

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 porcelainid crab *Petrolisthes laevis*. 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 porcelainid 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. laevis*. 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

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 porcelainid 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 porcelainid 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.

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

grazer populations (Halpern et al., 2006; Leleu et al., 2012; Hamilton & Caselle, 2015; Medrano et al., 2019). Furthermore, there are several examples of top-down effects in kelp forests, especially in marine reserves or marine protected areas, where predators are protected. In these cases, high predator abundances control grazers leading to increased algal biomass (Guidetti, 2006; Clemente et al., 2010; Leleu et al., 2012; Selden et al., 2017). Outside of protected areas, many of these predators are important marine resources that have been overharvested by humans (Jackson et al., 2001), thus indirectly leading to a higher grazer pressure.

The shallow rocky subtidal zone (0 – 20 m depth) of the Chilean coast is dominated by kelp forests (*Lessonia trabeculata* and *Macrocystis pyrifera*) and barren grounds, the latter characterized by high abundances of sea urchins *Tetrapygus niger* and *Loxechinus albus* and snails from the genus *Tegula* (Dayton, 1985; Vásquez & Buschmann, 1997; Stotz et al., 2016; Pérez-Matus et al., 2017a). In addition to direct human exploitation of seaweeds, these herbivorous species are also considered one of the main causes for the decrease of Chilean kelp forests and their associated fauna (Dayton, 1985; Vásquez & Santelices, 1990; Vásquez & Buschmann, 1997; Henríquez et al., 2011; Perreault et al., 2014). This can be due to a decrease in predation pressure on sea urchins. Some fish species, such as *Pinguipes chilensis*, *Semicossyphus darwini*, *Cheilodactylus variegatus*, *Oplegnathus insignis* and *Graus nigra*, are important predators in the shallow rocky communities of northern-central Chile (Muñoz & Ojeda, 1997; Vargas et al., 1999; Pérez-Matus et al., 2012; Pérez-Matus et al., 2017b) where they also prey on these grazer species. However, most of these fishes have been subject to an intense fishing activity with important population declines in northern-central Chile (Godoy et al., 2010), possibly resulting in the high number of sea urchins (Urriago et al., 2012).

Along the Chilean coast, the effects of sea urchins on kelp have been widely studied (e.g. Perreault et al., 2014), but the role of different coastal fish predators in controlling sea urchin populations and the effects of reduced abundances of these fishes in this system are less known. In order to fill this gap, we compared the effect of coastal fishes in kelp forests and on barren grounds in northern-central Chile by surveying fish assemblages and estimating predation on tethered live prey organisms in these contrasting habitats. Kelp forests are structurally complex systems that tend to have greater richness and abundance of predatory species compared to less complex systems (Hauser et al., 2006; Miller et al., 2018; Villegas et al., 2018) such as barren grounds (Sala & Zabala, 1996; Norderhaug & Christie, 2009). Therefore, we expected to find higher species richness and abundances of predatory fish in kelp forests than on barren grounds, and hence higher predation pressure on our baits at sites with a greater presence of predators.

Materials & Methods

Study location

The study was conducted at four locations in northern-central Chile (28°S – 30°S) between September 2016 and October 2017 (Table S1; Figure 1). Study locations were Caleta Angosta (CA), Punta Choros (PC), Chungungo (CH), and Guayacancito (GU), which are located within the biogeographic province north of latitude 30°S, considered as an important biogeographical break (Camus, 2001). These locations were chosen mainly because of the presence of one or both communities of interest (kelp forests and barren grounds) and accessibility to the sites. Kelp forests were mainly composed of *Lessonia trabeculata* with a minimum extension of 100 m along the shoreline and had at least a one-year absence of algal harvesting. They were extensive forests with densities that ranged from 0.5 ind. m² (PC and CH) to 2 ind. m² (CA). Barren grounds were composed of open rock fields, including bedrock and boulders.

Sampling was done at an average depth of 10 m on all sites. All study locations were exposed to the open sea. Data were collected in different seasons but considering that coastal fishes present in the study area are mainly non-migratory species (Angel & Ojeda, 2001; Pérez-Matus et al. 2007) and there are only minor seasonal variations among predatory fish assemblages (Pérez-Matus et al. 2007; Pérez-Matus et al. 2012), findings are comparable over time.

Two locations had both types of habitat (PC and CH), and kelp forests and barren grounds were separated by approximately 500 m at PC and by ~2,000 m at CH (Figure 1). PC and CH share general characteristics such as (a) distance to large urban centres (moderate potential for anthropogenic disturbances), (b) complex morphology and architecture of the coast and substratum, and (c) administrative regimes under the framework of Management Areas for Benthic Resources (AMERBs for Spanish abbreviation). There were also two distant locations with contrasting habitats, one with a large kelp forest (CA) located at the northern edge of our study area, and the other with an extensive barren ground (GU) located to the south. CA also is located within an AMERB, far from urban centers, while GU is an open access area close to Coquimbo, a major urban center. These locations with non-paired habitat types were included because they belong to coastal stretches of several km with extensive coverage of the respective habitat type (either kelp forest or barren ground). Along the coast of northern-central Chile, it is difficult to find an ideal kelp forest paired with an adjacent barren ground since some areas are heavily exploited for kelps (within and outside of AMERBs), leading to extensive barren grounds. On the other hand, in other areas kelp forests have remained untouched for many years (mostly due to logistic reasons impeding exploitation) and only small patches without kelps are found.

To facilitate the following descriptions, we term each habitat at each location a “study site”, and so we have 3 sites for kelp forest community (KF-CA, KF-PC, KF-CH) and 3 sites for barren ground community (BG-PC, BG-CH, BG-GU).

Experimental design

Fish surveys were conducted with baited remote underwater videos (BRUVs), which allowed us to determine fish abundances, predation pressure and identity of predators. BRUVs consisted of two different types of structures with GoPro cameras in vertical and horizontal orientation, respectively. The first structure (vertical orientation) was a metal frame with the camera fastened in the upper part, which allowed images to be taken from 80 cm above the bottom (vertical view) of an approximate area of 0.6 m² (Figure 2A and 2C). The second structure (horizontal orientation) was a plate with a metal arm to which the camera was fastened, which took panoramic images (horizontal view) where the bottom area was measured as a trapezium (Figure 2B and 2D). Each structure had on its base an eternit fibre cement plate of 40 x 40 cm side length, to which prey items were tethered. Each plate contained 6 tethered juveniles of the black sea urchin *Tetrapygus niger* or 6 juveniles of the porcelainid crab *Petrolisthes laevigatus*, respectively (see details below). Both types of structures were held on the bottom by concrete pieces of 1 kg or mesh filled with stones and a small and numbered plastic bottle was attached with a thin rope to each structure, allowing us to rapidly locate them from the boat.

Two different types of structures were used due to their respective advantages and/or shortcomings: vertical structures, with a small area, allowed more precise images (because the camera is closer to the plate), which is very useful to identify fish species and to observe predation events on tethered baits when visibility is low (see also Schettini & Corchs, 2010), but the vertical videos do not allow to observe the surrounding community; on the other hand,

horizontal structures produce a greater, but more imprecise observational area, allowing to see what happens in the surrounding community during the assay period, although high turbidity might occasionally limit visibility. Indeed, most studies that use cameras to describe subtidal fish assemblages have the cameras oriented in the horizontal plane (e.g. Malcolm et al., 2007; Duffy et al., 2015).

At each study site (KF-CA, KF-PC, KF-CH, BG-PC, BG-CH, BG-GU), five vertical and five horizontal structures were randomly distributed for each prey (not all of them with camera, because of camera availability). Deployment of the assays was repeated over two different days, because only 5 structures were available of each type (vertical and horizontal; see Table S2). So, after the two deployment days there were 5 replicates with *P. laevigatus* on horizontal structures and 5 replicates with *P. laevigatus* on vertical structures, and the same for *T. niger*. This was done during consecutive days for CA and PC, but not for CH and GU, due to logistic reasons (e.g. poor weather conditions delaying the continuation of field work for a few weeks). However, since fish assemblages do not vary much over the year (Pérez-Matus et al., 2007; Pérez-Matus et al., 2012), this should not affect the results. Assays were deployed between 9:00 am and 11:00 am, at ~10 m depth (at sites with abundant kelp coverage in the case of kelp forest habitats, see Figure S1), and separated from each other by similar distances (~10 m), following a line parallel to the coast. The distance of 10 meters between structures is considered sufficient to prevent the directional movement of fishes from one structure to the next. The fish species observed in our study move randomly and the most frequent fishes are small and territorial species, and thus movements between structures are unlikely and each structure can be considered an independent replicate. Furthermore, visibility in the system is limited due to kelp fronds, complex habitat structures with large boulders or rocky outcrops, and high turbidity, thus limiting visibility from

one structure to the next. Field work was conducted under the resolution 2,649 from “Subsecretaría de Pesca y Acuicultura” (SUBPESCA) published in the “Diario Oficial de la Republica de Chile”, num. 41,553 on 7 September 2016.

Fish species richness, frequency of occurrence and maximum abundance

We used video recordings to compare species richness (SR), frequency of occurrence (FO), and maximum abundance (MaxN) of fish between habitats, and to determine the total number of species (total species richness) per site. In each recording, we registered fish species and their abundances every 30 sec (video frame). When it was not possible to adequately scan a video frame (e.g. kelp blades in front of the camera), the closest visible frame was analysed. For horizontal videos, only fish observed within < 2 m distance from the camera (distance estimates based on reference points of the structures) were recorded, thereby generating a standardized survey area for all videos; there were no videos with a visibility of < 2 m. We obtained a total of 81 videos for both habitat and structure types (for details, see Table S2).

SR was the number of species per video for each study site, FO was calculated as the proportion of frames in which the respective species was observed over the total number of frames analysed in each video (80 frames; providing information about residence or staying time), and MaxN was the maximum number of individuals of the respective species in a video (recorded in one of the 80 examined frames, i.e. there is only one value of MaxN per species per video), which provides information about the relative abundance of the given species at the study site (Cappo et al., 2003). All fishes were identified to species based on their shape, colour, and swimming habits, with the exception of *Scartichthys*, of which two species occur in the study area, *S. viridis* and *S. gigas*. These species are common in northern Chile and display variable

colour patterns (Méndez-Abarca & Mundaca, 2016), making it sometimes difficult to distinguish among them, especially in videos with limited visibility. As both species are of similar size and ecological habits, we treated them as *Scartichthys viridis/gigas* (see also Villegas et al., 2018). To standardize the recordings, only the initial 40 min of each video were used (see also Willis & Babcock, 2000), obtaining 80 frames for counting data. This standardization was done for the analysis of SR, FO and MaxN, all with one single data point per video for analyses. Species accumulation curves for the two types of habitat confirmed that mean number of species recorded with the videos approached an asymptote before 40 min (Figure S2), a time frame also confirmed for a similar study system by Harasti et al. (2015). Only total species richness and predation events were assessed using the entire duration of the videos.

Predation assays and identity of predators

We measured predation pressure using tethered prey organisms (*T. niger* and *P. laevigatus*) as bait. Tethering has been used in different types of communities and with various types of prey, including snails (Reynolds et al., 2018), crustaceans (Heck & Wilson, 1987; Gutow et al., 2012; Ory et al., 2012), sea urchins (Urriago et al., 2011, 2012), and fishes (Pérez-Matus et al., 2016). Since refuge availability, prey behaviour, and other variables can affect the outcome of tethering assays, these should only be used to assess relative predation or predation pressure within the same ecosystem; following those basic recommendations (as done in our study) tethering assays continue to be a useful tool for comparing the predation rates among different habitats or environments (Aronson & Heck, 1995).

As small sea urchins tend to be susceptible to predation (McClanahan, 1988), juvenile sea urchins *T. niger* (15 - 25 mm test diameter) were tethered with monofilament fishing line (0.15

mm diameter) according to the methodology used by McClanahan & Muthiga (1989) and McClanahan & Shafir (1989). The porcelainid crab *P. laevigatus* was included in our study for comparative purposes, because along the Chilean coast decapod crustaceans are more frequent prey than sea urchins in the diet of common fish predators from subtidal hard bottoms (Pérez-Matus et al., 2012). Thus, this crab was used to validate background predation in the study area. Individuals of *P. laevigatus* (15-20 mm of cephalothorax) were tethered by gluing a piece of monofilament to the carapace with cyanoacrylate glue. Preliminary experiments of 24h duration were run in laboratory tanks with tethered individuals, and neither mortality (because of the tether) nor escapes were observed.

Prey organisms were tethered on eternit plates to provide a uniform surface to prey and predators across different types of habitats; this way different refuge structures and prey hiding behaviour in the two habitat types would not interfere with the estimates of predation pressure. After 24 hours, missing prey items were counted for each structure and divided by the total number of baits (n = 6 per structure), obtaining the proportion consumed. Using video recordings, we also identified predator species that consumed either sea urchins or crabs. It should be noted that data about predation events (from videos) only included the period until the cameras stopped recording (after ~40 – 60 minutes), and we may not have identified all species that might have fed on our prey organisms during the 24h of consumption assays.

Data analyses

We analysed fish species richness, FO and MaxN separately for vertical and horizontal structures, considering the differences in the view field of each structure. The predation data after

24h were pooled for both structures, because the plate areas with attached prey organisms were the same, irrespective of the structure.

For analysis, data from the two sampling days were pooled (see also above). All procedures were performed through stepwise model selection on the raw data, according to methods from Zuur et al. (2009). Species richness data were contrasted between habitats and sites using generalized linear models (GLM), pooling video data from both prey species; consumption was contrasted between habitat and prey using GLM, pooling video data from the two different structures; and FO and MaxN were contrasted between habitat and prey types using generalized linear mixed models (GLMMs), considering the values of FO or MaxN, respectively, of each species per video as duplicates. GLMMs allowed us to account for our unbalanced, over-dispersed and zero-inflated data set (Zuur et al., 2009). In GLMM analyses, we included habitat and prey type as fixed factors; and sites, fish species, and individual observations (replicates) were included as random factors. Zero inflation structure in FO GLMMs was attributed to habitat and prey type, whereas in MaxN GLMMs it was only attributed to habitat. Sample replicates were included as observational-level random effects in order to account for overdispersion, as recommended by Bolker et al. (2009). The best model fit was selected based on the lowest corrected Akaike Information Criterion (AICc) value. Model validation was then evaluated through graphical observations of the normality of residuals and the relationship between both observed and standardized residuals against fitted values (Bolker et al., 2009; Zuur et al., 2009).

All best-fit model validations exhibited an acceptable relationship of residuals against fitted values. Most residuals were normally distributed, while observed residual against fitted values did not show any pattern. However, subtle heterogeneities in standardized residuals

against fitted values were observed in some cases. Additional structural-zeros were not predicted for any of the final best-fit models.

Statistical analyses and graphics were done using the R environment (R core team 2019), and its libraries glmmTMB (Brooks et al., 2017), AICcmodavg (Mazerolle, 2019), DHARMA (Hartig, 2018), ggplot2 (Wickham, 2016), and MASS (Venables & Ripley, 2002).

Results

Fish species richness, frequency of occurrence and maximum abundance

We observed a total of 11 fish species analysing the entire video duration, 10 species in kelp forests and 8 on barren grounds (Figure 3). A species that was absent in kelp forests was *Paralabrax humeralis*, which was only observed at BG-PC, while the following species were not recorded on barren grounds: *Graus nigra*, *Semicossyphus darwini* and *Acanthistius pictus*. The latter two were only observed at KF-CA. The highest total number of species (9 species) were observed in the CA kelp forest, while only 4 species were seen on the GU barren ground. For PC and CH, where both habitats were present, BG and KF had similar total species richness (6 and 5 species, respectively, in both locations, Figure 3).

SR (mean \pm standard deviation) ranged from 1.2 ± 0.4 fish species in the CH kelp forest to 2.8 ± 1.6 in the CA kelp forest. The low values of SR were due to videos in which only one or two species were observed (see the dots in Figure 4). SR was similar between locations and habitats, both for videos with vertical and horizontal view (Figure 4, Table S4).

Scartichthys viridis/gigas was the most abundant species, followed by *Pinguipes chilensis* and *Cheilodactylus variegatus*, in both vertical and horizontal videos (Figure 5). *Scartichthys viridis/gigas* and *P. chilensis* used to be the first species to arrive in the visual field of the

cameras (in both habitats). It was very common to see these species within seconds after the structure was deployed, or even when the diver was still there. Other, less common species were observed in videos within minutes after deployment.

For vertical videos, there were no differences in FO between prey types, although barren grounds were significantly different from kelp forests (Wald $z=4.625$, df residual=359, $p < 0.001$). In addition, random effects were largely determined by fish species variance (Table S6). For horizontal videos, we also found no differences in FO between prey types and FO was higher on barren grounds (Wald $z=2.311$, df residual=341, $p = 0.0208$). Random effects were again determined by fish species variance (Table S7). For the FO of three species that generated the greatest random effect, *S. viridis/gigas* and *P. chilensis* reached higher values on barren grounds (mainly in vertical videos), whereas *C. variegatus* mostly had higher values of FO in kelp forests (Figure 5). Other predatory species, although present, occurred very infrequently, seen only in one video or in few frames.

MaxN for the same three most abundant predatory fish species followed a similar pattern as for FO, both in vertical and horizontal videos. For vertical videos, prey type did not exhibit a significant effect, although barren grounds were significantly different from kelp forests (Wald $z=4.793$, df residual=360, $p < 0.001$). Random effects were again largely determined by fish species variance (Table S8). For horizontal videos, there was no effect of prey type, although barren grounds exhibited marginal differences with kelp forests (Wald $z=2.032$, df residual=343, $p=0.0422$). Random effects were determined by fish species, although its variance was the smallest among the three previous analyses (Table S9). MaxN of *Scartichthys viridis/gigas* and *P. chilensis* followed a pattern similar to FO (Figure 6) and MaxN of *C. variegatus* was similar among study sites.

Even though the sizes of fishes were not consistently estimated in this study, all observed fishes were smaller than the plates (40 cm side length) to which prey items were tethered. The individuals of *Pinguipes chilensis* seen near the plates in videos were ~20 to 30 cm in body length. In the less abundant species *Graus nigra*, all individuals were juveniles of ~30 cm. Also, during the deployment of structures, no large individuals of these species were seen by the divers.

Predation assays and identity of predators

Predation pressure for both prey species did not vary across locations and habitats, but significant differences were observed between sea urchin and crab consumption. Predation of porcelainid crabs was significantly higher than that of sea urchins (Wald $z=-6.396$, df residual=116, $p<0.001$, Table S10). Consumption of *T. niger* ranged from $8.3 \pm 14.2\%$ on CH barren grounds to $29.6 \pm 28.6\%$ on GU barren grounds (Figure 7a). In contrast, predation of porcelainid crabs ranged from $38.3 \pm 34.3\%$ in the PC kelp forest to $86.7 \pm 31.2\%$ on CH barren grounds (Figure 7b).

Scartichthys viridis/gigas and *C. variegatus* were seen preying on bait in video recordings (Table S3). *Scartichthys viridis/gigas* was the principal consumer of crabs (82% of consumed prey) preying on 25 individuals of *P. laevigatus* on barren grounds and 7 individuals in kelp forests. *Scartichthys viridis/gigas* was also the only fish species recorded attacking (but not consuming) *Tetrapygus niger*. It was observed in 3 instances turning over sea urchins (solitary individuals) and attacking them orally on CH and PC barren grounds. One instance each of predation by the brachyuran crabs *Homalaspis plana* and *Romaleon setosum* was observed, consuming sea urchins *T. niger* on PC barren grounds. Additionally, a predation event by the

gastropod *Concholepas concholepas* over *P. laevigatus* was observed by the diver when cameras were removed (two hours after deployment), but this was not recorded in videos.

Discussion

Fish species richness showed no major differences across locations and habitats, contrary to what was expected (higher richness in kelp forests). Values of FO and MaxN showed minor differences between habitats, which when observed, were higher on barren grounds than in kelp forests. These differences were mainly due to the presence of two abundant species *Scartichthys viridis/gigas* and *Pinguipes chilensis*, while other large fish predators occurred very infrequently. Predation on *Petrolisthes laevigatus* was significantly higher than on *Tetrapygus niger*, possibly because crabs are a major diet component of coastal fishes, or because large predatory fish that could have consumed the sea urchins were mostly absent. *Scartichthys viridis/gigas* was the principal predator identified in this study, mainly consuming crabs; it was also the only fish that was observed attacking *T. niger*, confirming the predatory character of this species. Total consumption after 24h was similar between habitats, coinciding with the minor or lack of differences in MaxN and FO. Our findings suggest that *T. niger* might have increased in abundances on subtidal hard bottoms, because current predation pressure on this species is low, possibly due to overall reduced abundances of large, top fish predators.

Fish communities

Fish assemblages observed here were composed of typical species from the Chilean coast. The comparatively low total number of fish species per site was similar to species richness of reef-fish observed by other studies along the central and northern coast of Chile (Gelcich et al., 2008;

Ory et al., 2012; Villegas et al., 2018). Pérez-Matus et al. (2007) studied the structure of fish assemblages in northern Chile and found that CA was the site with the highest species richness. This site was also the location with the highest total number of species in our study, but when comparing average SR per video among study sites, no differences were observed. SR did not vary across locations and habitats, except for vertical videos where species richness was higher on barren grounds. This is not totally unexpected, because although kelp forests usually have higher diversity than other types of communities (Levin & Hay, 1996; Graham, 2004), a recent study in New Zealand also observed higher species richness, abundance and predation pressure by fish on barren grounds than in kelp forests (Hesse et al., 2016). On the other hand, Angel & Ojeda (2001) observed similar values in coastal fish abundances and diversity in northern Chile, when comparing a site with kelp forest and a site without forest.

Scartichthys viridis/gigas and *Pinguipes chilensis* were the most abundant species at all study sites, being more frequent on barren grounds albeit with small differences in horizontal videos (wider field of view). *Scartichthys viridis/gigas* are comparatively small fishes (10 – 20 cm adult size) that are not commercially fished (Méndez-Abarca & Mundaca, 2016) and are very common in subtidal habitats of northern Chile (Villegas et al., 2018; this study). On the other hand, *P. chilensis* was consistently present on barren grounds but not in kelp forests, which appears to be typical for this species, since previous studies had observed that its abundances increase when density of kelp forests decreases (Pérez-Matus et al., 2007). The third most abundant predatory species was *Cheilodactylus variegatus*, which despite being more common in kelp forests (Angel & Ojeda, 2001; Pérez-Matus et al., 2007; Villegas et al., 2018) did not show statistical differences in this study.

Several fish species that are typical members of kelp forest communities in northern Chile were rarely seen in our study (e.g. *Hemilutjanus macrophthalmos*, *Graus nigra* and *Semicossyphus darwini*; Pérez-Matus et al., 2012), possibly due to low abundances caused by high fishing pressure (Godoy et al., 2010, 2016). It should be noted that the method often used for the determination of species richness are visual transect surveys (e.g. Pérez-Matus et al., 2007; Ory et al., 2012). Static recordings (video), as used in our study, could underestimate richness and abundances, because less abundant or less mobile species will be less frequently seen compared to visual transect surveys covering more extensive areas (Pérez-Matus et al., 2007). This could be partly responsible for the low abundances observed; indeed, we generally observed higher abundances in the horizontal videos with wider visual field. On the other hand, visual surveys may underestimate the presence and abundance of fish species with cryptic behaviours (Willis, 2001), such as *S. viridis/gigas*, the most frequent and abundant species in our study. Using both methods (visual transect surveys, and BRUVs) in the same study could provide the best estimates of species richness and abundance of demersal fishes, since biology and behaviour of studied species could affect results when using different census methods (Willis et al., 2000).

Predation rates across communities

We observed no significant differences in predation rates between habitats for both prey species, which also coincides with findings of similar fish assemblages in kelp forests as well as on barren grounds. On the other hand, consumption was very different between the two prey species, with crabs being much more consumed than sea urchins. This was somewhat expected because crustaceans have a greater index of relative abundance in the stomach contents of

temperate reef fishes (Vargas et al., 1999; Medina et al., 2004; Pérez-Matus et al., 2012), thus being preferred over sea urchins. However, although echinoderms are not the most consumed prey items, they are frequently found in the stomach contents of these fish. The more abundant predators (*Scartichthys viridis/gigas* and *Pinguipes chilensis*) were ineffective in consuming sea urchins, while the other less abundant species (e.g. *Graus nigra*, *Semicossyphus darwini*, or *Cheilodactylus variegatus*) are recognized as important top predators along the Chilean coast (Pérez-Matus et al., 2007; Pérez-Matus et al., 2017b). Indeed, Selden et al. (2017) described a direct relationship between the rate of sea urchin consumption and the size of the predatory fish *Semicossyphus pulcher* in California. The lack of large individuals of *S. darwini* and similar fish predators in our study area could thus be an explanation for low predation pressure on sea urchins, thereby ultimately being responsible for their proliferation and the establishment of extensive barren grounds along the coast of northern Chile.

Seasonality could also affect results since this study was done over a year. Seasonal temperature variations may affect metabolic rates of organisms (Brown et al., 2004; Milazzo et al., 2013), and thereby influence their predation rates (Duffy et al., 2015). However, seasonal temperature variation along the exposed coast of Chile are rather moderate (Thiel et al., 2007) and might be insufficient to generate metabolic shifts in consumers as has been described for other latitudes (Brown et al., 2004). Furthermore, fish assemblages in the study region are similar across different seasons and fish species are characterized as being territorial and non-migratory (Angel & Ojeda, 2001; Pérez-Matus et al., 2007; Pérez-Matus et al., 2012). Consequently, it is unlikely that fish abundances and predation rates are affected by the season.

Scartichthys viridis/gigas was the species that consumed the most prey during video recordings. This species has originally been described as an herbivorous species with more than

90% of their stomach contents comprising seaweeds, mostly chlorophytes and rhodophytes (Ojeda & Muñoz, 1999; Muñoz & Ojeda, 2000). However, those studies were conducted on individuals from the intertidal zone, with little information on the foraging behaviour of this species in subtidal habitats. Ory et al. (2012) observed effective predation events of *S. viridis* on *Rhynchocinetes typus* in the shallow subtidal zone: the initial attack of an individual, usually adult, triggers a series of joint attacks by multiple conspecifics, forming a kind of feeding frenzy, which ends when the prey item is completely consumed. Similar observations had already been reported by Dumont et al. (2011), classifying *S. viridis* as the most efficient predator on the ascidian *Ciona intestinalis* within the Coastal System of Coquimbo (30°S). Our study not only confirms active predation but also group foraging in *S. viridis/gigas*. However, similar to reports by Urriago et al. (2012), *S. viridis/gigas* attacked and damaged *T. niger* but did not achieve successful predation in our videos. Whether the frenzy generated by this blennid fish might attract other predators of sea urchins is not known at present.

Cheilodactylus variegatus was the only other predatory fish preying on our baits, specifically on crabs, which is consistent with previous studies that observed porcelanid crabs in the diet of this species (Angel & Ojeda, 2001; Palma & Ojeda, 2002; Pérez-Matus et al., 2012). There are several other fish species that could have preyed on our baits, such as *G. nigra*, *S. darwini*, *H. macrophthalmos* and *P. chilensis*, among others (Muñoz & Ojeda, 1997; Medina et al., 2004; Pérez-Matus et al., 2012). These species, which could potentially be predators and controllers of sea urchins, were not identified as predators, most likely because they were only observed in low abundances in our study (except for *P. chilensis*). Possibly, low abundances and the small sizes of adult fishes observed in our videos (see also Selden et al., 2017) are the main reason for not recording them to prey on our baits. On the other hand, some of the species that

consumed our prey (during the 24h of the assay) may have nocturnal behaviours and were thus not captured by our diurnal video recordings.

In addition to fish predators, seastars *Heliaster helianthus* and *Meyenaster gelatinosus* are among the main consumers of sea urchins (Gaymer & Himmelman, 2008; Urriago et al., 2011, 2012), but in our study they seemed to be unimportant, not being interested in the tethered prey. On the other hand, brachyuran crabs *Homalaspis plana* and *Romaleon setosum* were observed attacking (and successfully preying on) tethered sea urchins. While our study is focused on fish predators, crabs also might be important controllers of black sea urchins, an interpretation that is supported by previous studies that have recognized these species as consumers of echinoids (Morales & Antezana, 1983; Cerda & Wolff, 1993). Future studies of subtidal predator assemblages should also take carnivorous crabs into account, because they seem to have an important role in subtidal rocky reefs.

Conclusion

We observed no differences in predation pressure between habitats, which could be related to the similar species richness and abundances of the observed fishes. We also recorded very low abundances of important top fish predators at all sites (e.g. *Semicossyphus darwini*), which might be due to overfishing (Godoy et al., 2010; Godoy et al., 2016) or due to the method used to count (stationary videos). The overall lack of large fish predators may also facilitate small and opportunistic predators such as *Scartichthys viridis/gigas* (not subject to fishing), which have been observed in this study as important predators in both habitats, kelp forests and barren grounds. The fact that these small fish were frequently observed in open areas during bright daylight furthermore suggests that large predatory fish are rare in the study area, which could

also have favoured sea urchin survival and spreading on subtidal hard bottoms. In summary, high fishing pressure and the consequent lack of top fish predators may have profound effects on shallow subtidal communities along the Chilean coast. This needs further attention, considering the ecological importance of kelp forests and their increasing exploitation (Almanza & Buschmann, 2013; Buschmann et al., 2014).

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References

- Almanza V, Buschmann AH, Hernández-González MC, Henríquez LA. 2012. Can giant kelp (*Macrocystis pyrifera*) forests enhance invertebrate recruitment in southern Chile? *Marine Biology Research* 8:855-864. <https://doi.org/10.1080/17451000.2012.692159>
- Almanza V, Buschmann AH. 2013. The ecological importance of *Macrocystis pyrifera* (Phaeophyta) forests towards a sustainable management and exploitation of Chilean coastal benthic co-management areas. *International Journal of Environment and Sustainable Development* 12:341-360. <https://doi.org/10.1504/IJESD.2013.056331>
- Angel A, Ojeda FP. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. *Marine Ecology Progress Series* 217:81-91. <https://doi.org/10.3354/meps217081>

500 **Aronson RB, Heck Jr KL. 1995.** Tethering experiments and hypothesis testing in ecology.
 501 *Marine Ecology Progress Series* **121**:307-309. <https://doi.org/10.3354/meps121307>

502 **Brown JH, Gillooly JF, Allen AP, Savage VM, Geoffrey BW. 2004.** Toward a metabolic
 503 theory of ecology. *Ecology* **85**:1771-1789. <https://doi.org/10.1890/03-9000>

504 **Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS. 2013.**
 505 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology*
 506 *and Evolution* **24**:127-135.

507 **Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug**
 508 **HJ, Maechler M, Bolker BM. 2017.** glmmTMB balances speed and flexibility among packages
 509 for zero-inflated Generalized Linear Mixed Modeling. *The R Journal* **9**: 378-400.

510 **Buschmann AH, Prescott S, Potin P, Faugeron S, Vasquez JA, Camus C, Infante J,**
 511 **Hernández-González MC, Gutiérrez A, Varela DA. 2014.** The status of kelp exploitation and
 512 marine agronomy, with emphasis on *Macrocystis pyrifera*, in Chile. *Advances in Botanical*
 513 *Research* **71**:161-188. <http://doi.org/10.1016/B978-0-12-408062-1.00006-8>

514 **Camus PA. 2001.** Biogeografía marina de Chile continental. *Revista Chilena de Historia*
 515 *Natural* **74**:587-617. <http://doi.org/10.4067/S0716-078X2001000300008>

516 **Cappo M, Harvey E, Malcolm H, Speare P. 2003.** Potential of video techniques to monitor
 517 diversity, abundance and size of fish in studies of Marine Protected Areas. in: Beumer JP, Grant
 518 A, Smith DC (Eds.). *Aquatic Protected Areas-what works best and how do we know?* Australian
 519 Society of Fish Biology, Cairns, Australia. 455-464.

520 **Cerda G, Wolff M. 1993.** Feeding ecology of the crab *Cancer polyodon* in La Herradura Bay,
 521 northern Chile. II. Food spectrum and prey consumption. *Marine Ecology Progress Series*
 522 **100**:119-125. <https://doi.org/10.3354/meps100119>

Clemente S, Hernández JC, Rodríguez A, Brito A. 2010. Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. *Marine Ecology Progress Series* **413**:55-67. <https://doi.org/10.3354/meps08700>

Dayton PK. 1985. The structure and regulation of some South American kelp communities. *Ecological Monographs* **55**:447-468. <https://doi.org/10.2307/2937131>

Duffy JE, Ziegler SL, Campbell JE, Bippus PM, Lefcheck JS. 2015. Squidpops: A simple tool to crowdsource a global map of marine predation intensity. *PLOS ONE* **10**:e0142994. <https://doi.org/10.1371/journal.pone.0142994>

Dumont CP, Gaymer CF, Thiel M. 2011. Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate *Ciona intestinalis*. *Biological Invasions* **13**:2023-2034. <https://doi.org/10.1007/s10530-011-0018-7>

Foster MS, Schiel DR. 2010. Loss of predators and the collapse of southern California kelp forests (?): Alternatives, explanations and generalizations. *Journal of Experimental Marine Biology and Ecology* **393**:59-70. <https://doi.org/10.1016/j.jembe.2010.07.002>

Gaymer CF, Himmelman JH. 2008. A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in the subtidal zone. *Marine Ecology Progress Series* **370**:143-153. <https://doi.org/10.3354/meps07663>

Gelcich S, Godoy N, Prado L, Castilla JC. 2008. Add-on conservation benefits of marine territorial user rights fishery policies in central Chile. *Ecological Applications* **18**:273-281. <https://doi.org/10.1890/06-1896.1>

Godoy N, Gelcich S, Vásquez JA, Castilla JC. 2010. Spearfishing to depletion: evidence from temperate reef fishes in Chile. *Ecological Applications* **20**:1504-1511. <https://doi.org/10.1890/09-1806.1>

- 546 **Godoy N, Gelcich S, Castilla JC, Lima M, Smith A. 2016.** Artisanal spearfishery in temperate
547 nearshore ecosystems of Chile: Exploring the catch composition, revenue, and management
548 needs. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **8**:436-
549 447. <https://doi.org/10.1080/19425120.2016.1185062>
- 550 **Graham MH. 2004.** Effects of local deforestation on the diversity and structure of southern
551 California giant kelp forest food webs. *Ecosystems* **7**:341-357 [https://doi.org/10.1007/s10021-](https://doi.org/10.1007/s10021-003-0245-6)
552 [003-0245-6](https://doi.org/10.1007/s10021-003-0245-6)
- 553 **Graham MH, Vásquez JA, Buschmann AH. 2007.** Global ecology of the giant kelp
554 *Macrocystis*: from ecotypes to ecosystems. *Oceanography and Marine Biology - an Annual*
555 *Review* **45**:39–88.
- 556 **Guidetti P, Fraschetti S, Terlizzi A, Boero F. 2003.** Distribution patterns of sea urchins and
557 barrens in shallow Mediterranean rocky reefs impacted by the ilegal fishery of the rock-boring
558 mollusc *Lithophaga lithophaga*. *Marine Biology* **143**:1135-1142.
- 559 **Guidetti P. 2006.** Marine reserves reestablish lost predatory interactions and cause community
560 changes in rocky reefs. *Ecological Applications* **16**:963-976. [https://doi.org/10.1890/1051-](https://doi.org/10.1890/1051-0761(2006)016[0963:MRRLPI]2.0.CO;2)
561 [0761\(2006\)016\[0963:MRRLPI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0963:MRRLPI]2.0.CO;2)
- 562 **Gutow L, Long JD, Cerda O, Hinojosa IA, Rothäusler E, Tala F, Thiel M. 2012.** Herbivorous
563 amphipods inhabit protective microhabitats within thalli of giant kelp *Macrocystis pyrifera*.
564 *Marine Biology* **159**:141-149. <https://doi.org/10.1007/s00227-011-1794-4>
- 565 **Halpern BS, Cottenie C, Broitman BR. 2006.** Strong top-down control in southern California
566 kelp forest ecosystems. *Science* **312**:1230-1232. <https://doi.org/10.1126/science.1128613>

Hamilton SL, Caselle JE. 2015. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings of the Royal Society B* **282**:20141817. <http://doi.org/10.1098/rspb.2014.1817>

Harasti D, Malcolm H, Gallen C, Coleman MA, Jordan A, Knott NA. 2015. Appropriate set times to represent patterns of rocky reef fishes using baited video. *Journal of Experimental Marine Biology and Ecology* **463**:173-180. <https://doi.org/10.1016/j.jembe.2014.12.003>

Hargrave MS, Foggo A, Pessarrodona A, Smale DA. 2017. The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia* **183**:531-543. <https://doi.org/10.1007/s00442-016-3776-1>

Hartig, F. 2018. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.0. <https://CRAN.R-project.org/package=DHARMA>

Hauser A, Attrill MJ, Cotton PA. 2006. Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts. *Marine Ecology Progress Series* **325**:93-100. <https://doi.org/10.3354/meps325093>

Heck KL, Wilson KA. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology* **107**:87–100. [https://doi.org/10.1016/0022-0981\(87\)90188-2](https://doi.org/10.1016/0022-0981(87)90188-2)

Henríquez LA, Buschmann AH, Maldonado MA, Graham MH, Hernández-González MC, Pereda SV, Bobadilla MI. 2011. Grazing on giant kelp microscopic phases and the recruitment success of annual population of *Macrocystis pyrifera* (Laminariales, Phaeophyta) in southern Chile. *Journal of Phycology* **47**: 252-258.

Hesse J, Stanley JA, Jeffs AG. 2016. Do predatory fish of benthic crustaceans vary between kelp and barren reef habitats in northeastern New Zealand? *New Zealand Journal of Marine and Freshwater Research* **50**:339-357. <https://doi.org/10.1080/00288330.2016.1146309>

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LV, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629-637. <https://doi.org/10.1126/science.1059199>

Konar B, Edwards MS, Estes JA. 2014. Biological interactions maintain the boundaries between kelp forests and urchin barrens in the Aleutian Archipelago. *Hydrobiologia* **724**:91-107. <https://doi.org/10.1007/s10750-013-1727-y>

Krumhansl KA, Okamoto, DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Conell SD, Johnson CR, Konar B, Ling SD, Micheli F, Norderhaug KM, Pérez-Matus A, Souza-Pinto I, Reed DC, Salomon AK, Shears NT, Wernberg T, Anderson RJ, Barrett NS, Buschmann AH, Carr MH, Caselle JE, Darrien-Courtél S, Edgar GJ, Edwards M, Estes JA, Goodwin C, Kenner MC, Kushner DJ, Moy FE, Nunn J, Steneck RS, Vásquez J, Watson J, Witman JD, Byrnes JEK. 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America* **113**:13785–13790. <https://doi.org/10.1073/pnas.1606102113>

Leleu K, Remy-Zephir B, Grace R, Costello MJ. 2012. Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. *Biological Conservation* **155**:193-201. <https://doi.org/10.1016/j.biocon.2012.05.009>

611 **Levin PS, Hay M. 1996.** Responses of temperate reef fishes to alterations in algal structure and
 612 species composition. *Marine Ecology Progress Series* **134**:37–47.

613 **Malcolm HA, Gladstone W, Lindfield S, Wraith J, Lynch TP. 2007.** Spatial and temporal
 614 variation in reef fish assemblages of marine parks in New South Wales, Australia—baited video
 615 observations. *Marine Ecology Progress Series* **350**:277-290. <https://doi.org/10.3354/meps07195>

616 **Mazerolle, MJ. 2019.** AICcmodavg: Model selection and multimodel inference based on
 617 (Q)AIC(c). R package version 2.2-1. <https://cran.r-project.org/package=AICcmodavg>

618 **McClanahan TR. 1988.** Coexistence in a sea urchin guild and its implications to coral reef
 619 diversity and degradation. *Oecologia* **77**:210-218. <http://doi.org/10.1007/BF00379188>

620 **McClanahan TR, Muthiga NA. 1989.** Patterns of predation on a sea urchin, *Echinometra*
 621 *mathaei* (de Blainville), on Kenyan coral reefs. *Journal Experimental Marine Biology and*
 622 *Ecology* **126**:77-94. [https://doi.org/10.1016/0022-0981\(89\)90125-1](https://doi.org/10.1016/0022-0981(89)90125-1)

623 **McClanahan TR, Shafir SH. 1989.** Causes and consequences of sea urchin abundance and
 624 diversity in Kenyan coral reef lagoons. *Oecologia* **83**:362-370.
 625 <https://doi.org/10.1007/BF00317561>

626 **Medina M, Araya M, Vega C. 2004.** Alimentación y relaciones tróficas de peces costeros de la
 627 zona norte de Chile. *Investigaciones Marinas* **32**:33-47. [http://doi.org/10.4067/S0717-](http://doi.org/10.4067/S0717-71782004000100004)
 628 [71782004000100004](http://doi.org/10.4067/S0717-71782004000100004)

629 **Medrano A, Linares C, Aspillaga E, Capdevila P, Montero-Serra I, Pagès-Escalà M, Hereu**
 630 **B. 2019.** No-take marine reserves control the recovery of sea urchin populations after mass
 631 mortality events. *Marine Environmental Research*: in Press.
 632 <https://doi.org/10.1016/j.marenvres.2019.02.013>

633 **Méndez-Abarca F, Mundaca EA. 2016.** Colouration patterns of two species of the genus
634 *Scartichthys* (Blenniidae: Perciformes) in the coastal area of northern Chile. *Revista de Biología*
635 *Marina y Oceanografía* **51**:475-481. <http://doi.org/10.4067/S0718-19572016000200026>

636 **Milazzo M, Mirto S, Domenici P, Gristina M. 2013.** Climate change exacerbates interspecific
637 interactions in sympatric coastal fishes. *Journal of Animal Ecology* **82**:468-477.
638 <https://doi.org/10.1111/j.1365-2656.2012.02034.x>

639 **Miller RJ, Lafferty KD, Lamy T, Kui L, Rassweiler A, Reed DC. 2018.** Giant kelp,
640 *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proceedings of the*
641 *Royal Society B* **285**:20172571. <https://doi.org/10.1098/rspb.2017.2571>

642 **Morales C, Antezana T. 1983.** Diet selection of the Chilean stone crab *Homalaspis plana*.
643 *Marine Biology* **77**:79-83. <https://doi.org/10.1007/BF00393212>

644 **Muñoz AA, Ojeda FP. 1997.** Feeding guild structure of a rocky intertidal fish assemblage in
645 central Chile. *Environmental Biology of Fishes* **49**:471-479.
646 <https://doi.org/10.1023/A:1007305426073>

647 **Muñoz AA, Ojeda FP. 2000.** Ontogenetic changes in the diet of the herbivorous *Scartichthys*
648 *viridis* in a rocky intertidal zone in central Chile. *Journal of Fish Biology* **56**:986-998.
649 <https://doi.org/10.1111/j.1095-8649.2000.tb00887.x>

650 **Norderhaug KM, Christie HC. 2009.** Sea urchin grazing and kelp re-vegetation in the NE
651 Atlantic. *Marine Biology Research* **5**:515-528. <https://doi.org/10.1080/17451000902932985>

652 **Ojeda P, Muñoz AA. 1999.** Feeding selectivity of the herbivorous fish *Scartichthys viridis*:
653 effects on macroalgal community structure in a temperate rocky intertidal coastal zone. *Marine*
654 *Ecology Progress Series* **184**:219-229.

- 655 **Oliver ECJ, Lago V, Hobday AJ, Holbrook NJ, Ling SD, Mundy CN. 2018.** Marine
656 heatwaves off eastern Tasmania: Trends, interannual variability, and predictability. *Progress in*
657 *Oceanography* **161**:116-130. <https://doi.org/10.1016/j.pocean.2018.02.007>
- 658 **Ory NC, Dudgeon D, Dumont CP, Miranda L, Thiel M. 2012.** Effects of predation and
659 habitat structure on the abundance and population structure of the rock shrimp *Rhynchocinetes*
660 *typus* (Caridea) on temperate rocky reefs. *Marine Biology* **159**:075-2089.
661 <https://doi.org/10.1007/s00227-012-1994-6>
- 662 **Palma ÁT, Ojeda FP. 2002.** Abundance, distribution and feeding patterns of a temperate reef
663 fish in subtidal environments of the Chilean coast: the importance of understory algal turf.
664 *Revista Chilena de Historia Natural* **75**:189-200. [http://doi.org/10.4067/S0716-](http://doi.org/10.4067/S0716-078X2002000100018)
665 [078X2002000100018](http://doi.org/10.4067/S0716-078X2002000100018).
- 666 **Pérez-Matus A, Ferry-Graham LA, Cea A, Vásquez JA. 2007.** Community structure of
667 temperate reef fishes in kelp-dominated subtidal habitats of northern Chile. *Marine and*
668 *Freshwater Research* **58**:1069-1085. <https://doi.org/10.1071/MF06200>
- 669 **Pérez-Matus A, Pledger S, Díaz FJ, Ferry LA, Vásquez JA. 2012.** Plasticity in feeding
670 selectivity and trophic structure of kelp forest associated fishes from northern Chile. *Revista*
671 *Chilena de Historia Natural* **85**:29-48. <http://doi.org/10.4067/S0716-078X2012000100003>
- 672 **Pérez-Matus A, Sánchez F, González-But JC, Lamb RW. 2016.** Understory algae
673 associations and predation risk influence broad-scale kelp habitat use in a temperate reef fish.
674 *Marine Ecology Progress Series* **559**:147-158. <https://doi.org/10.3354/meps11892>
- 675 **Pérez-Matus A, Carrasco SA, Gelcich S, Fernandez M, Wieters E. 2017a.** Exploring the
676 effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in
677 central Chile. *Ecosphere* **8**: e01808.10.1002/ecs2.1808. <https://doi.org/10.1002/ecs2.1808>

678 **Pérez-Matus A, Ospina-Alvarez A, Camus PA, Carrasco SA, Fernandez M, Gelcich S,**
679 **Godoy N, Ojeda FP, Prado LM, Rozbaczylo N, Subida MD, Thiel M, Wieters EA,**
680 **Navarrete SA. 2017b.** Temperate rocky subtidal reef community reveals human impacts across
681 the entire food web. *Marine Ecology Progress Series* **567**:1-16.
682 <https://doi.org/10.3354/meps12057>

683 **Perreault MC, Borgeaud IA, Gaymer CF. 2014.** Impact of grazing by the sea
684 urchin *Tetrapygus niger* on the kelp *Lessonia trabeculata* in northern Chile. *Journal of*
685 *Experimental Marine Biology and Ecology* **453**:22-27.
686 <https://doi.org/10.1016/j.jembe.2013.12.021>

687 **R Core Team. 2018.** R: A language and environment for statistical computing. R Foundation for
688 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>
689 (accessed 18 March 2019)

690 **Reynolds PL, Stachowicz JJ, Hovel K, Boström C, Boyer K, Cusson M, Eklöf JS, Engel**
691 **FG, Engelen AH, Eriksson BK, Fodrie FJ, Griffin JN, Hereu C, Hori M, Hanley T, Ivanov**
692 **M, Jorgensen P, Kruschel C, Lee KS, McGlathery K, Moksnes PO, Nakaoka M, O'Connor**
693 **MI, O'Connor N, Orth RJ, Rossi F, Ruesink J, Sotka E, Tomas F, Unsworth RKF, Whalen**
694 **MA, Duffy JE. 2018.** Latitude, temperature and habitat complexity predict predation pressure in
695 eelgrass beds across the northern Hemisphere. *Ecology* **99**:29–35.
696 <https://doi.org/10.1002/ecy.2064>

697 **Sala E, Zabala M. 1996.** Fish predation and the structure of the sea urchin *Paracentrotus lividus*
698 populations in the NW Mediterranean. *Marine Ecology Progress Series* **140**:71-81.
699 <https://doi.org/10.3354/meps140071>

Schettini R, Corchs S. 2010. Underwater image processing: State of the art of restoration and image enhancement methods. *EURASIP Journal on Advances in Signal Processing* 746052. <http://doi.org/10.1155/2010/746052>

Selden RL, Gaines SD, Hamilton SL, Warner RR. 2017. Protection of large predators in a marine reserve alters size-dependent prey mortality. *Proceedings of the Royal Society B* **284**: 20161936. <http://doi.org/10.1098/rspb.2016.1936>

Simonson EJ, Scheibling RE, Metaxas A. 2015. Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. *Marine Ecology Progress Series* **537**:89-104. <https://doi.org/10.3354/meps11438>

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**:436-459. <https://doi.org/10.1017/S0376892902000322>

Stotz WB, Aburto J, Caillaux LM, González SA. 2016. Vertical distribution of rocky subtidal assemblages along the exposed coast of north-central Chile. *Journal of Sea Research* **107**:34-47. <https://doi.org/10.1016/j.seares.2015.11.006>

Teagle H, Hawkins SJ, Moore PJ, Smale DA. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* **492**:81-98. <https://doi.org/10.1016/j.jembe.2017.01.017>

Tegner MJ, Dayton PK. 1987. El Niño Effects on Southern California Kelp Forest Communities. *Advances in Ecological Research* **17**:243-279.

Tegner MJ, Dayton PK. 2000. Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science* **57**:579–589. <https://doi.org/10.1006/jmsc.2000.0715>

Thiel M, Macaya EC, Acuña E, Arntz WE, Bastias H, Brokordt K, Camus PA, Castilla JC, Castro LR, Cortés M, Dumont CP, Escribano R, Fernández M, Gajardo JA, Gaymer CF, Gómez I, González AE, González HE, Haye PA, Illanes JE, Iriarte JL, Lancellotti DA, Luna-Jorquera G, Luxoroi C, Manríquez PH, Marín V, Muñoz P, Navarrete SA, Pérez E, Poulin E, Sellanes J, Sepúlveda HH, Stotz W, Tala F, Thomas A, Vargas CA, Vásquez JA, Vega JMA. 2007. The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology: Annual Review* **45**:195-344.

Urriago JD, Himmelman JH, Gaymer CF. 2011. Responses of the black sea urchin *Tetrapygus niger* to its sea-star predators *Heliaster helianthus* and *Meyenaster gelatinosus* under field conditions. *Journal of Experimental Marine Biology and Ecology* **399**:17-24. <https://doi.org/10.1016/j.jembe.2011.01.004>

Urriago JD, Himmelman JH, Gaymer CF. 2012. Sea urchin *Tetrapygus niger* distribution on elevated surfaces represents a strategy for avoiding predatory sea stars. *Marine Ecology Progress Series* **444**:85-95. <https://doi.org/10.3354/meps09396>

Vargas ME, Soto RA, Guzmán GL. 1999. Cambios interanuales en la alimentación de peces submareales del norte de Chile entre los 20°11' y 20°20'S. *Revista de Biología Marina y Oceanografía* **34**:197-210.

Vásquez JA, Santelices B. 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. *Hydrobiologia* **204/205**:41-47. <https://doi.org/10.1007/BF00040213>

Vásquez JA, Buschmann AH. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. *Revista Chilena de Historia Natural* **70**:41-52.

- 745 **Vega JMA, Vásquez JA, Buschmann AH. 2005.** Population biology of the subtidal kelps
746 *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling
747 ecosystem of northern Chile: interannual variability and El Niño 1997-1998. *Revista Chilena de*
748 *Historia Natural* **78**: 33-50. <https://doi.org/10.4067/S0716-078X2005000100004>
- 749 **Venables WN, Ripley BD. 2002.** MASS library of functions. *Modern Applied Statistics with S*.
750 Springer (Fourth Edition), New York. ISBN 0-387-95457-0. 495 p.
- 751 **Villegas M, Laudien J, Sielfeld W, Arntz W. 2018.** Effect of foresting barren ground with
752 *Macrocystis pyrifera* (Linnaeus) C. Agardh on the occurrence of coastal fishes off northern
753 Chile. *Journal of Applied Phycology*: in press, 1-13. <https://doi.org/10.1007/s10811-018-1657-1>
- 754 **Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD. 2010.**
755 Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications
756 for a warmer future. *Ecology Letters* **13**:685-694. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2010.01466.x)
757 [0248.2010.01466.x](https://doi.org/10.1111/j.1461-0248.2010.01466.x)
- 758 **Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Benett S,**
759 **Rousseaux CS. 2013.** An extreme climatic event alters marine ecosystem structure in a global
760 biodiversity hotspot. *Nature Climate Change* **3**:78-82. <https://doi.org/10.1038/nclimate1627>
- 761 **Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF. 2019.** Status and trends for the
762 world's kelp forests. In: Sheppard C, ed. *World Seas: An environmental evaluation*. Academic
763 Press (Second Edition), 57-78. <https://doi.org/10.1016/B978-0-12-805052-1.00003-6>
- 764 **Wickham, H. 2016.** ggplot2: Elegant graphics for data analysis. Springer-Verlag (Second
765 Edition), New York. 260 p. <https://doi.org/10.1007/978-0-387-98141-3>
- 766 **Willis TJ, Babcock RC. 2000.** A baited underwater video system for the determination of
767 relative density of carnivorous reef fish. *Marine and Freshwater Research* **51**:755-763.

Willis TJ, Millar RB, Babcock RC. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**:249-260.

Willis TJ. 2001. Visual census methods underestimate density and diversity of cryptic reef fishes. *Journal of Fish Biology* **59**:1408-1411. <https://doi.org/10.1111/j.1095-8649.2001.tb00202.x>

Zuur A, Ieno E, Walker N, Saveliev A, Smith G. 2009. Mixed effects models and extensions in ecology with R. In: Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, ed. *Statistics for biology and health*. Springer Science, New York, 563p.

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.

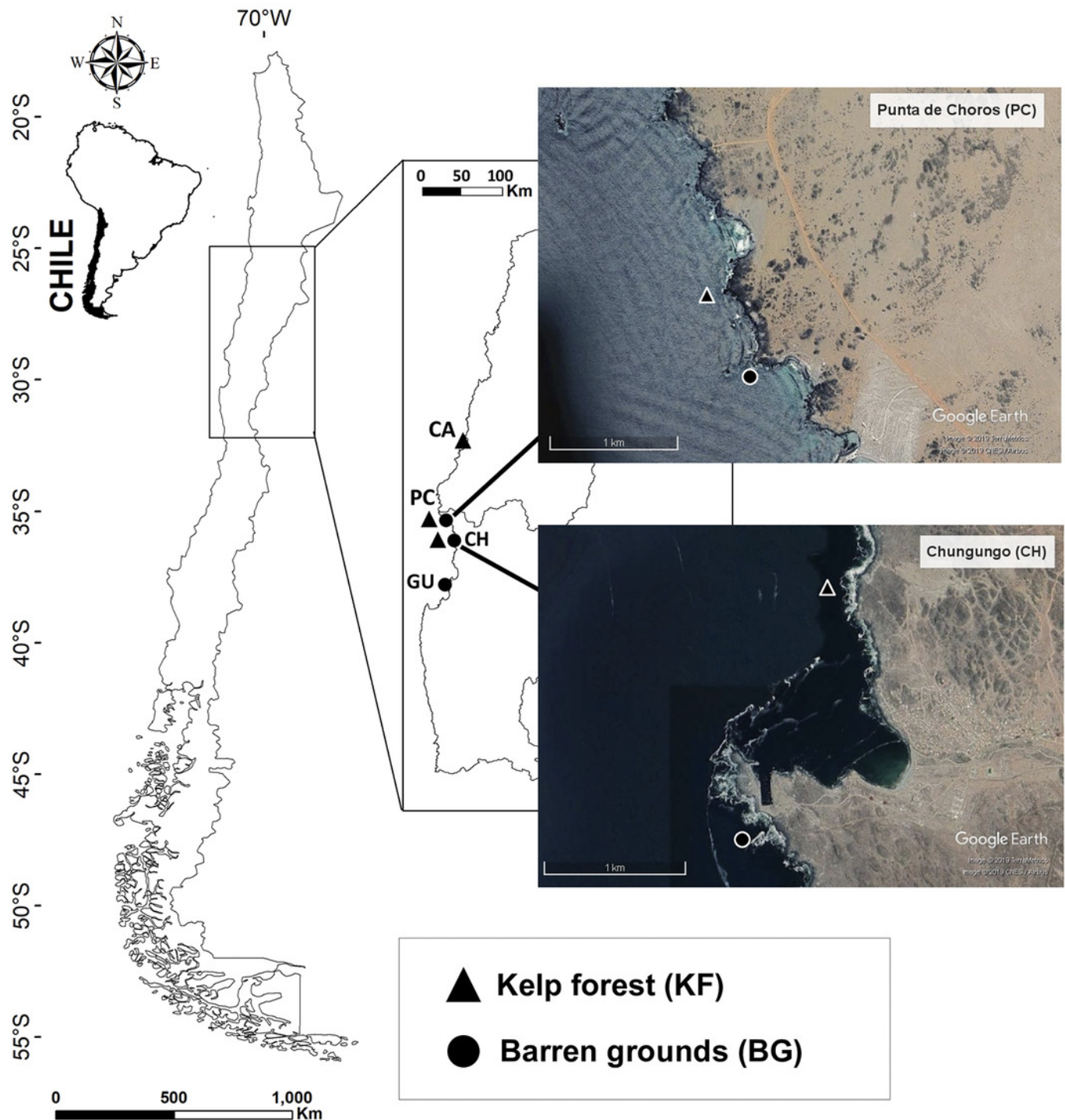


Figure 2

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.

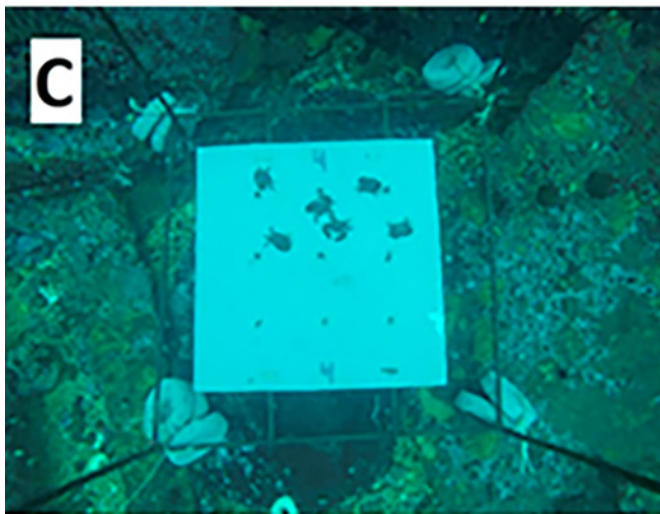


Figure 3

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.




































| | CA | PC | | CH | | GU |
|---|---|---|--|---|---|---|
| Species | KF | KF | BG | KF | BG | BG |
| <i>Scartichthys viridis/gigas</i> |  |  |  |  |  |  |
| <i>Pinguipes chilensis</i> |  | |  |  |  |  |
| <i>Cheilodactylus variegatus</i> |  |  |  |  |  |  |
| <i>Aplodactylus punctatus</i> |  |  |  |  | | |
| <i>Chromis crusma</i> | |  |  | |  |  |
| <i>Labrisomus philippii</i> |  |  | | |  | |
| <i>Hemilutjanus macrophthalmos</i> |  | | | |  | |
| <i>Graus nigra</i> |  | | |  | | |
| <i>Paralabrax humeralis</i> | | |  | | | |
| <i>Semicossyphus darwini</i> | *  | | | | | |
| <i>Acanthistius pictus</i> | *  | | | | | |
| 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.

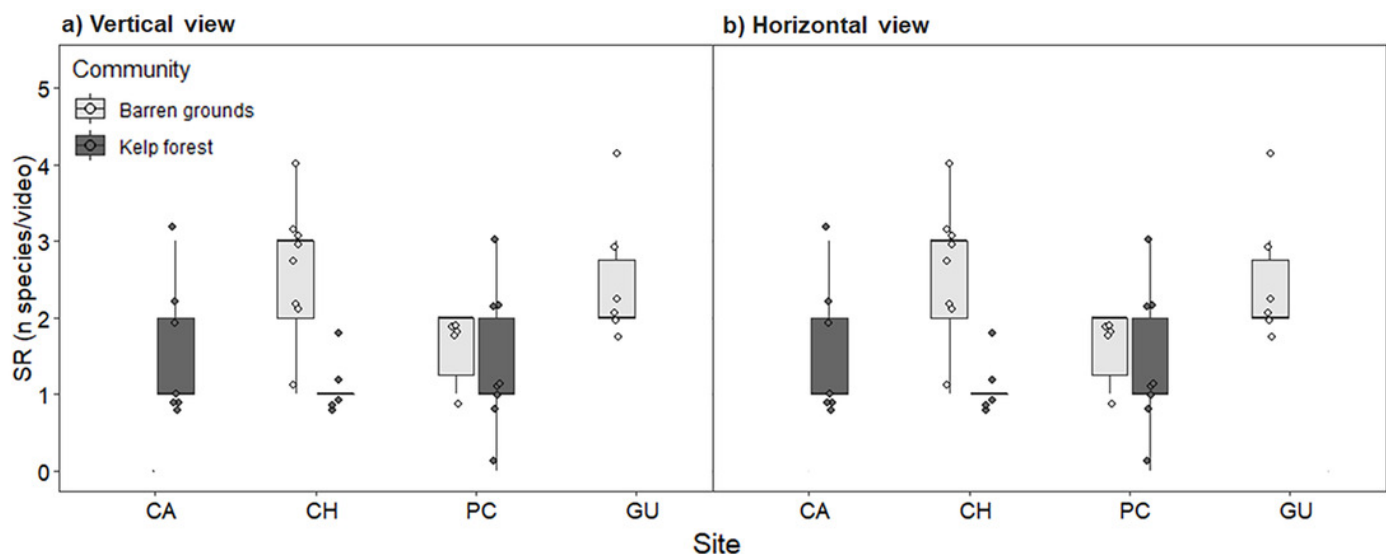


Figure 5

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 ($1.5 \times \text{IQR}$ 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.

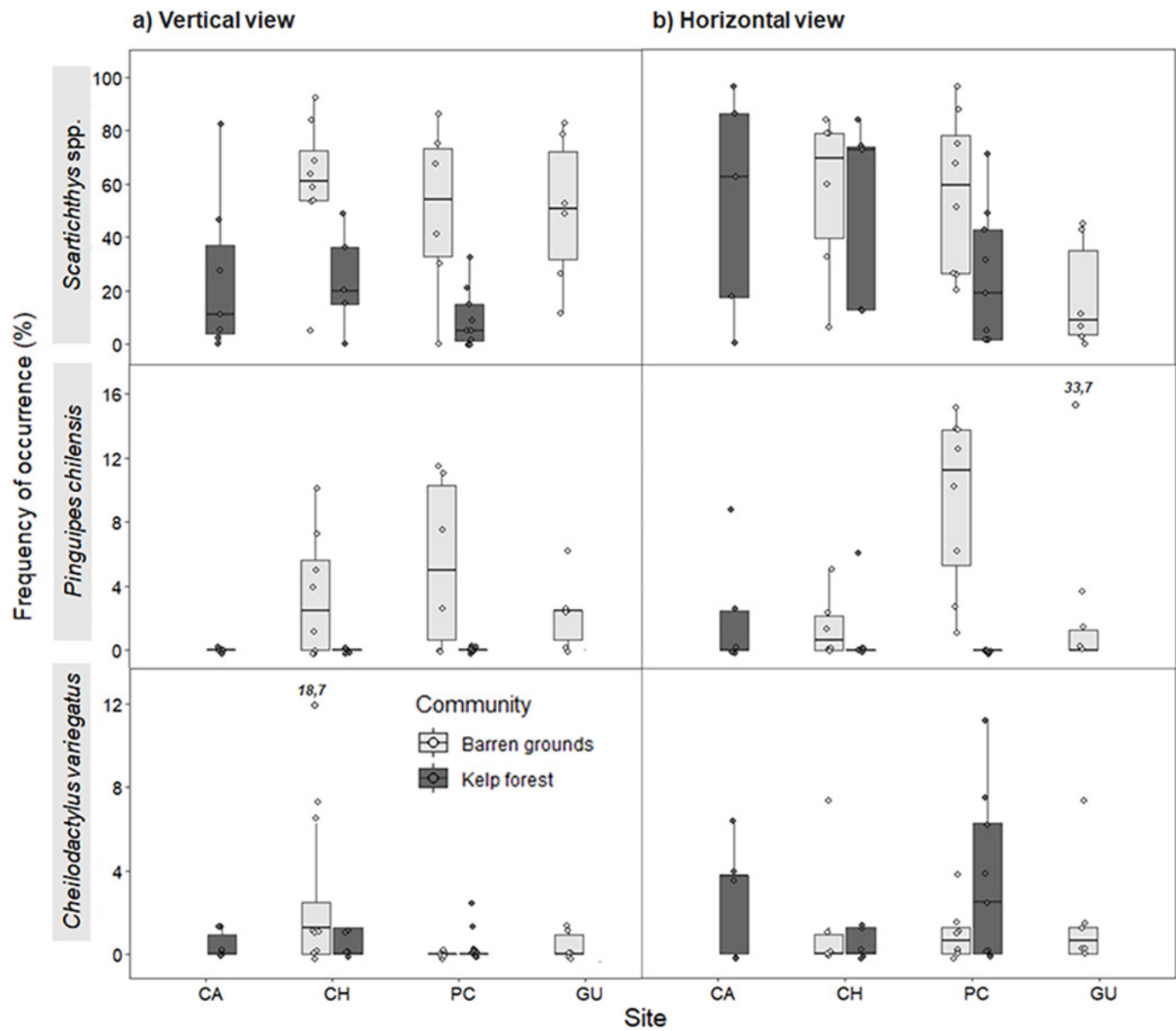


Figure 6

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 ($1.5 \times \text{IQR}$ 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.

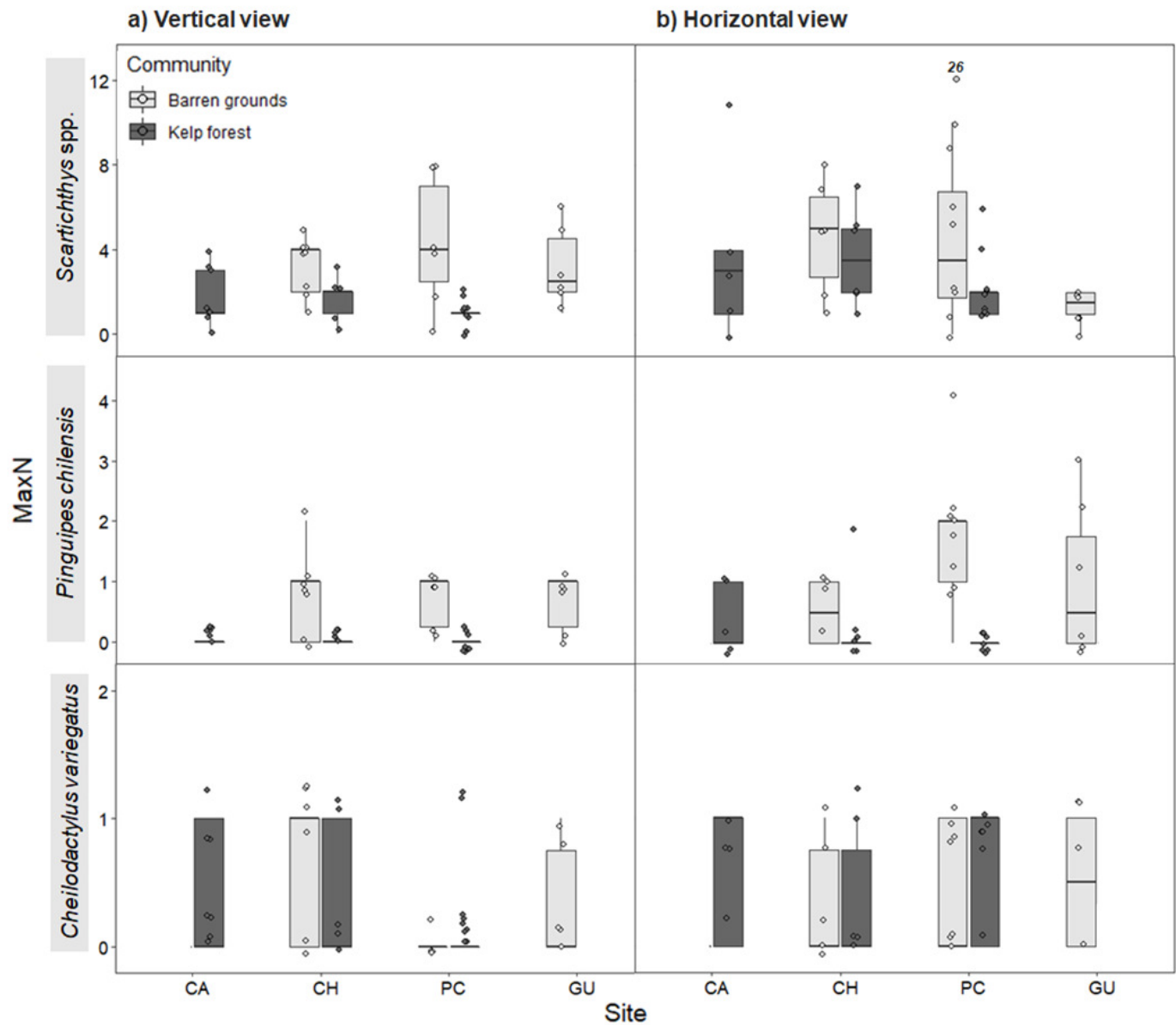


Figure 7

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 ($1.5 \times \text{IQR}$ or the interquartile range); dots show jittered raw data points and dots outside the range are outliers.

