Coastal fish assemblages and predation pressure in northern-central Chilean *Lessonia trabeculata* kelp forests and barren grounds

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Kelp forests are declining in many parts of the globe, which can lead to the spreading of barren grounds. Increased abundances of grazers, mainly due to reduction of their predators, are among the causes of this development. Here, we compared the species richness (SR), frequency of occurrence (FO) and maximum abundance (MaxN) of predatory fish and, their predation pressure between kelp forest and barren ground habitats of northern-central Chile. Sampling was done using baited underwater cameras with vertical and horizontal orientation. Two prey organisms were used as tethered baits, the black sea urchin *Tetrapygus niger* and the porcelanid crab *Petrolisthes laevigatus*. SR did not show major differences between habitats, while FO and MaxN were higher on barren grounds in vertical videos, with no major differences between habitats in horizontal videos. Predation pressure did not differ between habitats, but after 24h consumption of porcelanid crabs was significantly higher than that of sea urchins. *Scartichthys viridis/gigas* was the main predator, accounting for 82% of the observed predation events on *P. laevigatus*. Most of these attacks occurred on barren grounds. *Scartichthys viridis/gigas* was the only fish observed attacking (but not consuming) tethered sea urchins. High abundances of opportunistic predators (*S. viridis/gigas*) are probably related with low abundances of large predatory fishes. These results suggest that intense fishing activity on large predators, and their resulting low abundances, could result in low predation pressure on sea urchins, thereby contributing to the increase of *T. niger* abundances in subtidal rocky habitats.

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Abstract

20 Kelp forests are declining in many parts of the globe, which can lead to the spreading of barren

21 grounds. Increased abundances of grazers, mainly due to reduction of their predators, are among

22 the causes of this development. Here, we compared the species richness (SR), frequency of

23 occurrence (FO) and maximum abundance (MaxN) of predatory fish and, their predation

24 pressure between kelp forest and barren ground habitats of northern-central Chile. Sampling was

25 done using baited underwater cameras with vertical and horizontal orientation. Two prey

26 organisms were used as tethered baits, the black sea urchin *Tetrapygus niger* and the porcelanid

27 crab *Petrolisthes laevigatus*. SR did not show major differences between habitats, while FO and

28 MaxN were higher on barren grounds in vertical videos, with no major differences between

29 habitats in horizontal videos. Predation pressure did not differ between habitats, but after 24h

30 consumption of porcelanid crabs was significantly higher than that of sea urchins. *Scartichthys*

31 *viridis/gigas* was the main predator, accounting for 82% of the observed predation events on *P.*

32 *laevigatus*. Most of these attacks occurred on barren grounds. *Scartichthys viridis/gigas* was the

33 only fish observed attacking (but not consuming) tethered sea urchins. High abundances of

34 opportunistic predators (*S. viridis/gigas*) are probably related with low abundances of large

35 predatory fishes. These results suggest that intense fishing activity on large predators, and their

36 resulting low abundances, could result in low predation pressure on sea urchins, thereby

37 contributing to the increase of *T. niger* abundances in subtidal rocky habitats.

Introduction

Kelp forests are communities formed by large brown seaweeds, which can reach high densities and several meters in height (Wernberg et al., 2019). These ecosystems are vital to a wide diversity of invertebrate and fish species (Steneck et al., 2002; Almanza et al. 2012; Miller et al., 2018), providing them with food, shelter and habitat for larval settlement (Graham et al., 2007; Teagle et al., 2017). However, global trends indicate a decline in kelp forests (Krumhansl et al., 2016), as a consequence of poor habitat quality, pollution or sedimentation (Foster & Schiel, 2010), global warming (Wernberg et al., 2010), heatwaves (Wernberg et al., 2013; Oliver et al., 2018), or El Niño events (Tegner & Dayton, 1987; Vega et al., 2005), which affects the reproduction, settlement and physiology of kelp (Simonson et al., 2015; Hargrave et al., 2017). Kelp abundances also can be affected through direct extraction by humans or by increased abundances of grazers (Tegner & Dayton, 2000; Steneck et al., 2002). In the absence of these kelp forests, there are often extensive patches of rock devoid of vegetation called "barren grounds", which have low biodiversity and high abundances of grazers, such as sea urchins and snails (Norderhaug & Christie, 2009; Wernberg et al., 2019).

Grazers, especially sea urchins, are one of the most important factors controlling the distribution of kelp forests and can consume young kelp recruits, thereby suppressing the renewal and recovery of kelp populations (Norderhaug & Christie, 2009; Konar et al., 2014; Perreault et al., 2014; Wernberg et al., 2019). The increase of grazer populations can be due to natural and/or anthropogenic causes, which might generate favourable conditions for the survival and growth of grazers (Guidetti et al., 2003; Leleu et al., 2012; Konar et al., 2014). The best-documented process that affects grazer abundances is the alteration of trophic webs, with a reduced "top-down" pressure due to decreasing predator populations, which then leads to rising

65   grazer populations (Halpern et al., 2006; Leleu et al., 2012; Hamilton & Caselle, 2015; Medrano

66   et al., 2019). Furthermore, there are several examples of top-down effects in kelp forests,

67   especially in marine reserves or marine protected areas, where predators are protected. In these

68   cases, high predator abundances control grazers leading to increased algal biomass (Guidetti,

69   2006; Clemente et al., 2010; Leleu et al., 2012; Selden et al., 2017). Outside of protected areas,

70   many of these predators are important marine resources that have been overharvested by humans

71   (Jackson et al., 2001), thus indirectly leading to a higher grazer pressure.

72   The shallow rocky subtidal zone (0 – 20 m depth) of the Chilean coast is dominated by

73   kelp forests (*Lessonia trabeculata* and *Macrocystis pyrifera*) and barren grounds, the latter

74   characterized by high abundances of sea urchins *Tetrapygus niger* and *Loxechinus albus* and

75   snails from the genus *Tegula* (Dayton, 1985; Vásquez & Buschmann, 1997; Stotz et al., 2016;

76   Pérez-Matus et al., 2017a). In addition to direct human exploitation of seaweeds, these

77   herbivorous species are also considered one of the main causes for the decrease of Chilean kelp

78   forests and their associated fauna (Dayton, 1985; Vásquez & Santelices, 1990; Vásquez &

79   Buschmann, 1997; Henríquez et al., 2011; Perreault et al., 2014). This can be due to a decrease

80   in predation pressure on sea urchins. Some fish species, such as *Pinguipes chilensis*,

81   *Semicossyphus darwini*, *Cheilodactylus variegatus*, *Oplegnathus insignis* and *Graus nigra*, are

82   important predators in the shallow rocky communities of northern-central Chile (Muñoz &

83   Ojeda, 1997; Vargas et al., 1999; Pérez-Matus et al., 2012; Pérez-Matus et al., 2017b) where they

84   also prey on these grazer species. However, most of these fishes have been subject to an intense

85   fishing activity with important population declines in northern-central Chile (Godoy et al., 2010),

86   possibly resulting in the high number of sea urchins (Urriago et al., 2012).

87   Along the Chilean coast, the effects of sea urchins on kelp have been widely studied (e.g.

88   Perreault et al., 2014), but the role of different coastal fish predators in controlling sea urchin

89   populations and the effects of reduced abundances of these fishes in this system are less known.

90   In order to fill this gap, we compared the effect of coastal fishes in kelp forests and on barren

91   grounds in northern-central Chile by surveying fish assemblages and estimating predation on

92   tethered live prey organisms in these contrasting habitats. Kelp forests are structurally complex

93   systems that tend to have greater richness and abundance of predatory species compared to less

94   complex systems (Hauser et al., 2006; Miller et al., 2018; Villegas et al., 2018) such as barren

95   grounds (Sala & Zabala, 1996; Norderhaug & Christie, 2009). Therefore, we expected to find

96   higher species richness and abundances of predatory fish in kelp forests than on barren grounds,

97   and hence higher predation pressure on our baits at sites with a greater presence of predators.

98

Materials & Methods

Study location

101   The study was conducted at four locations in northern-central Chile (28°S – 30°S) between

102   September 2016 and October 2017 (Table S1; Figure 1). Study locations were Caleta Angosta

103   (CA), Punta Choros (PC), Chungungo (CH), and Guayacancito (GU), which are located within

104   the biogeographic province north of latitude 30ºS, considered as an important biogeographical

105   break (Camus, 2001). These locations were chosen mainly because of the presence of one or

106   both communities of interest (kelp forests and barren grounds) and accessibility to the sites. Kelp

107   forests were mainly composed of *Lessonia trabeculata* with a minimum extension of 100 m

108   along the shoreline and had at least a one-year absence of algal harvesting. They were extensive

109   forests with densities that ranged from 0.5 ind. m^2 (PC and CH) to 2 ind. m^2 (CA). Barren

110   grounds were composed of open rock fields, including bedrock and boulders.

111   Sampling was done at an average depth of 10 m on all sites. All study locations were

112   exposed to the open sea. Data were collected in different seasons but considering that coastal

113   fishes present in the study area are mainly non-migratory species (Angel & Ojeda, 2001; Pérez-

114   Matus et al. 2007) and there are only minor seasonal variations among predatory fish

115   assemblages (Pérez-Matus et al. 2007; Pérez-Matus et al. 2012), findings are comparable over

116   time.

117   Two locations had both types of habitat (PC and CH), and kelp forests and barren

118   grounds were separated by approximately 500 m at PC and by ~2,000 m at CH (Figure 1). PC

119   and CH share general characteristics such as (a) distance to large urban centres (moderate

120   potential for anthropogenic disturbances), (b) complex morphology and architecture of the coast

121   and substratum, and (c) administrative regimes under the framework of Management Areas for

122   Benthic Resources (AMERBs for Spanish abbreviation). There were also two distant locations

123   with contrasting habitats, one with a large kelp forest (CA) located at the northern edge of our

124   study area, and the other with an extensive barren ground (GU) located to the south. CA also is

125   located within an AMERB, far from urban centers, while GU is an open access area close to

126   Coquimbo, a major urban center. These locations with non-paired habitat types were included

127   because they belong to coastal stretches of several km with extensive coverage of the respective

128   habitat type (either kelp forest or barren ground). Along the coast of northern-central Chile, it is

129   difficult to find an ideal kelp forest paired with an adjacent barren ground since some areas are

130   heavily exploited for kelps (within and outside of AMERBs), leading to extensive barren

131   grounds. On the other hand, in other areas kelp forests have remained untouched for many years

132   (mostly due to logistic reasons impeding exploitation) and only small patches without kelps are

133   found.

134   To facilitate the following descriptions, we term each habitat at each location a "study

135 site", and so we have 3 sites for kelp forest community (KF-CA, KF-PC, KF-CH) and 3 sites for

136 barren ground community (BG-PC, BG-CH, BG-GU).

137

138 **Experimental design**

139 Fish surveys were conducted with baited remote underwater videos (BRUVs), which allowed us

140 to determine fish abundances, predation pressure and identity of predators. BRUVs consisted of

141 two different types of structures with GoPro cameras in vertical and horizontal orientation,

142 respectively. The first structure (vertical orientation) was a metal frame with the camera fastened

143 in the upper part, which allowed images to be taken from 80 cm above the bottom (vertical view)

144 of an approximate area of 0.6 m^2 (Figure 2A and 2C). The second structure (horizontal

145 orientation) was a plate with a metal arm to which the camera was fastened, which took

146 panoramic images (horizontal view) where the bottom area was measured as a trapezium (Figure

147 2B and 2D). Each structure had on its base an eternit fibre cement plate of 40 x 40 cm side

148 length, to which prey items were tethered. Each plate contained 6 tethered juveniles of the black

149 sea urchin *Tetrapygus niger* or 6 juveniles of the porcelanid crab *Petrolisthes laevigatus*,

150 respectively (see details below). Both types of structures were held on the bottom by concrete

151 pieces of 1 kg or mesh filled with stones and a small and numbered plastic bottle was attached

152 with a thin rope to each structure, allowing us to rapidly locate them from the boat.

153   Two different types of structures were used due to their respective advantages and/or

154 shortcomings: vertical structures, with a small area, allowed more precise images (because the

155 camera is closer to the plate), which is very useful to identify fish species and to observe

156 predation events on tethered baits when visibility is low (see also Schettini & Corchs, 2010), but

157 the vertical videos do not allow to observe the surrounding community; on the other hand,

158   horizontal structures produce a greater, but more imprecise observational area, allowing to see

159   what happens in the surrounding community during the assay period, although high turbidity

160   might occasionally limit visibility. Indeed, most studies that use cameras to describe subtidal fish

161   assemblages have the cameras oriented in the horizontal plane (e.g. Malcolm et al., 2007; Duffy

162   et al., 2015).

163   At each study site (KF-CA, KF-PC, KF-CH, BG-PC, BG-CH, BG-GU), five vertical and

164   five horizontal structures were randomly distributed for each prey (not all of them with camera,

165   because of camera availability). Deployment of the assays was repeated over two different days,

166   because only 5 structures were available of each type (vertical and horizontal; see Table S2). So,

167   after the two deployment days there were 5 replicates with *P. laevigatus* on horizontal structures

168   and 5 replicates with *P. laevigatus* on vertical structures, and the same for *T. niger*. This was

169   done during consecutive days for CA and PC, but not for CH and GU, due to logistic reasons

170   (e.g. poor weather conditions delaying the continuation of field work for a few weeks). However,

171   since fish assemblages do not vary much over the year (Pérez-Matus et al., 2007; Pérez-Matus et

172   al., 2012), this should not affect the results. Assays were deployed between 9:00 am and 11:00

173   am, at ~10 m depth (at sites with abundant kelp coverage in the case of kelp forest habitats, see

174   Figure S1), and separated from each other by similar distances (~10 m), following a line parallel

175   to the coast. The distance of 10 meters between structures is considered sufficient to prevent the

176   directional movement of fishes from one structure to the next. The fish species observed in our

177   study move randomly and the most frequent fishes are small and territorial species, and thus

178   movements between structures are unlikely and each structure can be considered an independent

179   replicate. Furthermore, visibility in the system is limited due to kelp fronds, complex habitat

180   structures with large boulders or rocky outcrops, and high turbidity, thus limiting visibility from

181   one structure to the next. Field work was conducted under the resolution 2,649 from

182   "Subsecretaría de Pesca y Acuicultura" (SUBPESCA) published in the "Diario Oficial de la

183   Republica de Chile", num. 41,553 on 7 September 2016.

184

185   **Fish species richness, frequency of occurrence and maximum abundance**

186   We used video recordings to compare species richness (SR), frequency of occurrence (FO), and

187   maximum abundance (MaxN) of fish between habitats, and to determine the total number of

188   species (total species richness) per site. In each recording, we registered fish species and their

189   abundances every 30 sec (video frame). When it was not possible to adequately scan a video

190   frame (e.g. kelp blades in front of the camera), the closest visible frame was analysed. For

191   horizontal videos, only fish observed within < 2 m distance from the camera (distance estimates

192   based on reference points of the structures) were recorded, thereby generating a standardized

193   survey area for all videos; there were no videos with a visibility of < 2 m. We obtained a total of

194   81 videos for both habitat and structure types (for details, see Table S2).

195   SR was the number of species per video for each study site, FO was calculated as the

196   proportion of frames in which the respective species was observed over the total number of

197   frames analysed in each video (80 frames; providing information about residence or staying

198   time), and MaxN was the maximum number of individuals of the respective species in a video

199   (recorded in one of the 80 examined frames, i.e. there is only one value of MaxN per species per

200   video), which provides information about the relative abundance of the given species at the study

201   site (Cappo et al., 2003). All fishes were identified to species based on their shape, colour, and

202   swimming habits, with the exception of *Scartichthys*, of which two species occur in the study

203   area, *S. viridis* and *S. gigas*. These species are common in northern Chile and display variable

204   colour patterns (Méndez-Abarca & Mundaca, 2016), making it sometimes difficult to distinguish

205   among them, especially in videos with limited visibility. As both species are of similar size and

206   ecological habits, we treated them as *Scartichthys viridis/gigas* (see also Villegas et al., 2018).

207   To standardize the recordings, only the initial 40 min of each video were used (see also Willis &

208   Babcock, 2000), obtaining 80 frames for counting data. This standardization was done for the

209   analysis of SR, FO and MaxN, all with one single data point per video for analyses. Species

210   accumulation curves for the two types of habitat confirmed that mean number of species

211   recorded with the videos approached an asymptote before 40 min (Figure S2), a time frame also

212   confirmed for a similar study system by Harasti et al. (2015). Only total species richness and

213   predation events were assessed using the entire duration of the videos.

214

215   **Predation assays and identity of predators**

216   We measured predation pressure using tethered prey organisms (*T. niger* and *P. laevigatus*) as

217   bait. Tethering has been used in different types of communities and with various types of prey,

218   including snails (Reynolds et al., 2018), crustaceans (Heck & Wilson, 1987; Gutow et al., 2012;

219   Ory et al., 2012), sea urchins (Urriago et al., 2011, 2012), and fishes (Pérez-Matus et al., 2016).

220   Since refuge availability, prey behaviour, and other variables can affect the outcome of tethering

221   assays, these should only be used to assess relative predation or predation pressure within the

222   same ecosystem; following those basic recommendations (as done in our study) tethering assays

223   continue to be a useful tool for comparing the predation rates among different habitats or

224   environments (Aronson & Heck, 1995).

225   As small sea urchins tend to be susceptible to predation (McClanahan, 1988), juvenile sea

226   urchins *T. niger* (15 - 25 mm test diameter) were tethered with monofilament fishing line (0.15

227   mm diameter) according to the methodology used by McClanahan & Muthiga (1989) and

228   McClanahan & Shafir (1989). The porcelanid crab *P. laevigatus* was included in our study for

229   comparative purposes, because along the Chilean coast decapod crustaceans are more frequent

230   prey than sea urchins in the diet of common fish predators from subtidal hard bottoms (Pérez-

231   Matus et al., 2012). Thus, this crab was used to validate background predation in the study area.

232   Individuals of *P. laevigatus* (15-20 mm of cephalothorax) were tethered by gluing a piece of

233   monofilament to the carapace with cyanoacrylate glue. Preliminary experiments of 24h duration

234   were run in laboratory tanks with tethered individuals, and neither mortality (because of the

235   tether) nor escapes were observed.

236   Prey organisms were tethered on eternit plates to provide a uniform surface to prey and

237   predators across different types of habitats; this way different refuge structures and prey hiding

238   behaviour in the two habitat types would not interfere with the estimates of predation pressure.

239   After 24 hours, missing prey items were counted for each structure and divided by the total

240   number of baits (n = 6 per structure), obtaining the proportion consumed. Using video

241   recordings, we also identified predator species that consumed either sea urchins or crabs. It

242   should be noted that data about predation events (from videos) only included the period until the

243   cameras stopped recording (after ~40 – 60 minutes), and we may not have identified all species

244   that might have fed on our prey organisms during the 24h of consumption assays.

245

246   **Data analyses**

247   We analysed fish species richness, FO and MaxN separately for vertical and horizontal

248   structures, considering the differences in the view field of each structure. The predation data after

249   24h were pooled for both structures, because the plate areas with attached prey organisms were

250   the same, irrespective of the structure.

251   For analysis, data from the two sampling days were pooled (see also above). All

252   procedures were performed through stepwise model selection on the raw data, according to

253   methods from Zuur et al. (2009). Species richness data were contrasted between habitats and

254   sites using generalized linear models (GLM), pooling video data from both prey species;

255   consumption was contrasted between habitat and prey using GLM, pooling video data from the

256   two different structures; and FO and MaxN were contrasted between habitat and prey types using

257   generalized linear mixed models (GLMMs), considering the values of FO or MaxN, respectively,

258   of each species per video as duplicates. GLMMs allowed us to account for our unbalanced, over-

259   dispersed and zero-inflated data set (Zuur et al., 2009). In GLMM analyses, we included habitat

260   and prey type as fixed factors; and sites, fish species, and individual observations (replicates)

261   were included as random factors. Zero inflation structure in FO GLMMs was attributed to habitat

262   and prey type, whereas in MaxN GLMMs it was only attributed to habitat. Sample replicates

263   were included as observational-level random effects in order to account for overdispersion, as

264   recommended by Bolker et al. (2009). The best model fit was selected based on the lowest

265   corrected Akaike Information Criterion (AICc) value. Model validation was then evaluated

266   through graphical observations of the normality of residuals and the relationship between both

267   observed and standardized residuals against fitted values (Bolker et al., 2009; Zuur et al., 2009).

268   All best-fit model validations exhibited an acceptable relationship of residuals against

269   fitted values. Most residuals were normally distributed, while observed residual against fitted

270   values did not show any pattern. However, subtle heterogeneities in standardized residuals

271   against fitted values were observed in some cases. Additional structural-zeros were not predicted

272   for any of the final best-fit models.

273   Statistical analyses and graphics were done using the R environment (R core team 2019),

274   and its libraries glmmTMB (Brooks et al., 2017), AICcmodavg (Mazerolle, 2019), DHARMa

275   (Hartig, 2018), ggplot2 (Wickham, 2016), and MASS (Venables & Ripley, 2002).

276

277   **Results**

278   **Fish species richness, frequency of occurrence and maximum abundance**

279   We observed a total of 11 fish species analysing the entire video duration, 10 species in kelp

280   forests and 8 on barren grounds (Figure 3). A species that was absent in kelp forests was

281   *Paralabrax humeralis*, which was only observed at BG-PC, while the following species were not

282   recorded on barren grounds: *Graus nigra, Semicossyphus darwini* and *Acanthistius pictus*. The

283   latter two were only observed at KF-CA. The highest total number of species (9 species) were

284   observed in the CA kelp forest, while only 4 species were seen on the GU barren ground. For PC

285   and CH, where both habitats were present, BG and KF had similar total species richness (6 and 5

286   species, respectively, in both locations, Figure 3).

287   SR (mean ± standard deviation) ranged from 1.2 ± 0.4 fish species in the CH kelp forest

288   to 2.8 ± 1.6 in the CA kelp forest. The low values of SR were due to videos in which only one or

289   two species were observed (see the dots in Figure 4). SR was similar between locations and

290   habitats, both for videos with vertical and horizontal view (Figure 4, Table S4).

291   *Scartichthys viridis/gigas* was the most abundant species, followed by *Pinguipes chilensis*

292   and *Cheilodactylus variegatus*, in both vertical and horizontal videos (Figure 5). *Scartichthys*

293   *viridis/gigas* and *P. chilensis* used to be the first species to arrive in the visual field of the

294   cameras (in both habitats). It was very common to see these species within seconds after the

295   structure was deployed, or even when the diver was still there. Other, less common species were

296   observed in videos within minutes after deployment.

297   For vertical videos, there were no differences in FO between prey types, although barren

298   grounds were significantly different from kelp forests (Wald z=4.625, df residual=359, p <

299   0.001). In addition, random effects were largely determined by fish species variance (Table S6).

300   For horizontal videos, we also found no differences in FO between prey types and FO was higher

301   on barren grounds (Wald z=2.311, df residual=341, p =0.0208). Random effects were again

302   determined by fish species variance (Table S7). For the FO of three species that generated the

303   greatest random effect, *S. viridis/gigas* and *P. chilensis* reached higher values on barren grounds

304   (mainly in vertical videos), whereas *C. variegatus* mostly had higher values of FO in kelp forests

305   (Figure 5). Other predatory species, although present, occurred very infrequently, seen only in

306   one video or in few frames.

307   MaxN for the same three most abundant predatory fish species followed a similar pattern

308   as for FO, both in vertical and horizontal videos. For vertical videos, prey type did not exhibit a

309   significant effect, although barren grounds were significantly different from kelp forests (Wald

310   z=4.793, df residual=360, p<0.001). Random effects were again largely determined by fish

311   species variance (Table S8). For horizontal videos, there was no effect of prey type, although

312   barren grounds exhibited marginal differences with kelp forests (Wald z=2.032, df residual=343,

313   p=0.0422). Random effects were determined by fish species, although its variance was the

314   smallest among the three previous analyses (Table S9). MaxN of *Scartichthys viridis/gigas* and

315   *P. chilensis* followed a pattern similar to FO (Figure 6) and MaxN of *C. variegatus* was similar

316   among study sites.

317   Even though the sizes of fishes were not consistently estimated in this study, all observed

318   fishes were smaller than the plates (40 cm side length) to which prey items were tethered. The

319   individuals of *Pinguipes chilensis* seen near the plates in videos were ~20 to 30 cm in body

320   length. In the less abundant species *Graus nigra*, all individuals were juveniles of ~30 cm. Also,

321   during the deployment of structures, no large individuals of these species were seen by the

322   divers.

323

324   **Predation assays and identity of predators**

325   Predation pressure for both prey species did not vary across locations and habitats, but

326   significant differences were observed between sea urchin and crab consumption. Predation of

327   porcelanid crabs was significantly higher than that of sea urchins (Wald $z=-6.396$, df

328   residual$=116$, $p<0.001$, Table S10). Consumption of *T. niger* ranged from $8.3 \pm 14.2\%$ on CH

329   barren grounds to $29.6 \pm 28.6\%$ on GU barren grounds (Figure 7a). In contrast, predation of

330   porcelanid crabs ranged from $38.3 \pm 34.3\%$ in the PC kelp forest to $86.7 \pm 31.2\%$ on CH barren

331   grounds (Figure 7b).

332   *Scartichthys viridis/gigas* and *C. variegatus* were seen preying on bait in video recordings

333   (Table S3). *Scartichthys viridis/gigas* was the principal consumer of crabs (82% of consumed

334   prey) preying on 25 individuals of *P. laevigatus* on barren grounds and 7 individuals in kelp

335   forests. *Scartichthys viridis/gigas* was also the only fish species recorded attacking (but not

336   consuming) *Tetrapygus niger*. It was observed in 3 instances turning over sea urchins (solitary

337   individuals) and attacking them orally on CH and PC barren grounds. One instance each of

338   predation by the brachyuran crabs *Homalaspis plana* and *Romaleon setosum* was observed,

339   consuming sea urchins *T. niger* on PC barren grounds. Additionally, a predation event by the

340   gastropod *Concholepas concholepas* over *P. laevigatus* was observed by the diver when cameras

341   were removed (two hours after deployment), but this was not recorded in videos.

342

Discussion

344   Fish species richness showed no major differences across locations and habitats, contrary to what

345   was expected (higher richness in kelp forests). Values of FO and MaxN showed minor

346   differences between habitats, which when observed, were higher on barren grounds than in kelp

347   forests. These differences were mainly due to the presence of two abundant species *Scartichthys*

348   *viridis/gigas* and *Pinguipes chilensis*, while other large fish predators occurred very infrequently.

349   Predation on *Petrolisthes laevigatus* was significantly higher than on *Tetrapygus niger*, possibly

350   because crabs are a major diet component of coastal fishes, or because large predatory fish that

351   could have consumed the sea urchins were mostly absent. *Scartichthys viridis/gigas* was the

352   principal predator identified in this study, mainly consuming crabs; it was also the only fish that

353   was observed attacking *T. niger*, confirming the predatory character of this species. Total

354   consumption after 24h was similar between habitats, coinciding with the minor or lack of

355   differences in MaxN and FO. Our findings suggest that *T. niger* might have increased in

356   abundances on subtidal hard bottoms, because current predation pressure on this species is low,

357   possibly due to overall reduced abundances of large, top fish predators.

358

Fish communities

360   Fish assemblages observed here were composed of typical species from the Chilean coast. The

361   comparatively low total number of fish species per site was similar to species richness of reef-

362   fish observed by other studies along the central and northern coast of Chile (Gelcich et al., 2008;

363 Ory et al., 2012; Villegas et al., 2018). Pérez-Matus et al. (2007) studied the structure of fish

364 assemblages in northern Chile and found that CA was the site with the highest species richness.

365 This site was also the location with the highest total number of species in our study, but when

366 comparing average SR per video among study sites, no differences were observed. SR did not

367 vary across locations and habitats, except for vertical videos where species richness was higher

368 on barren grounds. This is not totally unexpected, because although kelp forests usually have

369 higher diversity than other types of communities (Levin & Hay, 1996; Graham, 2004), a recent

370 study in New Zealand also observed higher species richness, abundance and predation pressure

371 by fish on barren grounds than in kelp forests (Hesse et al., 2016). On the other hand, Angel &

372 Ojeda (2001) observed similar values in coastal fish abundances and diversity in northern Chile,

373 when comparing a site with kelp forest and a site without forest.

374   *Scartichthys viridis/gigas* and *Pinguipes chilensis* were the most abundant species at all

375 study sites, being more frequent on barren grounds albeit with small differences in horizontal

376 videos (wider field of view). *Scartichthys viridis/gigas* are comparatively small fishes (10 – 20

377 cm adult size) that are not commercially fished (Méndez-Abarca & Mundaca, 2016) and are very

378 common in subtidal habitats of northern Chile (Villegas et al., 2018; this study). On the other

379 hand, *P. chilensis* was consistently present on barren grounds but not in kelp forests, which

380 appears to be typical for this species, since previous studies had observed that its abundances

381 increase when density of kelp forests decreases (Pérez-Matus et al., 2007). The third most

382 abundant predatory species was *Cheilodactylus variegatus*, which despite being more common in

383 kelp forests (Angel & Ojeda, 2001; Pérez-Matus et al., 2007; Villegas et al., 2018) did not show

384 statistical differences in this study.

385   Several fish species that are typical members of kelp forest communities in northern

386   Chile were rarely seen in our study (e.g. *Hemilutjanus macrophthalmos*, *Graus nigra* and

387   *Semicossyphus darwini*; Pérez-Matus et al., 2012), possibly due to low abundances caused by

388   high fishing pressure (Godoy et al., 2010, 2016). It should be noted that the method often used

389   for the determination of species richness are visual transect surveys (e.g. Pérez-Matus et al.,

390   2007; Ory et al., 2012). Static recordings (video), as used in our study, could underestimate

391   richness and abundances, because less abundant or less mobile species will be less frequently

392   seen compared to visual transect surveys covering more extensive areas (Pérez-Matus et al.,

393   2007). This could be partly responsible for the low abundances observed; indeed, we generally

394   observed higher abundances in the horizontal videos with wider visual field. On the other hand,

395   visual surveys may underestimate the presence and abundance of fish species with cryptic

396   behaviours (Willis, 2001), such as *S. viridis/gigas*, the most frequent and abundant species in our

397   study. Using both methods (visual transect surveys, and BRUVs) in the same study could

398   provide the best estimates of species richness and abundance of demersal fishes, since biology

399   and behaviour of studied species could affect results when using different census methods

400   (Willis et al., 2000).

401

402   Predation rates across communities

403   We observed no significant differences in predation rates between habitats for both prey species,

404   which also coincides with findings of similar fish assemblages in kelp forests as well as on

405   barren grounds. On the other hand, consumption was very different between the two prey

406   species, with crabs being much more consumed than sea urchins. This was somewhat expected

407   because crustaceans have a greater index of relative abundance in the stomach contents of

408   temperate reef fishes (Vargas et al., 1999; Medina et al., 2004; Pérez-Matus et al., 2012), thus

409   being preferred over sea urchins. However, although echinoderms are not the most consumed

410   prey items, they are frequently found in the stomach contents of these fish. The more abundant

411   predators (*Scartichthys viridis/gigas* and *Pinguipes chilensis*) were ineffective in consuming sea

412   urchins, while the other less abundant species (e.g. *Graus nigra*, *Semicossyphus darwini*, or

413   *Cheilodactylus variegatus*) are recognized as important top predators along the Chilean coast

414   (Pérez-Matus et al., 2007; Pérez-Matus et al., 2017b). Indeed, Selden et al. (2017) described a

415   direct relationship between the rate of sea urchin consumption and the size of the predatory fish

416   *Semicossyphus pulcher* in California. The lack of large individuals of *S. darwini* and similar fish

417   predators in our study area could thus be an explanation for low predation pressure on sea

418   urchins, thereby ultimately being responsible for their proliferation and the establishment of

419   extensive barren grounds along the coast of northern Chile.

420   Seasonality could also affect results since this study was done over a year. Seasonal

421   temperature variations may affect metabolic rates of organisms (Brown et al., 2004; Milazzo et

422   al., 2013), and thereby influence their predation rates (Duffy et al., 2015). However, seasonal

423   temperature variation along the exposed coast of Chile are rather moderate (Thiel et al., 2007)

424   and might be insufficient to generate metabolic shifts in consumers as has been described for

425   other latitudes (Brown et al., 2004). Furthermore, fish assemblages in the study region are similar

426   across different seasons and fish species are characterized as being territorial and non-migratory

427   (Angel & Ojeda, 2001; Pérez-Matus et al., 2007; Pérez-Matus et al., 2012). Consequently, it is

428   unlikely that fish abundances and predation rates are affected by the season.

429   *Scartichthys viridis/gigas* was the species that consumed the most prey during video

430   recordings. This species has originally been described as an herbivorous species with more than

431   90% of their stomach contents comprising seaweeds, mostly chlorophytes and rhodophytes

432   (Ojeda & Muñoz, 1999; Muñoz & Ojeda, 2000). However, those studies were conducted on

433   individuals from the intertidal zone, with little information on the foraging behaviour of this

434   species in subtidal habitats. Ory et al. (2012) observed effective predation events of *S. viridis* on

435   *Rhynchocinetes typus* in the shallow subtidal zone: the initial attack of an individual, usually

436   adult, triggers a series of joint attacks by multiple conspecifics, forming a kind of feeding frenzy,

437   which ends when the prey item is completely consumed. Similar observations had already been

438   reported by Dumont et al. (2011), classifying *S. viridis* as the most efficient predator on the

439   ascidian *Ciona intestinalis* within the Coastal System of Coquimbo (30°S). Our study not only

440   confirms active predation but also group foraging in *S. viridis/gigas.* However, similar to reports

441   by Urriago et al. (2012), *S. viridis/gigas* attacked and damaged *T. niger* but did not achieve

442   successful predation in our videos. Whether the frenzy generated by this blennid fish might

443   attract other predators of sea urchins is not known at present.

444   *Cheilodactylus variegatus* was the only other predatory fish preying on our baits,

445   specifically on crabs, which is consistent with previous studies that observed porcelanid crabs in

446   the diet of this species (Angel & Ojeda, 2001; Palma & Ojeda, 2002; Pérez-Matus et al., 2012).

447   There are several other fish species that could have preyed on our baits, such as *G. nigra, S.*

448   *darwini, H. macrophthalmos* and *P. chilensis*, among others (Muñoz & Ojeda, 1997; Medina et

449   al., 2004; Pérez-Matus et al., 2012). These species, which could potentially be predators and

450   controllers of sea urchins, were not identified as predators, most likely because they were only

451   observed in low abundances in our study (except for *P. chilensis*). Possibly, low abundances and

452   the small sizes of adult fishes observed in our videos (see also Selden et al., 2017) are the main

453   reason for not recording them to prey on our baits. On the other hand, some of the species that

454 consumed our prey (during the 24h of the assay) may have nocturnal behaviours and were thus

455 not captured by our diurnal video recordings.

456   In addition to fish predators, seastars *Heliaster helianthus* and *Meyenaster gelatinosus* are

457 among the main consumers of sea urchins (Gaymer & Himmelman, 2008; Urriago et al., 2011,

458 2012), but in our study they seemed to be unimportant, not being interested in the tethered prey.

459 On the other hand, brachyuran crabs *Homalaspis plana* and *Romaleon setosum* were observed

460 attacking (and successfully preying on) tethered sea urchins. While our study is focused on fish

461 predators, crabs also might be important controllers of black sea urchins, an interpretation that is

462 supported by previous studies that have recognized these species as consumers of echinoids

463 (Morales & Antezana, 1983; Cerda & Wolff, 1993). Future studies of subtidal predator

464 assemblages should also take carnivorous crabs into account, because they seem to have an

465 important role in subtidal rocky reefs.

466

467 **Conclusion**

468 We observed no differences in predation pressure between habitats, which could be related to the

469 similar species richness and abundances of the observed fishes. We also recorded very low

470 abundances of important top fish predators at all sites (e.g. *Semicossyphus darwini*), which might

471 be due to overfishing (Godoy et al., 2010; Godoy et al., 2016) or due to the method used to count

472 (stationary videos). The overall lack of large fish predators may also facilitate small and

473 opportunistic predators such as *Scartichthys viridis/gigas* (not subject to fishing), which have

474 been observed in this study as important predators in both habitats, kelp forests and barren

475 grounds. The fact that these small fish were frequently observed in open areas during bright

476 daylight furthermore suggests that large predatory fish are rare in the study area, which could

477   also have favoured sea urchin survival and spreading on subtidal hard bottoms. In summary, high

478   fishing pressure and the consequent lack of top fish predators may have profound effects on

479   shallow subtidal communities along the Chilean coast. This needs further attention, considering

480   the ecological importance of kelp forests and their increasing exploitation (Almanza &

481   Buschmann, 2013; Buschmann et al., 2014).

482

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488

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Figure 1

Map of the 4 sampling locations along the Chilean coast and their corresponding habitats.

Black triangles indicate kelp forest sites at Caleta Angosta (CA), Punta de Choros (PC) and Chungungo (CH) and black dots indicate barren ground sites at PC, CH, and Guayacancito (GU). All sites are within management areas (AMERBs), except for GU, which is an open access area. Images were extracted from Google Earth Pro program. Image © 2018 Google, CNES/ airbus 2019, Terrametrics 2019.

CA ▲

PC ▲●

▲● CH

GU ●

Punta de Choros (PC)

Google Earth

Chungungo (CH)

Google Earth

▲ Kelp forest (KF)

● Barren grounds (BG)
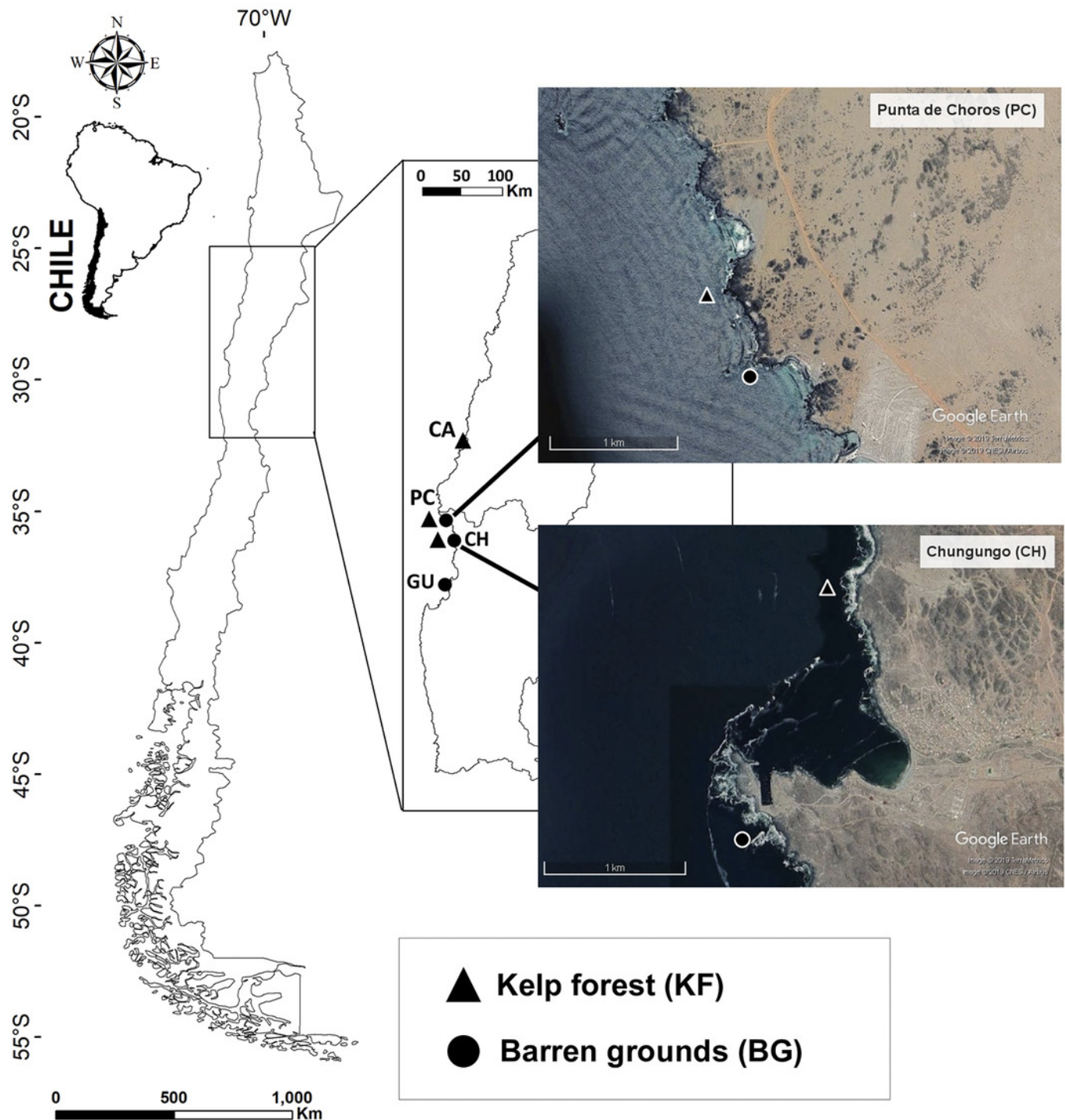
Figure 2

Structures used to record communities, to carry out predation assays and to document predation events.

(A) Metal frame structure to generate vertical view, (B) Metal arm structure to generate horizontal view, (C) vertical view perpendicular to the bottom, and (D) horizontal view parallel to the bottom. Square structures on the base of the structures were eternity fibre cement plates of 40 x 40 cm. Photo Credits: Nicolás Riquelme-Pérez.
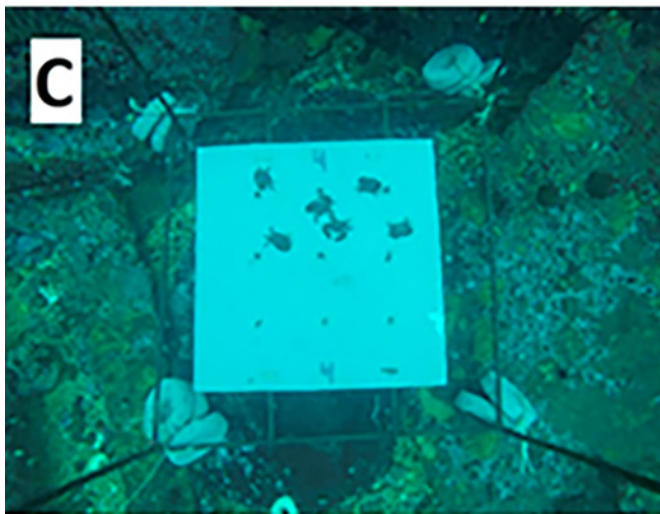
Figure 3

Species of fish observed in videos by location and habitat (KF= Kelp forest, BG= Barren grounds), black fish shapes show presence.

Fish species richness is the number of fish species observed at the respective location and habitat. *Species observed outside the 40 min standardized video duration for quantitative evaluation.

Species	CA	PC		CH		GU
	KF	KF	BG	KF	BG	BG
Scartichthys viridis/gigas	✓	✓	✓	✓	✓	✓
Pinguipes chilensis	✓		✓	✓	✓	✓
Cheilodactylus variegatus	✓	✓	✓	✓	✓	✓
Aplodactylus punctatus	✓	✓	✓	✓		
Chromis crusma		✓	✓		✓	✓
Labrisomus philippii	✓	✓			✓	
Hemilutjanus macrophthalmos	✓				✓	
Graus nigra	✓			✓		
Paralabrax humeralis				✓		
Semicossyphus darwini	*✓					
Acanthistius pictus	*✓					
Total fish species richness:	9	5	6	5	6	4
Number of videos (Vertical/Horizontal):	7/5	9/9	6/8	5/6	8/6	6/6

Figure 4

Fish species richness (SR, number of species video^{-1}) by study site, observed in videos with (a) vertical, and (b) horizontal view.

Only the first 80 frames were considered, each frame was scanned every 30 sec during the first 40 min of the video. The box plots present first and third quartile, while the bold lines in the boxes show the medians of SR. Vertical lines are the minimum and maximum values (1.5*IQR, interquartile range); dots show jittered raw data points and dots outside the range are outliers.
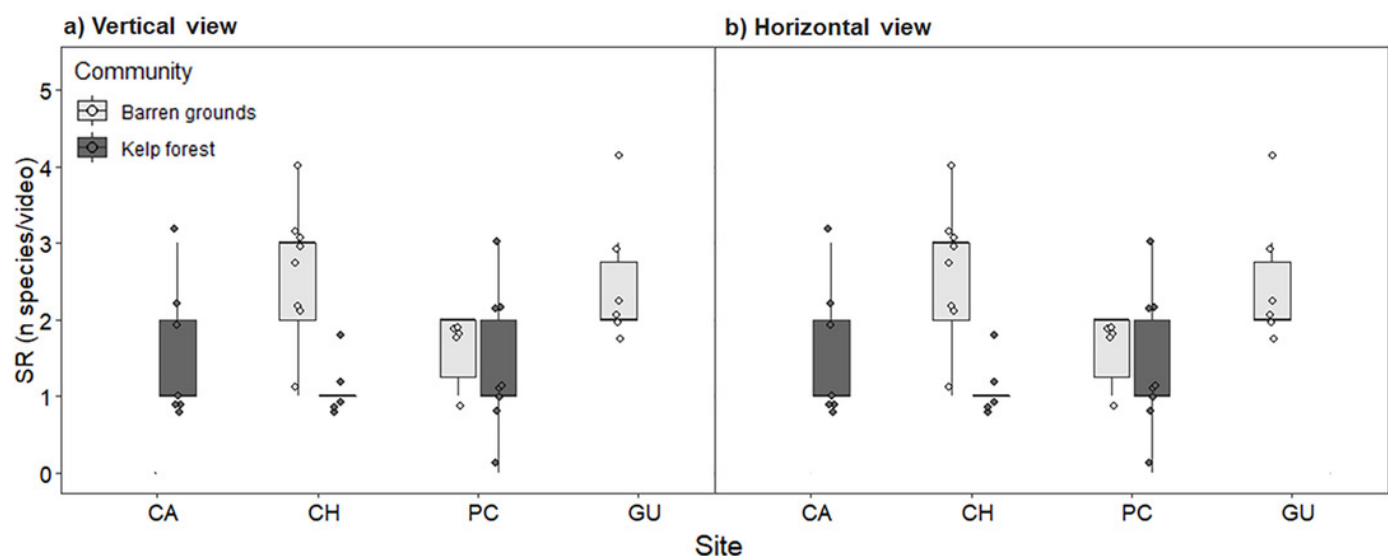
Figure 5

Frequency of occurrence (%) (FO) of the three most common predatory fish species by study site in videos with (a) vertical, and (b) horizontal view.

FO was percentage of frames in which at least one individual of each species was observed (of a total of 80 frames that were scanned every 30 sec during the first 40 min of the video). The box plots present first and third quartile, while the bold lines in the boxes show the medians of FO; vertical lines are the minimum and maximum values (1.5*IQR or the interquartile range); dots show jittered raw data points and dots outside the range are outliers; dots with a number above them (which correspond to a FO value), represent outliers outside the y-axis scale.

a) Vertical view   b) Horizontal view
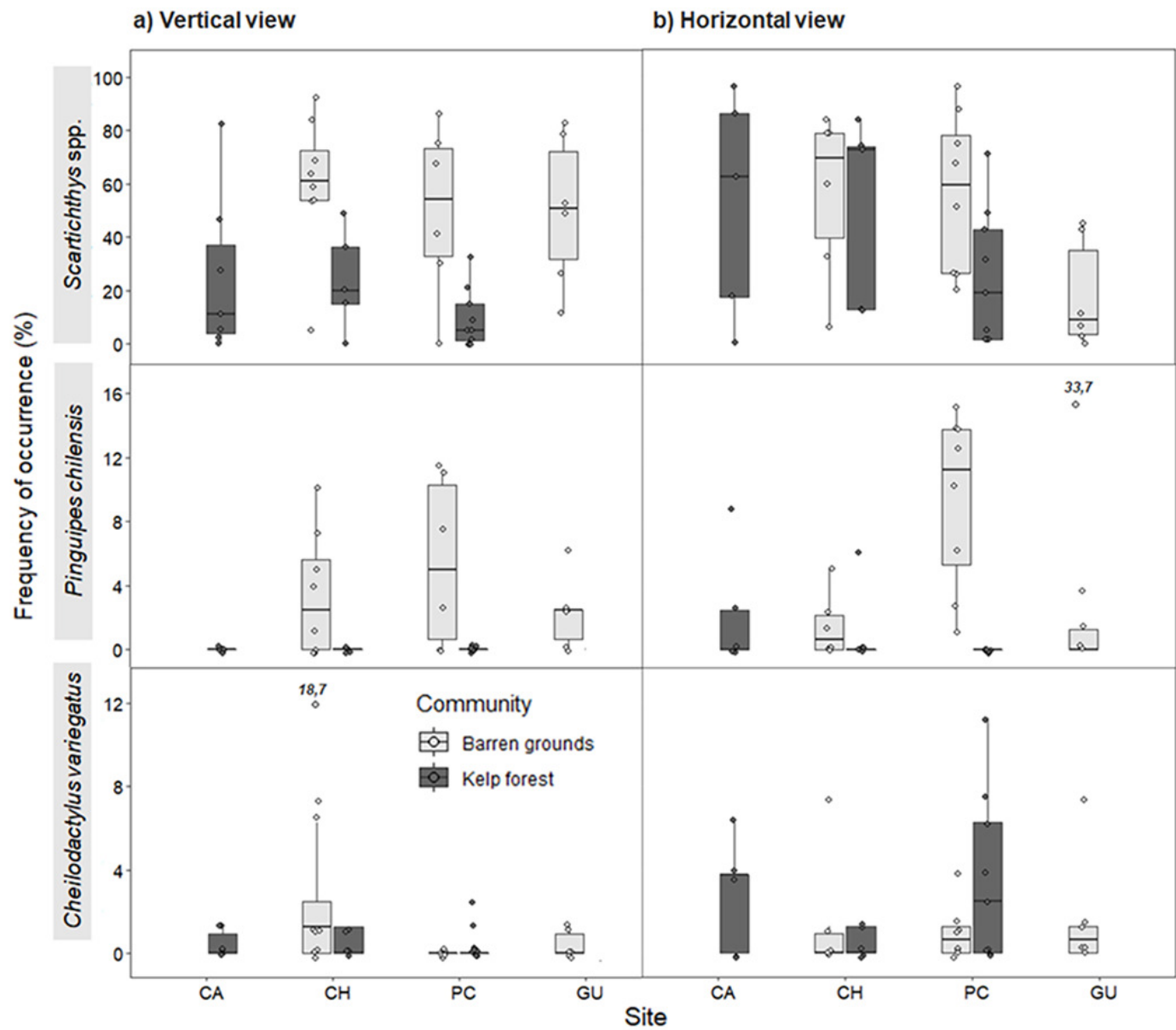
Figure 6

Maximum abundance (MaxN) of the three most common predatory fish species by study site in videos with (a) vertical, and (b) horizontal view.

MaxN indicates the maximum abundance of any species observed in one of the 80 frames that were surveyed every 30 sec during the first 40 min of the video recordings. The box plots present first and third quartile, while the bold lines in the boxes show the medians of MaxN; vertical lines are the minimum and maximum values (1.5*IQR or the interquartile range); dots show jittered raw data points and dots outside the range are outliers; dots with a number above them (which correspond to a MaxN value) represent outliers outside the y-axis scale.

a) Vertical view   b) Horizontal view
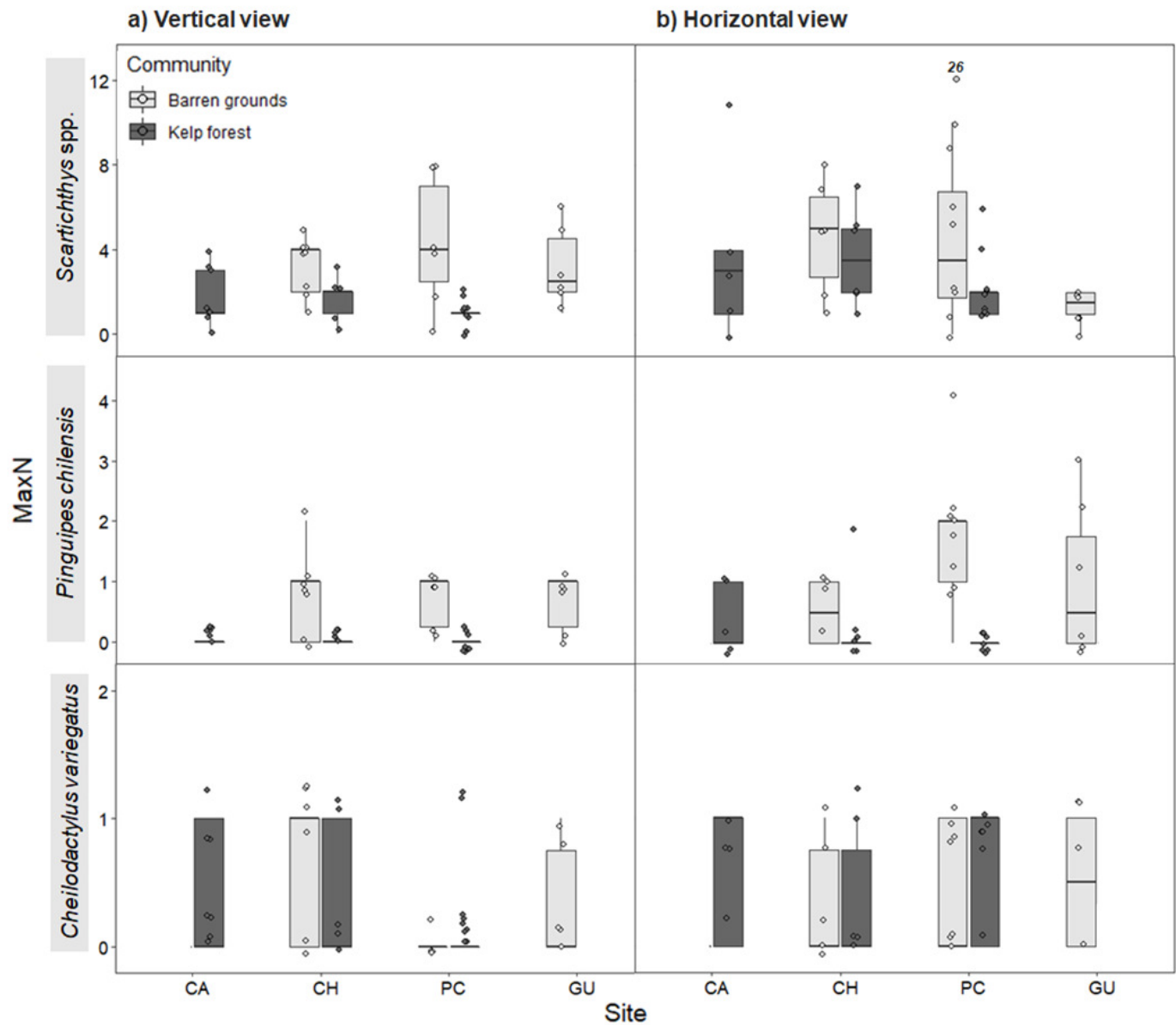
Figure 7

Percentage of (a) *T. niger* (sea urchin), and (b) *P. laevigatus* (crab) consumed at each study site.

The box plots present first and third quartile, while the bold lines in the boxes show the medians of consumption (%); vertical lines are the minimum and maximum values (1.5*IQR or the interquartile range); dots show jittered raw data points and dots outside the range are outliers.

a) *Tetrapygus niger*

b) *Petrolisthes laevigatus*