmobranch species.

379

#### 380 *Limitations and future directions*

381 Previous research has identified two distinct biogeographic provinces based on  
382 multiple taxa along the Chilean coast, the Peruvian province in the north (4° – 30° S) and the  
383 Magellanic province in the south (42° – 56° S) (Camus, 2001). There is also an “intermediate  
384 area” between these two provinces that has been described as a rich, mixed-origin species’  
385 transition zone for teleost fishes (Pequeño, 2000; Ojeda, Labra & Muñoz, 2000). Considering

386 the limitations of geographic scale, the single main biogeographic province (assemblage II)  
387 that was identified between 29.5° S and 38.5° S only showed limited evidence of species  
388 more usually associated with the Peruvian and Magellenic provinces.

389 Fishery-independent surveys allowed us to explore an extensive area, including  
390 traditional commercial trawling zones and non-traditional fishing zones with similar effort. It  
391 should be mentioned that the methodology used was designed to sample demersal and  
392 bottom-dwelling species, and therefore the cartilaginous fish community' definitions used  
393 here effectively excludes species that occur in mid- to surface waters and likely  
394 underestimates species richness (Pakhomov et al., 2006). Potential limitations of our analysis  
395 include differential vulnerability to fishing gear, which could be species-specific or relate to  
396 swimming performance or the size of individuals. Also, the sampling effort was not evenly  
397 distributed throughout the whole of the latitudinal range with sites clustered within each zone,  
398 as such is unlikely that all habitat types were sampled. This may be important as rocky  
399 substrates and other irregular habitats such as coral reefs and seamounts have been described  
400 as high diversity areas (hotspots), especially for cartilaginous fishes (Henry et al., 2013). The  
401 clusters of sample sites also resulted in a relatively low resolution 'picture', and precluded a  
402 fine scale description of species' distributions and abundance, and how these might be  
403 influenced by local conditions (e.g., habitat type).

404 Our results provide a quantitative description of species richness and abundance of the  
405 cartilaginous fish community on the outer continental shelf and slope of Chile to complement  
406 and extend knowledge of biological and ecological interactions of this demersal ecosystem.  
407 More than 90% of elasmobranch species worldwide inhabit demersal ecosystems on  
408 continental shelves and slopes (Compagno, 1990), which makes them vulnerable to trawl  
409 fishing (Shepherd & Myers, 2005) and we are just beginning to understand the potential  
410 ecological consequences of removal and declines of cartilaginous fishes. The information

411 presented here is of immediate value in the assessment of the conservation status of species  
412 and the threats to their populations posed by demersal trawling. The study is also of particular  
413 value for future assessment of how natural or anthropogenic activities may impact the various  
414 species by providing quantitative baseline information against which change can be assessed.

415

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417

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426

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562 **Table 1** Depth and latitudinal range of cartilaginous fishes caught during surveys.

563

Order	Family	Species	Depth range (m)	Latitudinal range (°S)
Hexanchiformes	Hexanchidae	<i>Hexanchus griseus</i> (Bonnaterre 1788)	358–376	35–35.1
Squaliformes	Etmopteridae	<i>Aculeola nigra</i> de Buen 1959	262–492	29.4–36.5
Squaliformes	Somniosidae	<i>Centroscymnus macracanthus</i> Regan 1906	455	33.3
Squaliformes	Etmopteridae	<i>Centroscyllium granulatum</i> Günther 1887	262–482	33.2–38.9
Squaliformes	Etmopteridae	<i>Centroscyllium nigrum</i> Garman 1899	335–455	32–38.8
Squaliformes	Centrophoridae	<i>Deania calcea</i> (Lowe 1839)	362–492	29.5–38.9
Carcharhiniformes	Scyliorhinidae	<i>Apristurus brunneus</i> (Gilbert 1892)	443–461	34.5–36.5
Carcharhiniformes	Scyliorhinidae	<i>Apristurus nasutus</i> de Buen 1959	338–482	29.5–38.9
Carcharhiniformes	Scyliorhinidae	<i>Bythaelurus canescens</i> (Günther 1878)	237–492	29.4–38.9
Rajiformes	Arhynchobatidae	<i>Bathyraja albomaculata</i> (Norman 1937)	356–436	37.8–38.7
Rajiformes	Arhynchobatidae	<i>Bathyraja brachyurops</i> (Fowler 1910)	482	38.9
Rajiformes	Arhynchobatidae	<i>Bathyraja multispinis</i> (Norman 1937)	445	36.4
Rajiformes	Arhynchobatidae	<i>Bathyraja peruana</i> McEachran & Miyake 1984	243–492	29.6–38.9
Rajiformes	Arhynchobatidae	<i>Psammobatis rudis</i> Günther 1870	240–475	32–38.8
Rajiformes	Rajidae	<i>Gurgesiella furvescens</i> de Buen 1959	362–484	29.4–32
Rajiformes	Rajidae	<i>Zearaja chilensis</i> (Guichenot 1848)	159–476	33.3–38.7
Rajiformes	Rajidae	<i>Dipturus trachyderma</i> (Kreffft & Stehmann 1975)	234–482	32–38.9
Rajiformes	Rajidae	<i>Rajella sadowskii</i> (Kreffft & Stehmann 1974)	475	33.4
Rajiformes	Torpedinidae	<i>Torpedo tremens</i> de Buen 1959	149–376	34.5–38.9
Chimaeriformes	Chimaeridae	<i>Hydrolagus macrophthalmus</i> de Buen 1959	430–483	29.6–37.8

564

565 **Table 2** Percentage of tows with cartilaginous fishes in the catch, species richness (S) and  
 566 total number (N) of cartilaginous fishes caught in each zone (n=16) and each depth stratum  
 567 (n=32).

568

<b>Zone</b>	<b>Catch (%)</b>	<b>S</b>	<b>N</b>	<b>Depth stratum (m)</b>	<b>Catch (%)</b>	<b>S</b>	<b>N</b>
1	37.5	7	2,921	100–200	3.13	2	203
2	56.25	10	14,871	200–300	65.63	8	18,907
3	56.25	11	12,199	300–400	78.13	14	58,597
4	62.5	11	15,058	400–500	90.63	18	116,998
5	68.75	10	23,224				
6	56.25	12	60,651				
7	75	12	47,862				
8	62.5	12	17,919				

569

570 **Table 3** Abundance, as total CPUE (ind km<sup>-2</sup> h<sup>-1</sup>) of cartilaginous fishes caught during  
 571 surveys in each zone (geographic location of zones is indicated in Fig. 1).

572

Species	Zone							
	1	2	3	4	5	6	7	8
<i>H. griseus</i>	--	--	--	--	54.7	--	--	--
<i>A. nigra</i>	130	249.4	208	390	10	11	--	--
<i>C. macracanthus</i>	--	--	9.2	--	--	--	--	--
<i>C. granulatum</i>	--	770.6	109.9	259.8	64.7	4,611	1,730	577.6
<i>C. nigrum</i>	--	257.5	752.6	363.8	2,845.1	1,639.8	435.7	5.2
<i>D. calcea</i>	15	54.7	68.5	37.8	41.5	28.4	122.1	85.1
<i>A. brunneus</i>	15	--	--	--	--	15.5	326.3	206.7
<i>A. nasutus</i>	--	--	--	30.6	--	59.2	--	--
<i>B. canescens</i>	272.7	312.5	403.8	476.5	483.2	1084.4	361.4	160.5
<i>B. albomaculata</i>	--	--	--	--	--	--	14.5	5
<i>B. brachyurops</i>	--	--	--	--	--	--	--	4.7
<i>B. multispinis</i>	--	--	--	--	--	8.4	--	--
<i>B. multispinis</i>	42.4	52	65.7	121.8	21.5	50.2	29	92
<i>P. rudis</i>	--	32.7	71.0	38.5	192.2	77.1	154.2	14.9
<i>G. furvescens</i>	239.5	55.5	--	--	--	--	--	--
<i>Z. chilensis</i>	--	--	9.2	--	--	21	984.1	5
<i>D. trachyderma</i>	--	55.8	--	127.8	159.3	336.2	100.6	395.3
<i>R. sadowskii</i>	--	--	38.2	--	--	--	--	--
<i>T. tremens</i>	--	--	--	18.7	--	--	10.1	4.4
<i>H. macrophthalmus</i>	14.2	17.6	9.2	15.2	63.9	--	5.9	--
<b>Total</b>	728.8	1,858.3	1,745.3	1,880.5	3,936.1	7,942.2	4,273.9	1,556.4

573

574

575 **Table 4** Frequency of occurrence of cartilaginous fishes caught during surveys in each zone  
 576 (geographic location of zones is indicated in Fig. 1).

577

Species	Zone							
	1	2	3	4	5	6	7	8
<i>H. griseus</i>	--	--	--	--	100	--	--	--
<i>A. nigra</i>	7.2	27.6	20.1	43.2	0.8	1.2	--	--
<i>C. macracanthus</i>	--	--	100	--	--	--	--	--
<i>C. granulatum</i>	--	8.7	1.1	2.9	0.5	49.6	27.2	10
<i>C. nigrum</i>	--	4.6	11.8	6.5	37.7	28.2	10.9	0.1
<i>D. calcea</i>	1.4	10.5	11.5	7.3	5.9	5.9	32.8	25.2
<i>A. brunneus</i>	0.9	--	--	--	--	1.9	57.3	39.9
<i>A. nasutus</i>	--	--	--	35.2	--	64.8	--	--
<i>B. canescens</i>	4	9.1	10.3	13.9	10.4	30.3	14.7	7.2
<i>B. albomaculata</i>	--	--	--	--	--	--	72.6	27.4
<i>B. brachyurops</i>	--	--	--	--	--	--	--	100
<i>B. multispinis</i>	--	--	--	--	--	100	--	--
<i>B. peruana</i>	4.3	10.4	11.5	24.5	3.2	9.6	8.1	28.4
<i>P. rudis</i>	--	5.6	10.6	6.6	24.2	12.5	36.7	3.9
<i>G. furvescens</i>	68.4	31.6	--	--	--	--	--	--
<i>Z. chilensis</i>	--	--	0.6	--	--	1.4	97.5	0.5
<i>D. trachyderma</i>	--	94.5	--	10.4	9.5	26.1	12.6	36.9
<i>R. sadowskii</i>	--	--	100	--	--	--	--	--
<i>T. tremens</i>	--	--	--	18.7	--	--	35.6	17
<i>H. macrophthalmus</i>	6.9	17	7.7	14.8	45.6	--	8	--

578

579 **Table 5** Abundance, as total CPUE (ind km<sup>-2</sup> h<sup>-1</sup>) and frequency of occurrence (Fo) of  
 580 cartilaginous fishes caught in each depth stratum†

581

Species	CPUE				F <sub>o</sub>			
	Depth stratum				Depth stratum			
	A	B	C	D	A	B	C	D
<i>H. griseus</i>	--	--	54.7	--	--	--	100	--
<i>A. nigra</i>	--	4.1	45.8	948.1	--	0.4	4.6	95
<i>C. macracanthus</i>	--	--	--	9.2	--	--	--	100
<i>C. granulatum</i>	--	85.4	3,258.8	4,779.3	--	1.1	40.1	58.8
<i>C. nigrum</i>	--	--	1,541.1	4,758.6	--	--	24.5	75.5
<i>D. calcea</i>	--	--	220.9	232.3	--	--	48.7	51.3
<i>A. brunneus</i>	--	--	23.2	540.2	--	--	4.1	95.9
<i>A. nasutus</i>	--	--	--	89.8	--	--	--	100
<i>B. canescens</i>	--	18.7	1,121.4	2,415.4	--	0.5	31.6	67.9
<i>B. albomaculata</i>	--	--	9.4	10.0	--	--	48.4	51.6
<i>B. brachyurops</i>	--	--	--	4.7	--	--	--	100
<i>B. multispinis</i>	--	--	--	8.4	--	--	--	100
<i>B. peruana</i>	--	61.1	214.2	199.3	--	12.9	45.1	42
<i>P. rudis</i>	--	430.1	122.4	28.1	--	74.1	21.1	4.8
<i>G. furvescens</i>	--	--	38.4	254.3	--	--	13.1	86.9
<i>Z. chilensis</i>	13.7	951.1	39.9	14.5	1.3	93.3	3.9	1.4
<i>D. trachyderma</i>	--	375.4	431.2	278.5	--	34.6	39.7	25.7
<i>R. sadowskii</i>	--	--	--	38.2	--	--	--	100
<i>T. tremens</i>	5.3	6.5	21.4	--	16.1	19.6	64.3	--
<i>H. macrophthalmus</i>	--	--	--	126.0	--	--	--	100
<b>Total</b>	19.0	1,932.4	7,142.8	14,734.9				

582

583 †Depth strata are A: 100–199 m; B: 200–299 m; C: 300–399; D: 400–499.

584

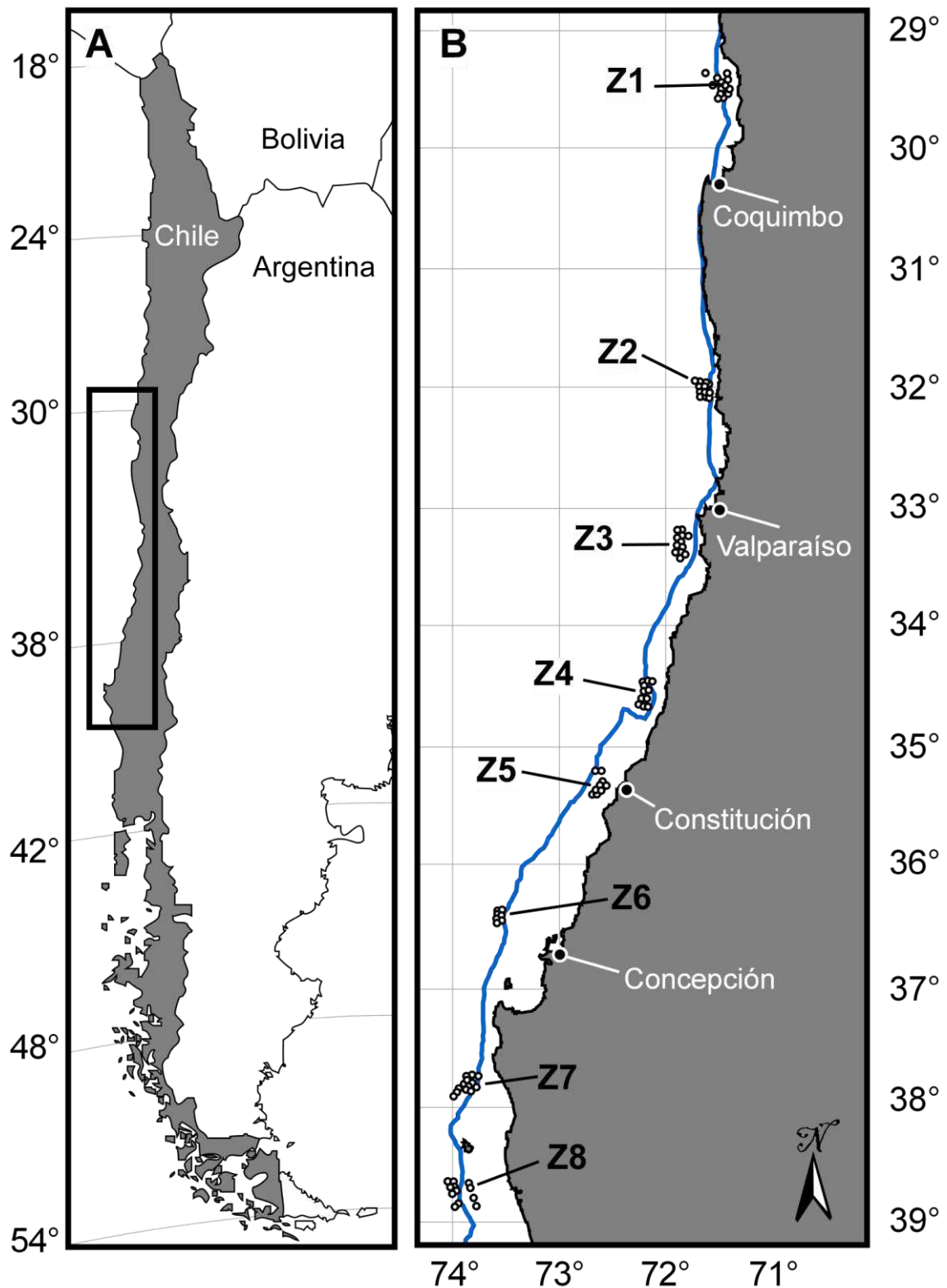
585 **Table 6** Average abundance (ind km<sup>-2</sup> h<sup>-1</sup>) and percentage of contribution per species in each  
 586 assemblage (*n* indicates the number of sites included per assemblage).

587

Species/Assemblage	I ( <i>n</i> = 11)		II ( <i>n</i> = 45)		III ( <i>n</i> = 9)		IV ( <i>n</i> = 10)	
	Avg.	%	Avg.	%	Avg.	%	Avg.	%
<i>H. griseus</i>	--	--	1.2	0.3	--	--	--	--
<i>A. nigra</i>	4.1	7.2	21.1	4.4	--	--	0.4	1.0
<i>C. macracanthus</i>	--	--	0.2	0.0	--	--	--	--
<i>C. granulatum</i>	--	--	178.5	37.6	1.1	0.7	8.1	20.4
<i>C. nigrum</i>	19.3	34.3	135.3	28.5	--	--	--	--
<i>D. calcea</i>	1.4	2.4	9.7	2.0	--	--	--	--
<i>A. brunneus</i>	1.4	2.4	12.2	2.6	--	--	--	--
<i>A. nasutus</i>	--	--	2.0	0.4	--	--	--	--
<i>B. canescens</i>	12.5	22.2	75.9	16.0	--	--	--	--
<i>B. albomaculata</i>	--	--	0.4	0.1	--	--	--	--
<i>B. brachyurops</i>	--	--	0.1	0.0	--	--	--	--
<i>B. multispinis</i>	--	--	0.2	0.0	--	--	--	--
<i>B. peruana</i>	2.5	4.5	8.9	1.9	4.1	2.6	--	--
<i>P. rudis</i>	6.5	11.5	2.0	0.4	18.3	11.6	25.3	63.4
<i>G. furvescens</i>	2.8	4.9	5.9	1.2	--	--	--	--
<i>Z. chilensis</i>	0.8	1.5	1.2	0.3	106.2	67.4	--	--
<i>D. trachyderma</i>	5.1	9.0	16.3	3.4	26.8	17.0	5.7	14.2
<i>R. sadowskii</i>	--	--	0.8	0.2	--	--	--	--
<i>T. tremens</i>	--	--	0.5	0.1	1.1	0.7	--	--
<i>H. macrophthalmus</i>	--	--	2.8	0.6	--	--	--	--

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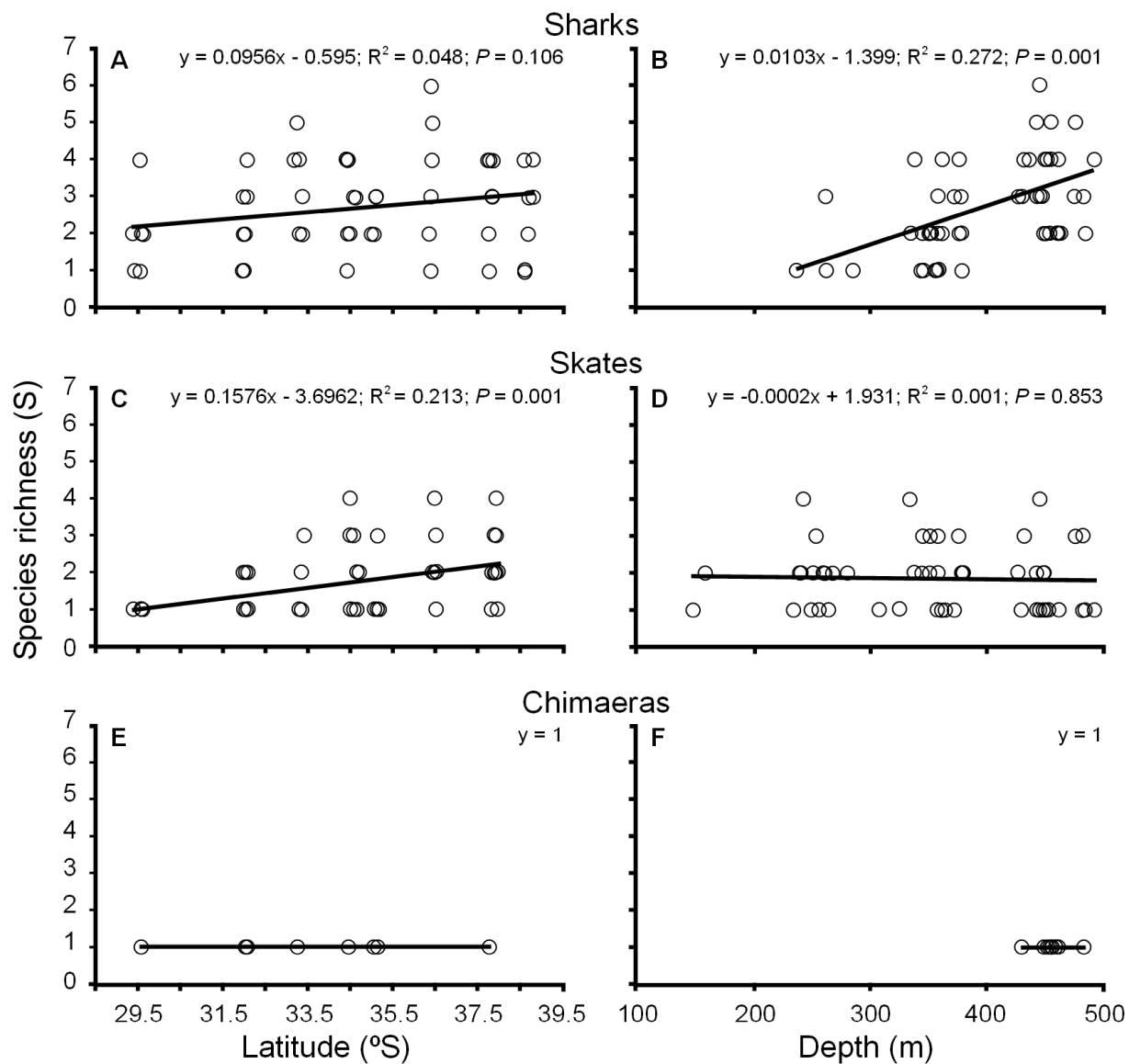
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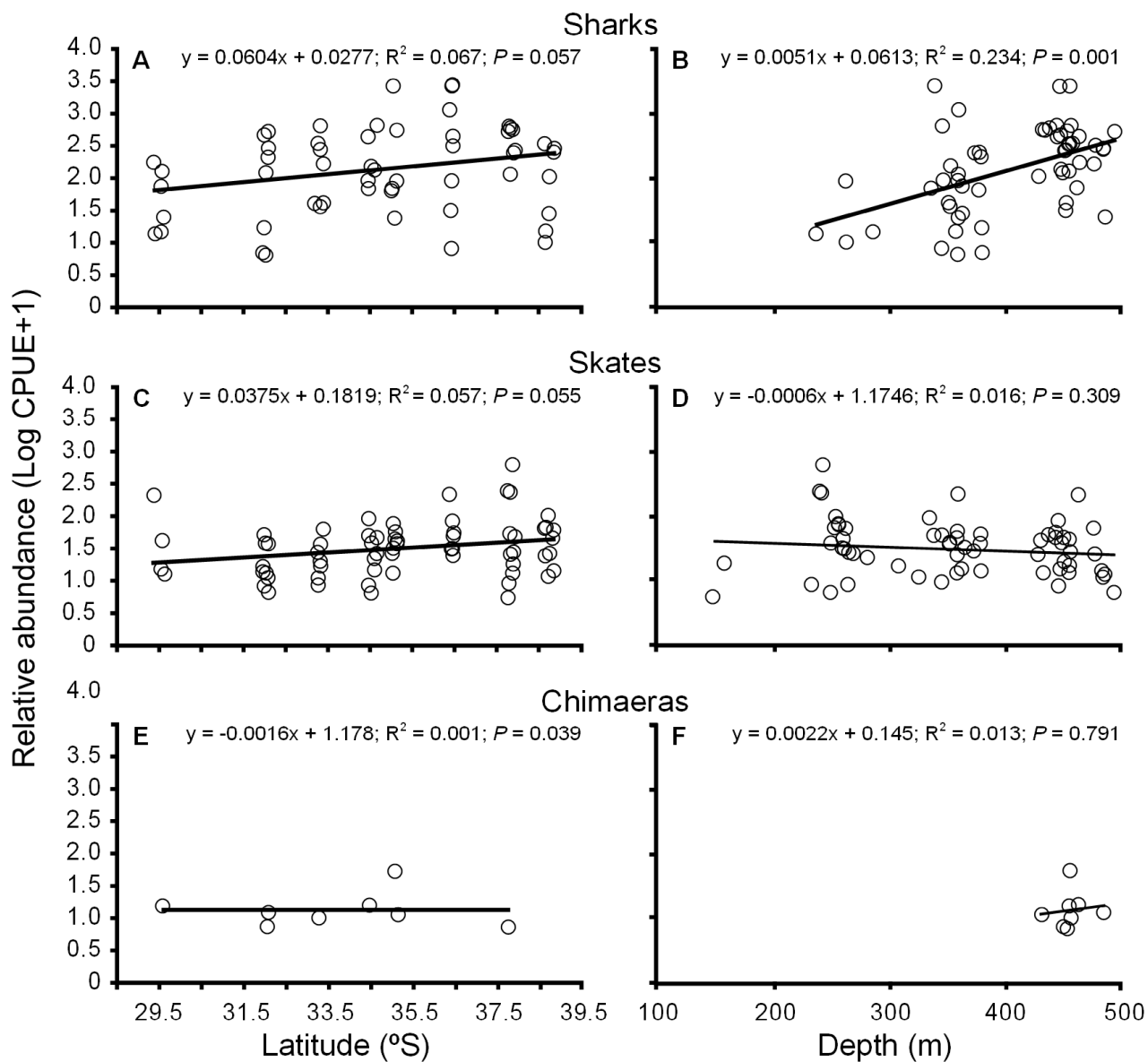
591 **Figure 1** Map of (A) Chile showing location of study area (inset box) and (B) location of  
592 zones (Z1 to Z8) and sampling sites (with circles). Isobath of 500 m (blue line) is indicated  
593 in (B).





594

595 **Figure 2** Latitudinal and bathymetric changes of species richness of sharks (A–B), skates (C–  
 596 D) and chimaeras (E–F) across the study area. Fitted least-square regression model (solid line)  
 597 and statistical significance are indicated in each case.

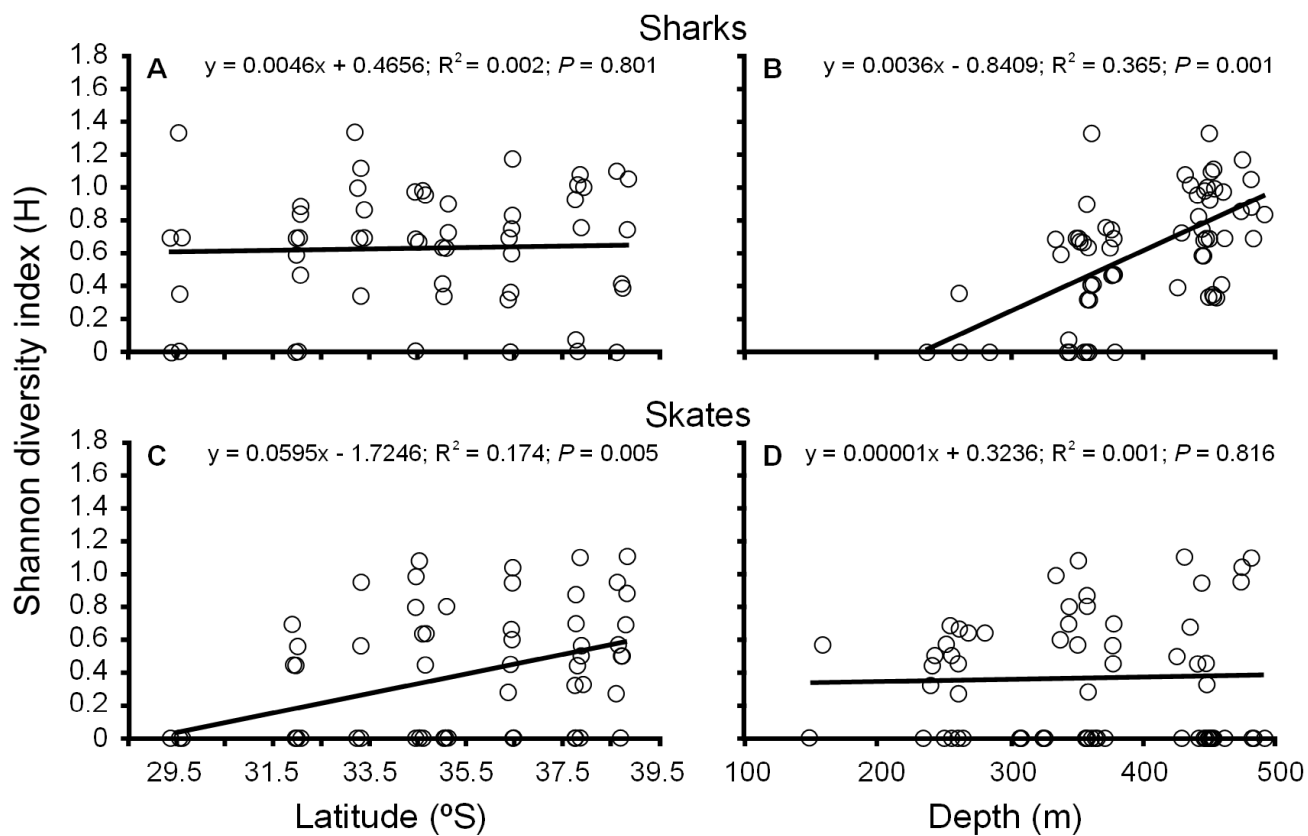


598

599 **Figure 3** Latitudinal and bathymetric changes of relative abundance (Log CPUE+1) of sharks

600 (A–B), skates (C–D) and chimaeras (E–F) across the study area. Fitted least-square regression

601 model (solid line) and statistical significance are indicated in each case.

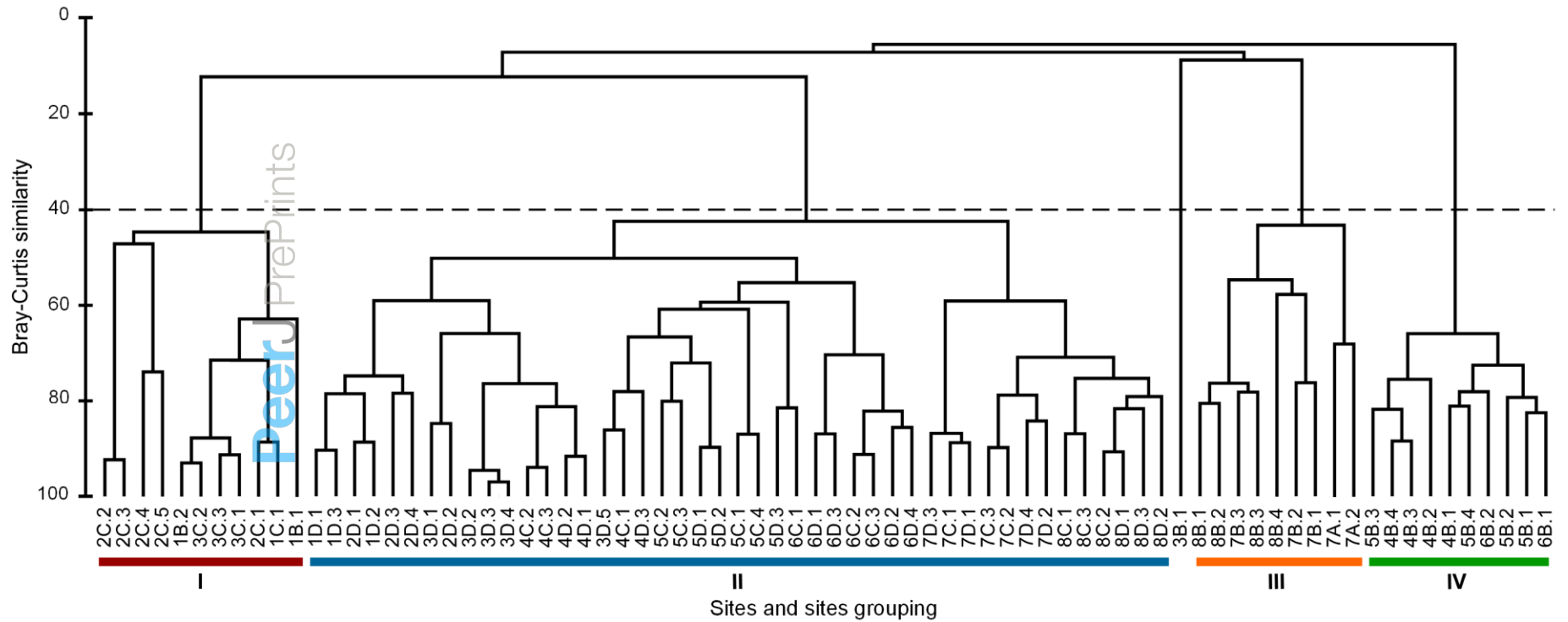


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603 **Figure 4** Latitudinal and bathymetric changes of Shannon diversity index ( $H$ ) of sharks (A–

604 B) and skates (C–D) across the study area. Fitted least-square regression model (solid line)

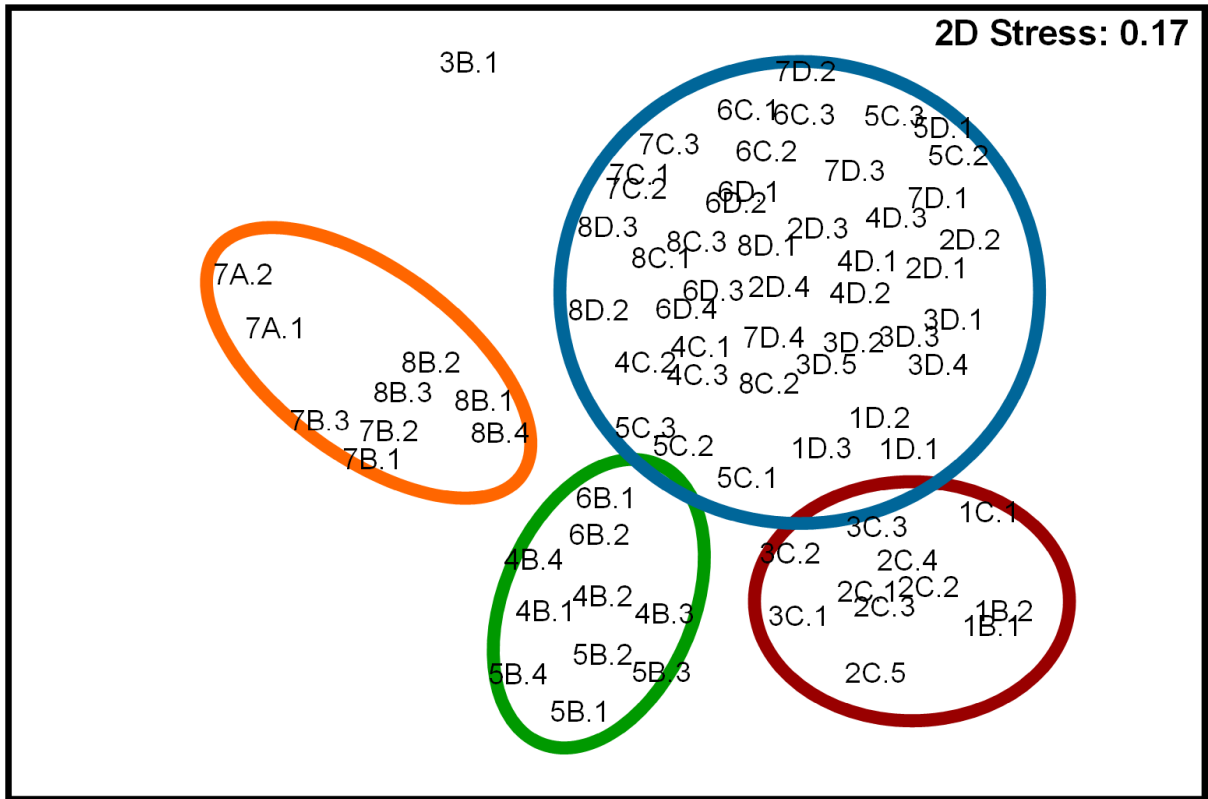
605 and statistical significance are indicated in each case.



607

608 **Figure 5** Agglomerative hierarchical cluster indicating the clustering of the four assemblages. Sites grouping is colour coded and indicate 40%

609 similarity.



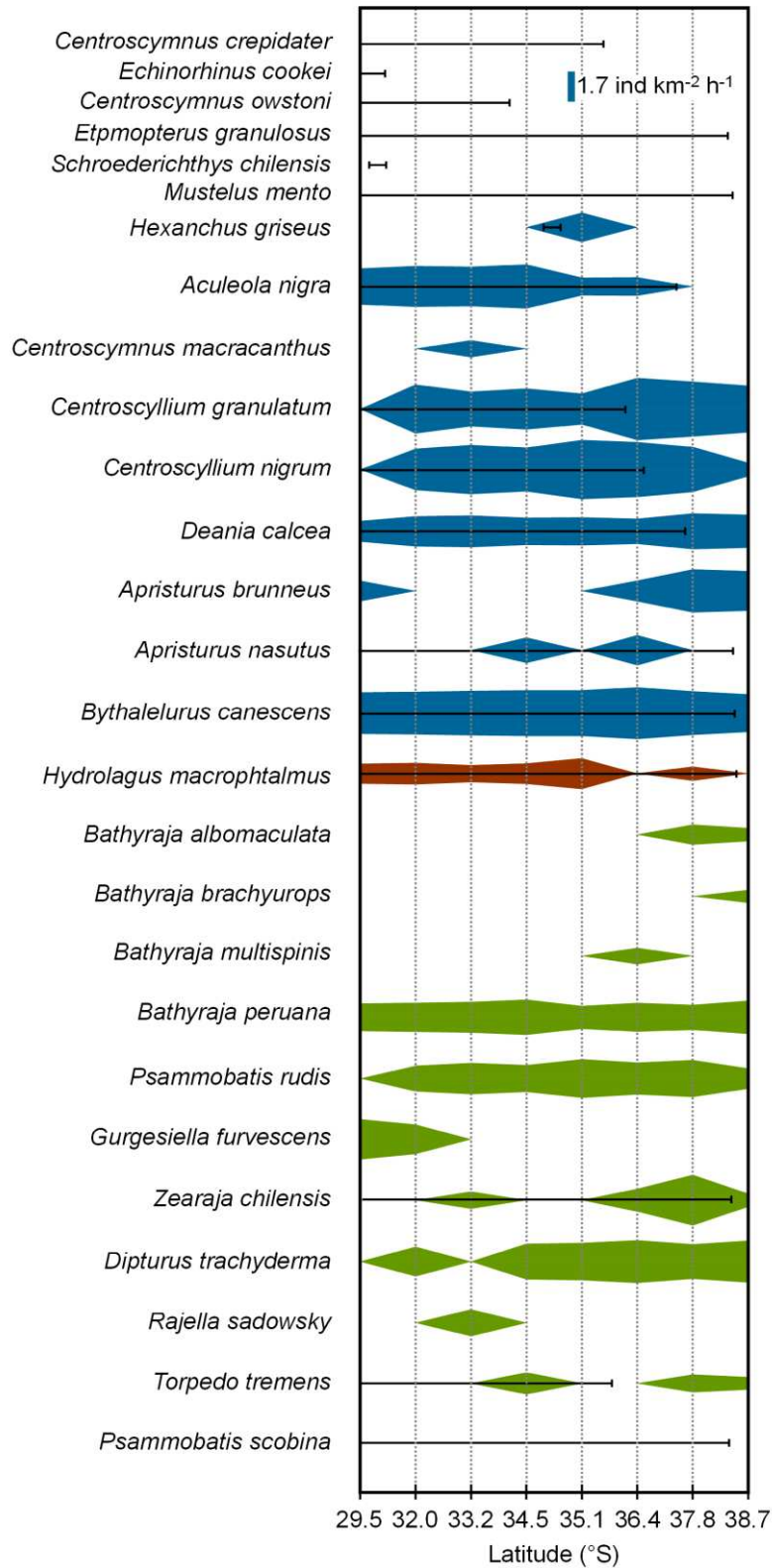
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**Figure 6** Ordination in two-dimensions using non-dimensional metric scaling indicating the clustering of the four assemblages. Sites grouping is colour coded and indicate 40% similarity.



614

615 **Figure 7** Latitudinal distribution and abundance (Log CPUE+1) of cartilaginous fishes  
 616 present in the continental shelf and slope of Chile. Black lines represent species range  
 617 reported by Acuña et al. (2005).