Research Article

The natural diet of *Prolatilus jugularis* inhabiting *Lessonia trabeculata* kelp forests of south-central Chile

Simon Gartenstein[1,2,3] **, Eliseo Fica-Rojas**[4] **, Alejandro Pérez-Matus**[5,6]
Natalio Godoy[3] **, Felipe Torres-Cañete**[3] **& Nelson Valdivia**[1,7]

[1]Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias
Universidad Austral de Chile, Valdivia, Chile
[2]The Rufford Foundation (http://www.rufford.org/)
[3]The Nature Conservancy, Providencia, Santiago, Chile
[1,4]Programa de Doctorado en Ciencias mención Ecología y Evolución
Instituto de Ciencias Ambientales & Evolutivas, Facultad de Ciencias
Universidad Austral de Chile, Valdivia, Chile
[5]Subtidal Ecology Laboratory, Estación Costera de Investigaciones Marinas
Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
[6]Millennium Nucleus for Ecology and Conservation of Temperate
Mesophotic Reef Ecosystem (NUTME), Valparaiso, Chile
[7]Centro FONDAP de Investigación de Dinámicas de Ecosistemas Marinos de Altas Latitudes (IDEAL)
Universidad Austral de Chile, Valdivia, Chile
Corresponding author: Simon Gartenstein (simon.gartenstein@alumnos.uach.cl)

ABSTRACT. Kelp forests support species-rich food webs that predator-prey interactions may sustain. Here, we analyze prey availability and stomach contents of the predatory fish *Prolatilus jugularis* in an unexplored subtidal kelp forest of *Lessonia trabeculata* in south-central Chile. In the kelp forest, 42 invertebrate taxa and 1016 individuals were observed. In the diet of *P. jugularis*, 21 taxa and 130 individuals were identified. Crustacea, particularly amphipods, were the dominant and more frequent taxa in the kelp forest and stomach contents. Annelida and Mollusca were also present in the kelp forest and diets but were less abundant. We did not find a statistically significant correlation between kelp forest and stomach-content prey abundances and frequencies. Also, dominance structure significantly differed between kelps and stomach contents. Our results indicate that *P. jugularis* could feed in other habitats outside the survey area. Seven predatory fish were sampled in the kelp forest. *Pinguipes chilensis* was the dominant fish, with 65% of the total fish biomass, followed by *P. jugularis* with 20%.

Keywords: *Prolatilus jugularis*; *Lessonia trabeculata*; kelps; stomach content analysis; predatory reef fish; benthic invertebrates

INTRODUCTION

Kelp species are found along 25% of the world's coastlines, providing many ecosystem goods and services (Smale et al. 2020). They constitute a structurally complex type of habitat that supports the assemblages of highly diverse communities and food webs (Dayton 1985, Thiel et al. 2007, Trujillo et al. 2019, Velasco-Charpentier et al. 2021), providing food, shelter, and habitat for larval settlement (Teagle et al. 2017, Riquelme-Pérez et al. 2019). These areas not only provide favorable habitat options for reef fishes (e.g.

---

feeding grounds, nursery habitat, and refuge from predators) (Norderhaug et al. 2005, Witman & Lamb 2018) but also for the prey species on which they feed (Angel & Ojeda 2001, Pérez-Matus et al. 2007).

The trophic organization, dynamics, and diversity of kelp forest communities may be influenced by predator-prey interactions (Ojeda & Dearborn 1991, Angel & Ojeda 2001, Pérez-Matus et al. 2007, 2017). Large predatory fish can maintain biodiversity by controlling smaller fish and invertebrates at interme-diate and lower trophic levels (Campanella et al. 2019), e.g. sea urchins, that can otherwise consume entire kelp forests (Dayton et al. 1998, Estes et al. 2011). The ability of predatory fish to control local community structure is related to variations in feeding, foraging tactics, migratory behavior, individual prey behavior, morphological specializations, and predator gape allometry (Scharf et al. 2000, Pérez-Matus et al. 2012). Along the Chilean coast, the role of different coastal fish predators in controlling prey species, such as sea urchin populations, is less known (Riquelme-Pérez et al. 2019). Many predatory fishes have been subject to intense fishing activity, and the population of the fish has declined in north-central Chile (Godoy et al. 2010, Riquelme-Pérez et al. 2019).

Prolatilus jugularis (Valenciennes, 1833) is a carnivorous predatory fish that is distributed in the southeast Pacific from Huacho, Peru (11°11'S) to Chiloé Island, Chile (43°43'S) (Vera-Duarte & Landaeta 2017). It is an important artisanal fisheries species in Chile, especially in the central to northern regions (Moreno & Flores 2002). This fish has mostly been known to inhabit shallow demersal rocky and sandy bottom habitats in coastal areas up to 20 m (Pequeño & Lamilla 1995, Pérez-Matus et al. 2007, 2017), but also in deeper waters to 200 m (Mann 1954, Pequeño 1975, Nakamura et al. 1986). Previous studies have shown that *P. jugularis* principally feeds on benthic and demersal organisms in which sedentary polychaetes and, to a lesser extent, crustaceans are the main prey (Meléndez 1989, Moreno & Flores 2002, Vera-Duarte & Landaeta 2017). *P. jugularis* has been studied in central Chile (Moreno & Flores 2002), but little is known about this species in southern Chile, where it can reach relatively large abundances.

Unlike the central to northern coastlines of Chile, where kelp forests are heavily exploited (Pérez-Matus et al. 2017, Riquelme-Pérez et al. 2019, Gouraguine et al. 2021), in the south-central region kelp forests are still abundant and mostly unexplored (Trujillo et al. 2019). Therefore, there is a need and opportunity to increase our knowledge about fish predators and their

role in these kelp forests, where very little data exists on how kelp forests function and support ecosystem services for predators.

Here, we describe the dietary composition of a predatory fish, the Pacific sand perch *P. jugularis*, and its potential food sources in a *Lessonia trabeculata* kelp forest in south-central Chile. In addition, we collected survey data on the predatory fish community to compare the abundance and biomass of *P. jugularis* to the other species. If kelp forests harbor potential prey for fish, we predicted a positive association between the abundance of species found within the kelp forest and those found in the stomach contents of *P. jugularis*.

MATERIALS AND METHODS

Study site

Sampling was conducted on the south-central coast of Chile at Morro Gonzalo, Corral (39°51'05.27"S, 73°27'02.38"W) (Fig. 1a). The site is semi-protected from the prevailing southerly swell. The *L. trabeculata* kelp forest at this site is around 500 m^2 with depths of up to 12 m (Trujillo et al. 2019). The substratum within the kelp forest consists of boulders, large rocks, and sand bottom. The understorey assemblage encompasses fish, invertebrates, and algae (Fig. 1b). Observations from our dive surveys indicated that *P. jugularis* (Fig. 1c) and other fish predators patrol the kelp forests of this region, especially *Pinguipes chilensis*, *Calliclinus geniguttatus*, and *Sebastes oculatus* (Table 1).

Sampling of benthic invertebrates and fishes

Benthic invertebrates were sampled on March 15 and 18, 2020 (Fig. 1d). On each date, five 50×50 cm quadrats were haphazardly deployed in the kelp forest along transects at depths between 7 and 10 m. Scraping knives were used to remove all mobile species within each quadrat, based on the methods of Palma & Ojeda (2002) and Pérez-Matus et al. (2012). All samples were labeled and preserved in glass jars with 90% ethanol until processing in the facilities of Universidad Austral de Chile in Valdivia. On the same dates, 13 adult individuals of *P. jugularis* were fished above the kelp forest by handline in approximately 7 m of water, using fresh local clams as bait. Fish were immediately frozen after capture to prevent further digestion of stomach contents. To determine the prey composition of *P. jugularis*, all stomachs and intestines were removed and sampled following the methods of Buckland et al. (2017). Using a Euromex dissecting microscope (20x), invertebrates were identified to the lowest possible taxonomic level using taxonomic references (Palma
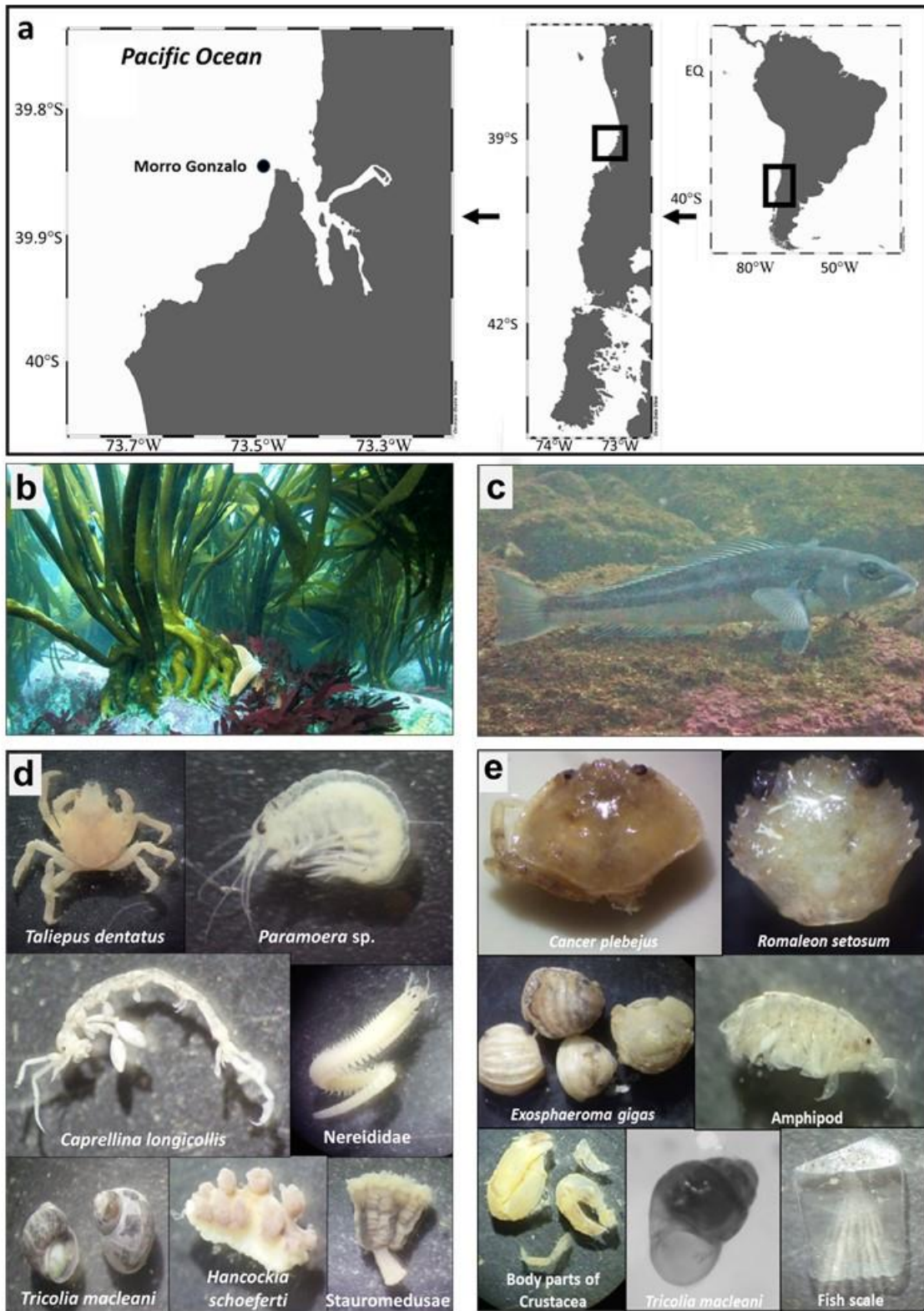
Figure 1. Sampling site at Morro Gonzalo, south-central Chile. a) Map of sampling site, b) understory habitat in kelp forest of *Lessonia trabeculata*, c) *Prolatilus jugularis* in benthic habitat of *L. trabeculata*, d) taxa sampled from the understorey habitat in the kelp forest, e) taxa sampled from stomachs of *P. jugularis*. Simon Gartenstein took all photographs except photograph (c), which was taken by Eliseo Fica.

Table 1. The number of individuals, total biomass (g), fork length range (cm), and average fork length (cm) of predatory fish that were surveyed from October 2020 to May 2021 using underwater visual census (UVC) along six transects in kelp forests of *Lessonia trabeculata* at Morro Gonzalo, south-central Chile. The mean length for *Prolatilus jugularis* also includes measurements of individuals fished from the kelp forest for stomach analyses (n = 13 fish; average length = 23.6 cm). The length range for all individuals of *P. jugularis* was 15-35 cm.

Taxa			Number of individuals (ind per transect area 200 m^{-2})	Total biomass (g)	Mean length (cm)	Length range (cm)
Perciformes	Pinguipedidae	*Pinguipes chilensis* (Valenciennes, 1833)	46	11,670	25.6	10-40
		Prolatilus jugularis (Valenciennes, 1833)	36	3598	23	15-35
	Cheilodactylidae	*Cheilodactylus variegatus* (Valenciennes, 1833)	4	1340	27.5	25-35
	Eleginopsidae	*Patagonotothen* sp. (Cuvier, 1830)	109	740	8.7	7.5-15
	Labrisomidae	*Calliclinus geniguttatus* (Valenciennes, 1836)	9	67	8.6	7.5-10
Scorpaeniformes	Congiopodidae	*Congiopodus peruvianus* (Cuvier, 1829)	1	101	20	20
	Sebastidae	*Sebastes oculatus* (Valenciennes, 1833)	6	357	14.2	7.5-25
		Total	211	17,873		

& Ojeda 2002, Thiel et al. 2003, Zagal et al. 2007, Thiel & Hinojosa 2009) (Fig. 1e, Table 2).

During fish surveys between October 2019 and May 2021, the size of *P. jugularis* and the most abundant predatory fish species were measured along six 50×8 m transects (Table 1). The size of each fish was estimated to the nearest centimeter using an underwater visual census (UVC) based on the methodology of Frid et al. (2013) and Edgar et al. (2020). To ensure accuracy in size estimation, divers used a 'reference pole' (an 80 cm length of PVC, labeled with centimeter increments and mounted at the end of a 1.5 m pole) to benchmark visual estimates (Frid et al. 2013). Individual fish weights were calculated from lengths using species-specific length-weight conversions from FishBase (www. fishbase.org).

Statistical analysis

Species accumulation curves were produced to assess whether the sampling effort was enough to represent the species diversity of kelp forests and the diet of *P. jugularis* (Colwell & Coddington 1995). To that aim, taxonomic richness was expressed as the number of taxonomic identities occurring in each sample. The representativeness of our sample size was further assessed by calculating the bias-corrected Chao estimator of extrapolated species richness separately for kelp forest and stomach contents (Chao 1987). Chao quantifies the number of unseen species and adds them to the observed species richness (Colwell & Coddington 1995).

To quantify the relative abundances and incidence of species from the kelp forest and diets of *P. jugularis*, we calculated the numerical frequency (N) and frequency of occurrence (F) (Pinkas et al. 1971, Hyslop 1980, Castañeda-Fernández-de-Lara et al. 2005, Buckland et al. 2017, Tripp-Valdez et al. 2023). For N, we calculated the number of individuals of each taxon as a percentage of the total number of individuals of all taxa from kelp forest samples and stomach samples. For F, we calculated the percentage of observations in which each taxon occurred for kelp forest samples and stomachs.

Spearman rank correlation coefficient (r_s) was used to calculate the correlation between kelp forest samples and stomach contents. N and F were analyzed separately. A general linear model (LM) was used to compare rank abundance curves between the kelp forest assemblage and stomach contents. The relative abundance of each species was log$_{10}$-transformed for this analysis. Analyses were conducted using R version 4.3.2 (R Development Core Team 2023).

RESULTS

Predatory fish community

The size of *P. jugularis* in this study indicated that all fish sampled were adults (Meléndez 1989, Angel & Ojeda 2001, Medina et al. 2004). The adult size range for *P. jugularis* in a population from Pisco, Peru, started at 9.1 cm (Vélez et al. 2003). Seven predatory fish species were observed in the kelp forest during fish surveys. Fish abundance (number of individuals) was dominated by *Patagonotothen* sp., followed by *P. chilensis* and *P. jugularis* (109, 46, and 36 ind 200 m^{-2}, respectively, Table 1). Biomass, however, mostly accounted for *P. chilensis*, *P. jugularis*, and *Cheilodactylus variegatus* (11,670, 3598, and 1340 g 200 m^{-2}, respectively, Table 1). The largest individuals of the assemblage belonged to *C. variegatus* (mean = 27.5 cm, range = 25-35 cm), *P. chilensis* (mean = 25.6 cm, range = 10-40 cm), and *P. jugularis* (mean = 23 cm, range =15-35 cm, Table 1).

Prey diversity in kelp forest and diet of *Prolatilus jugularis*

In the kelp forest, there were 42 invertebrate taxa and 1016 individuals (Fig. 2, Table 2). The species-accumulation curve suggested the presence of a relatively small number of unseen species associated with the kelp forest, as indicated by the Chao estimator of 45.3 (SE = 3.03) (Fig. 2). Crustacea was the dominant taxa category with 27 species (N = 53.3%; F = 40%) (Table 2). The Amphipoda were the most abundant (N = 34%), common (F = 62%), and diverse (10 taxa) in the kelp forest. Annelida (Polychaeta and Sipuncula) were relatively abundant/common (N = 12.5%; F = 25.6%) and diverse (9 taxa). Mollusca (Gastropoda, Nudibranchia, and Bivalvia) represented 18.5% (N) of the total abundance, occurred in 36.3 samples (F), and encompassed seven taxa (Table 2). The most abundant and frequent taxon in the kelp forest was Stauromedusae larvae (N = 14.6%; F = 100%), followed by the bivalve *Tricolia macleani* (N = 14.3%; F = 90%; Table 2).

For the diets*, P. jugularis,* 21 taxa, and 130 individuals were sampled (Fig. 2, Table 2). In this case, the Chao estimator suggested the occurrence of a relatively large number of unseen species as indicated by the Chao estimator of 30.2 (SE = 7.76). All of the 13 *P. jugularis* stomachs contained identifiable prey. Crustacea was the dominant taxa category with 14 species (N = 87.7%; F = 19%). The Amphipoda were the most abundant and frequent with five taxa (N = 36.2%; F = 26%), but the Decapoda were most diverse with six taxa (N = 14.6%; F = 13%; Table 2). Other taxa identified in the diets of *P. jugularis* were the Annelida with three taxa (N = 6.2%; F = 15%) and the Mollusca with two taxa (N = 3.1%; F = 12%). The most abundant taxon in all stomachs was the isopod *Exosphaeroma gigas* (N = 33.1%; F = 31%), followed by unidentified amphipods (N = 25.4%), which were very frequent (F = 69%; Table 2).

Fish scales were present in the stomachs of 7 out of 13 fish. Digestion in the stomachs and intestines of *P. jugularis* was evident due to the presence of a thick, sticky mucus consisting of unidentifiable body parts (mostly crustaceans but also soft-bodied taxa such as polychaetes) and benthic material (sand, sediment, shell fragments, and pebbles) (Table 2). We observed a non-statistically significant correlation between invertebrate species of the kelp forest and in the stomachs of *P. jugularis*, for N (r_s = -0.04, *P* = 0.79) and F (r_s = 0.11, *P* = 0.46). In addition, the slope of the species-rank abundance curves differed between kelp forest and stomach assemblages (between-slope difference = 0.02 [CI = 0.01-0.02], R^2 = 0.96, *P* < 0.001; Fig. 3). The slope of the kelp forest assemblage was steeper than that of the stomach content, indicating a stronger dominance (e.g. lower evenness) in the former than the latter.

DISCUSSION

In this study, evidence suggests that kelp forests of *L. trabeculata* are resource-rich and may serve as an important food source for fish species. However, we must reject our hypothesis as there was no correlation between invertebrate species in the kelp forest and stomachs of *P. jugularis*. Perhaps *P. jugularis* feed in areas outside the sampling zone, e.g. other kelp forests or reefs. Larger mobile fish, such as the adult *P. jugularis* surveyed in this study, may have access to external food sources outside local kelp forests (Trebilco et al. 2013, Gartenstein et al. 2024). Mobile reef fishes that forage and aggregate locally or between habitats could be important conduits for increasing local reef production at various trophic levels (Trebilco et al. 2016, Gartenstein et al. 2024).

In the kelp forests of *L. trabeculata*, crustaceans were the most abundant and diverse taxa (Vásquez et al. 2001, Palma & Ojeda 2002, Pérez-Matus et al. 2012). Crustaceans are a high-energy resource (Palma & Ojeda 2002, Pérez-Matus et al. 2012). They are abundant in diets of predatory reef fish of coastal Chile (Ojeda & Dearborn 1991, Palma & Ojeda 2002, González & Oyarzún 2003, Medina et al. 2004, Pérez-
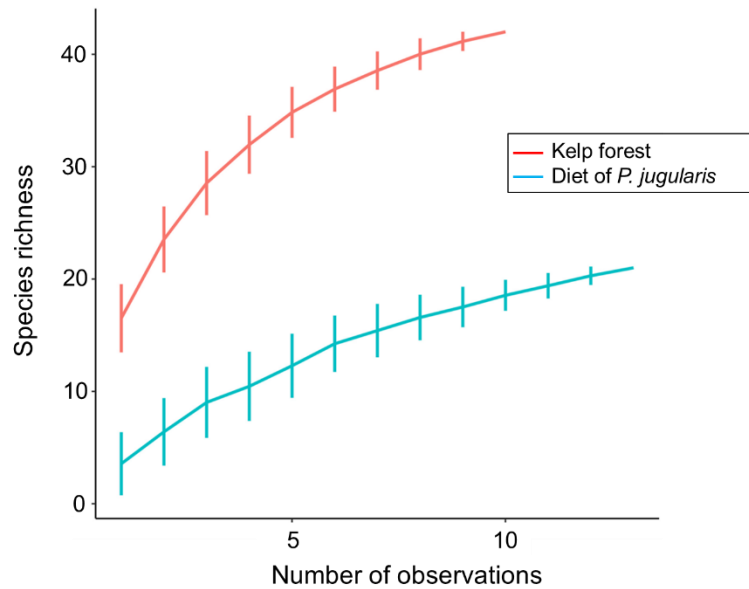
Figure 2. Species accumulation curves showing species richness for the number of samples (number of quadrats, n = 10) and diet of *Prolatilus jugularis* (n = 13 stomachs) from kelp forests of *Lessonia trabeculata*.

Matus et al. 2012). The high content of proteins, lipids, and carbohydrates in crustaceans most likely makes them a valuable trophic resource for predatory fish (Manly et al. 2002, Baeza-Rojano et al. 2014).

All stomachs of *P. jugularis* contained identifiable taxa in this study. In contrast, in northern Chile's kelp forests, the stomachs of *P. jugularis* were 67% empty (Medina et al. 2004). In another study, *P. jugularis* was removed from the analysis because most of its stomachs were empty (Angel & Ojeda 2001). Variations in diet composition and stomach fullness may be due to digestion rate, degree of mastication, type of prey ingested (e.g. soft-bodied prey such as polychaetes and molluscs are digested faster than crustaceans), and capture and storage methods (Rindorf & Lewy 2004, Buckland et al. 2017). The physiology and behavior of fish predators and seasonal changes in prey type and availability can also affect diets (Ojeda & Muñoz 1999, Pérez-Matus et al. 2012). In our study, the fact that all stomachs of *P. jugularis* had taxa indicates that the kelp forest habitat is resource-rich with the availability of substantial prey.

In the kelp forest and diet of *P. jugularis*, the most abundant and diverse taxa were crustaceans and, to a lesser degree, molluscs and polychaetes. Although the information on the diets of fish in kelp forests of *L. trabeculata* of south-central Chile is scarce, a study by Cornejo-Acevedo et al. (2014) at Morro Gonzalo showed that the predatory fish *P. chilensis* and *C.*

variegatus had a similar diet composition to *P. jugularis* in our study, which was composed mostly of crustaceans, with less abundance and diversity of molluscs and polychaetes. Of the crustaceans, amphipods were the most abundant and diverse in the kelp forest and the most abundant in the diet of *P. jugularis*. Other investigations in kelp forests of *L. trabeculata* have also shown the predominance of amphipods in the diets of *P. chilensis* (Moreno & Zamorano 1980, González & Oyarzún 2003), *C. geniguttatus* (Moreno & Zamorano 1980), and *C. variegatus* (Palma & Ojeda 2002, Medina et al. 2004, Pérez-Matus et al. 2012). Amphipods were probably not limited in the kelp forests due to their high abundance and diversity (Palma & Ojeda 2002), which may reduce the costs required by predatory fish to search, capture, and handle larger and more mobile prey (Scharf et al. 2000, Sih & Christensen 2001). Although decapods were less abundant and frequent than amphipods in the kelp forest, they were the most diverse taxa in the stomachs of *P. jugularis*.

Furthermore, decapods were more abundant and diverse in the stomachs compared to the kelp forest, suggesting plasticity in prey selection. Decapods have been mentioned as the preferred prey for many predatory reef fish species (Pérez-Matus et al. 2012, Cornejo-Acevedo et al. 2014). In our study, perhaps *P. jugularis* selected the decapods because of their larger size and greater energy potential (Manly et al. 2002,

Table 2. Results for numerical frequency (N) and frequency of occurrence (F) for benthic invertebrate taxa sampled in kelp forests of *Lessonia trabeculata* and from stomachs of *Prolatilus jugularis* at Morro Gonzalo, south-central Chile.

| Taxa			N(%)		F(%)	
Crustacea	Amphipoda	*Peramphithoe* sp.	11.7	5.4	100	23
		Heterophoxus sp.	3.3	0.8	60	8
		Aora typica	0.6	2.3	50	23
		Melita sp.	1.8	2.3	60	8
		Paramoera sp.	0.8	0	20	0
		Jassa sp.	1.7	0	20	0
		Caprellina longicollis	2.1	0	60	0
		Caprella scaura	2.5	0	50	0
		Paracaprella pusilla	0.1	0	100	0
		Unid. amphipod	9.5	25.4	100	69
	Tanaidacea	*Zeuxo marmoratus*	1.8	0	70	0
	Decapoda	*Hemigrapsus* sp.	0.1	0.8	10	8
		Alpheidae	0.1	0	10	0
		Romaleon setosum	0	1.5	0	8
		Cancer plebejus	0	3.9	0	8
		Taliepus dentatus	2	1.5	100	15
		Crab megalopa	0	2.3	0	8
		Unid. decapod	0	4.6	0	31
	Isopoda	*Exosphaeroma gigas*	0.3	33.1	20	31
		Ischyromene menziesi	0.8	0	20	0
		Meridiosignum menziesi	0.8	0	40	0
		Ianiropsis sp.	5.7	0	40	0
		Anthuroidea	0.1	0	10	0
	Copepoda	Copepoda	6.3	0	60	0
	Ostracoda	Ostracoda	0.4	3.1	20	15
	Pycnogonida	Pantopoda	0.7	0	40	0
	Insect larvae	Unidentifiable	0.4	0.8	20	8
Annelida	Polychaeta	Ampharetidae	2.3	0	10	0
		Capitellidae	0.3	0	10	0
		Hesionidae	0.4	0	30	0
		Nereididae	4.5	1.5	90	15
		Phyllodocidae	0.3	0	20	0
		Sabellidae	0.5	0	40	0
		Paraonidae	0	1.5	0	8
		Unid. polychaete	0.2	3.1	20	23
	Sipuncula	Golfingiidae	4.1	0	10	0
Nemertea	Neonemertea	Unidentifiable	0.7	0.8	30	8
Mollusca	Gastropodia	*Tricolia macleani*	14.3	2.3	90	15
	Nudibranchia	*Phidiana lottini*	0.3	0	20	0
		Hancockia schoeferti	0.4	0	30	0
		Diaulula punctuolata	0.2	0	20	0
		Doto uva	1.2	0	40	0
		Unid. nudibranch	0	0.8	0	8
	Bivalvia	*Gaimardia trapesina*	2	0	70	0
		Brachidontes granulata	0.2	0	20	0
Echinodermata	Echinoidea	*Loxechinus albus*	0.1	0	10	0
	Asteroidea	*Patiria obesa*	0.2	0	10	0
Cnidaria	Stauromedusae	Unidentifiable	14.6	2.3	100	15
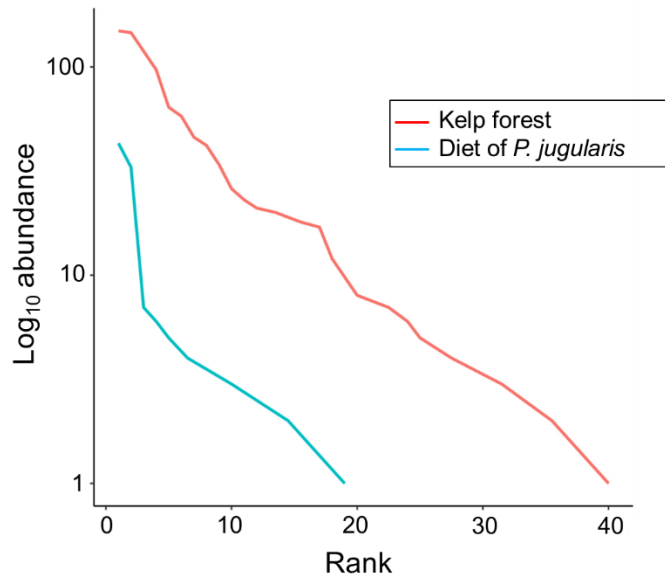
Figure 3. Species-rank abundance curves show the number of individuals ($\log_{10}$ abundance) for species in the kelp forest and diet of *Prolatilus jugularis*.

Pérez-Matus et al. 2012), which could also be the case for the isopod *Exosphaeroma gigas*, one of the largest and most abundant taxa in the diet of *P. jugularis* (N = 22.1%), yet scarce in kelp forest samples (N = 0.3%) (Table 2).

Molluscs were more abundant and diverse in the kelp forest compared to the diet of *P. jugularis*, suggesting they were not preferred prey. However, other studies of predatory fish in kelp forests have shown molluscs to be more prominent in their diets (Palma & Ojeda 2002, Medina et al. 2004, Pérez-Matus et al. 2012) when compared to *P. jugularis* in our study. Polychaetes were also less abundant and diverse in the diet of *P. jugularis*, as shown in other dietary studies of predatory fish (Medina et al. 2004, Cornejo-Acevedo et al. 2014). Perhaps the greater availability of better-quality prey, such as crustaceans, which are high in energy due to their content of proteins, lipids, and carbohydrates (Palma & Ojeda 2002, Pérez-Matus et al. 2012, Baeza-Rojano et al. 2014), may reduce the need for *P. jugularis* to select molluscs and polychaetes. However, an investigation by Meléndez (1989) in soft-sediment habitats found that *P. jugularis* fed principally on sedentary polychaetes (86% of all taxa) and, to a lesser degree, crustaceans, suggesting that *P. jugularis* is a generalist predator and can change its dietary habits to be consistent with the type of habitat and availability of local resources (Medina et al. 2004). This demonstration of plasticity has also been shown for other

predatory fishes in kelp forests of *L. trabeculata* (Medina et al. 2004, Pérez-Matus et al. 2012).

Small pebbles, shell grit, and sediment in the stomachs mirrored the benthic composition in the kelp forest, providing further evidence for its benthic and demersal feeding behavior (Meléndez 1989, Reyes & Hüne 2012). Stomach content analyses also revealed the presence of fish scales in the diets of *P. jugularis*. However, there was no other evidence for piscivory (i.e. the presence of bones). Although *P. jugularis* is piscivorous (Mann 1954, Moreno & Flores 2002, Vélez et al. 2003, Reyes & Hüne 2012), the presence of scales in the stomachs may also be due to the ingestion of detached scales when they swim in schools or scales in the ingested sediments.

Identification of taxa from the stomachs of *P. jugularis* was most likely affected by the ingested organisms that were partly digested and fragmented, which is probably one of the reasons correlations between kelp forest species and diet were weak and statistically non-significant. Additional samples (benthic invertebrates and *P. jugularis*) at an increased temporal and spatial scale would clarify food source potential in the kelp forest and diet composition. It is recommended that future studies combine traditional stomach content analyses with DNA-based (DNA barcoding) techniques with stable isotope analysis (Morais & Bellwood 2019), which will give a more

accurate description of abundances and species richness of consumed taxa and will avoid problems associated with the difficulty in identification of taxa, especially partially digested soft-bodied prey. Further studies of *P. jugularis* and *P. chilensis* at Morro Gonzalo are recommended to improve our understanding of the role of predatory fish and interactions with their habitat and prey, especially since together they contributed to 85.4% of the predatory fish biomass (15,277 g).

CONCLUSION

The study gives a snapshot of the predator-prey relationship of the Pacific sand perch *P. jugularis* in a kelp forest of *L. trabeculata*. We show that the feeding grounds of *L. trabeculata* are potentially resource-rich and may serve as important food sources for *P. jugularis* and, most likely, other predatory fish. Its carnivorous benthic diet indicated that it exploited mostly crustaceans, molluscs, and polychaetes. The species differences between the kelp forest and diet indicate that *P. jugularis* could feed in other habitats outside the survey area. *P. jugularis* was the second most common predatory fish in the kelp forest.

ACKNOWLEDGMENTS

REFERENCES

Angel, A. & Ojeda, F.P. 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. doi: 10.3354/meps217081

Baeza-Rojano, E., Hachero-Cruzado, I. & Guerra-García, J.M. 2014. Nutritional analysis of freshwater and marine amphipods from the Strait of Gibraltar and potential aquaculture applications. Journal of Sea Research, 85: 29-36. doi: 10.1016/j.seares.2013.09.007

Buckland, A., Baker, R., Loneragan, N. & Heaves, M.S. 2017. Standardizing fish stomach content analysis: The importance of prey condition. Fisheries Research, 196: 126-140. doi: 10.1016/j.fishres.2017.08.003

Campanella, F., Auster, P.J., Christopher-Taylor, J. & Muñoz, R.C. 2019. Dynamics of predator-prey habitat use and behavioral interactions over diel periods at sub-tropical reefs. Plos One, 14: 0211886. doi: 10.1371/journal.pone.0211886

Castañeda-Fernández-de-Lara, V., Serviere-Zaragoza, E., Hernández-Vázquez, S. & Butler, M. 2005. Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico. New Zealand Journal of Marine and Freshwater Research, 39: 425-435. doi: 10.1080/00288330.2005.9517322

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics, 43: 783. doi: 10.2307/2531532

Colwell, R.K. & Coddington, J.A. 1995. Estimating terrestrial biodiversity through extrapolation. Biodiversity: Measurement and Estimation, 345: 101-118. doi: 10.1098/rstb.1994.0091

Cornejo-Acevedo, M.F., Fierro, P., Bertrán, C. & Vargas-Chacoff, L. 2014. Composición y sobreposición dietaria de *Pinguipes chilensis* (Perciformes: Pinguipedidae), *Cheilodactylus variegatus* (Perciformes: Cheilodactylidae) y *Aplodactylus punctatus* (Perciformes: Aplodactylidae) en el litoral costero valdiviano, Chile. Gayana, 78: 98-108. doi: 10.4067/s 0717-65382014000200003

Dayton, P.K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics, 16: 215-245. doi: 10.1146/annurev.es.16.110185.001243

Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecological Applications, 8: 309-322. doi: 10.2307/2641070

Edgar, G.J., Cooper, A., Baker, S.C., Barker, W., Barrett, N.S., Becerro, M.A., et al. 2020. Reef life survey: establishing the ecological basis for conservation of shallow marine life. Biological Conservation, 252: 1-14. doi:10.1016/j.biocon.2020.108855

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., et al. 2011. Trophic downgrading of planet Earth. Science, 333: 301-306. doi: 10.1126/science.1205106

Frid, A., Connors, B., Cooper, A.B. & Marliave, J. 2013. Size-structured abundance relationships between upper-and mid-trophic level predators on temperate rocky reefs. Ethology Ecology and Evolution, 25: 253-268. doi: 10.1080/03949370.2013.798350

Gartenstein, S., Pérez-Matus, A., Heather, F.J., Godoy, N., Torres-Cañete, F., Catalán, A.M. & Valdivia, N. 2024. The limited effects of management and ecological subsidies on the size spectra of kelp forest fish communities. Marine Ecology Progress Series, 732: 135-147. doi: 10.3354/meps14528

Godoy, N., Gelcich, S., Vásquez, J.A. & Castilla, J.C. 2010. Spearfishing to depletion: evidence from temperate reef fishes in Chile. Ecological Applications, 20: 1504-1511. doi: 10.1890/09-1806.1

González, P. & Oyarzún, C. 2003. Diet of the Chilean sandperch, *Pinguipes chilensis* (Perciformes, Pinguipedidae) in southern Chile. Journal of Applied Ichthyology, 19: 371-375. doi: 10.1111/j.1439-0426.2003.00444.x

Gouraguine, A., Moore, P., Burrows, M.T., Velasco, E., Ariz, L., Figueroa-Fábrega, L., et al. 2021. The intensity of kelp harvesting shapes the population structure of the foundation species *Lessonia trabeculata* along the Chilean coastline. Marine Biology, 168: 1-9. doi: 10.1007/s00227-021-03870-7

Hyslop, E.J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology, 17: 411-429. doi: 10.1111/j.1095-8649.1980.tb02775.x

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht. doi: 10.22621/cfn.v117i2.717

Mann, G. 1954. Vida de los peces en aguas chilenas. Ministerio de Agricultura, Santiago.

Medina, M., Araya, M. & Vega, C. 2004. Alimentación y relaciones tróficas de peces costeros de la zona norte de Chile. Investigaciones Marinas, 32: 33-47. doi: 10.4067/S0717-71782004000100004

Meléndez, R. 1989. Alimentación y consideraciones somatométricas de *Prolatilus jugularis* (Valenciennes) (Teleostei, Branchiostegidae). Museo Nacional de Historia Natural (Chile), 316: 3-8.

Morais, R.A. & Bellwood, D.R. 2019. Pelagic subsidies underpin fish productivity on a degraded coral reef. Current Biology, 29:1521-1527. doi: 10.1016/j.cub.2019.03.044

Moreno, M. & Flores, H. 2002. Contenido estomacal de *Cheilodactylus variegatus* Valenciennes 1833, *Pinguipes chilensis* Valenciennes 1833 y *Prolatilus jugularis* Valenciennes, 1833 en bahía de la Herradura, Coquimbo, durante primavera del 2001. Gayana (Concepción), 66: 213-217. doi: 10.4067/S0717-6538 2002000200017

Moreno, C.A. & Zamorano, J.H. 1980. Selectividad del alimento en dos peces bentofagos (*Mugiloides chilensis* y *Calliclinus geniguttatus*). Brazilian Journal of Oceanography, 29: 245-249. doi: 10.1590/S0373-55241980000200051

Nakamura, I., Inada, T., Takeda, M. & Hatanaka, H. 1986. Important fishes trawled off Patagonia. Japan Marine Fishery Resource Research Center, Tokyo.

Norderhaug, K.M., Christie, H., Fosså, J.H. & Fredriksen, S. 2005. Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. Journal of the Marine Biological Association of the United Kingdom, 85: 1279-1286. doi: 10.1017/S0025315405012439

Ojeda, F. & Dearborn, J. 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. Journal of Experimental Marine Biology and Ecology, 149: 13-44. doi: 10.1016/0022-0981(91)90 114-C

Ojeda, F.P. & Muñoz, A.A. 1999. Feeding selectivity of the herbivorous fish *Scartichthys viridis*: effects on macroalgal community structure in a temperate rocky intertidal coastal zone. Marine Ecology Progress Series, 184: 219-229. doi: 10.3354/meps184219

Palma, A.T. & Ojeda, F.P. 2002. Abundance, distribution and feeding patterns of a temperate reef fish in subtidal environments of the Chilean coast: the importance of understory algal turf. Revista Chilena de Historia Natural, 75: 189-200. doi: 10.4067/S0716-078X20 02000100018

Pequeño, G. 1975. Peces del crucero Merluza V efectuado con el B/C Carlos Darwin entre Corral y Coquimbo. Enero-febrero de 1970. Boletín del Museo Nacional de Historia Natural, 34: 227-232. doi: 10.54830/bmnhn. v34.1975.535

Pequeño, G. & Lamilla, J. 1995. Peces intermareales de la costa de Llanquihue (Chile): composición taxonómica, abundancia relativa y gradiente de distribución longitudinal. Revista de Biología Marina y Oceanografía, 30: 7-27

Pérez-Matus, A., Ferry-Graham, L., Cea, A. & Vásquez, J.A. 2007. Community structure of temperate reef fishes in kelp-dominated subtidal habitats of northern Chile. Marine and Freshwater Research, 58: 1069-1085. doi: 10.1071/MF06200

Pérez-Matus, A.P., Carrasco, S.A., Gelcich, S., Fernandez, M. & Wieters, E.A. 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. Ecosphere, 8: 1-18. doi: 10.1002/ecs2.1808

Pérez-Matus, A., Pledger, S., Díaz, F.J., Ferry, L.A. & Vásquez, J.A. 2012. Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile. Revista Chilena de Historia Natural, 85: 29-48. doi: 10.4067/S0716-078X2012000100003

Pinkas, L., Oliphant, M.S. & Iverson, I.L.K. 1971. Food habits of albacore, bluefin tuna, and bonito. California Fish Game, 152: 1-105.

R Development Core Team. 2020. R a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reyes, P.L. & Hüne, M.B. 2012. Peces del sur de Chile. Ocho Libros Editorial, Santiago.

Rindorf, A. & Lewy, P. 2004. Bias in estimating food consumption of fish by stomach-content analysis. Canadian Journal of Fisheries and Aquatic Sciences, 61: 2487-2498. doi: 10.1139/f04-200

Riquelme-Pérez, N., Musrri, C.A., Stotz, W.B., Cerda, O., Pino-Olivares, O. & Thiel, M. 2019. Coastal fish assemblages and predation pressure in northern-central Chilean *Lessonia trabeculata* kelp forests and barren grounds. PeerJ, 7: e6964. doi: 10.7717/peerj.6964

Scharf, F.S., Juanes, F. & Rountree, R.A. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series, 208: 229-248. doi: 10.3354/meps208229

Sih, A. & Christensen, B. 2001. Optimal diet theory: when does it work, and when and why does it fail? Animal Behaviour, 61: 379-390. doi: 10.1006/anbe.2000.1592

Smale, D.A., Epstein, G., Hughes, E., Mogg, A.O.M. & Moore, P.J. 2020. Patterns and drivers of understory macroalgal assemblage structure within subtidal kelp forests. Biodiversity and Conservation, 29: 4173-4192. doi: 10.1007/s10531-020-02070-x

Teagle, H., Hawkins, S.J., Moore, P.J. & Smale, D.A. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology, 492: 81-98. doi: 10.1016/j.jembe.2017.01.017

Thiel, M. & Hinojosa, I.A. 2009. Peracarida - anfípodos, isópodos, tanaidáceos y cumáceos. In: Häussermann, V. & Försterra, G. (Eds.). Fauna marina bentónica de la Patagonia Chilena. Nature in Focus, Puerto Montt, pp. 671-739.

Thiel, M., Guerra-García, J.M., Lancellotti, D.A. & Vasquez, N. 2003. The distribution of littoral caprellids (Crustacea : Amphipoda : Caprellidea) along the Pacific coast of continental Chile. Revista Chilena de Historia Natural, 76: 297-312. doi: 10.4067/S0716-078X2003000200014

Thiel, M., Macaya, E.C., Acuna, E., Arntz, W.E., Bastias, H., Brokordt, K., et al. 2007. The Humboldt Current System of northern and central Chile oceanographic processes, ecological interactions and socioeconomic feedback. Oceanography and Marine Biology, 45: 195-345. doi: 10.1201/9781420050943.ch6

Trebilco, R., Baum, J.K., Salomon, A.K. & Dulvy, N.K. 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends in Ecology & Evolution, 28: 423-431. doi: 10.1016/j.tree.2013.03.008

Trebilco, R., Dulvy, N.K., Anderson, S.C. & Salomon, A.K. 2016. The paradox of inverted biomass pyramids in kelp forest fish communities. Proceedings of the Royal Society B: Biological Sciences, 283: 0816. doi: 10.1098/rspb.2016.0816

Tripp-Valdez, A., Pinon-Gimate, A., Jakes-Cota, U. & Lopez-Fuerte, F.O. 2023. Diet of the stone scorpion-fish (*Scorpaena mystes*) from the coastal region of Santa Rosalia, Gulf of California, Mexico using stomach contents and stable isotope analyses. Regional Studies in Marine Science, 62: 102942. doi: 10.1016/j.rsma.2023.102942

Trujillo, J.E., Pardo, L.M., Vargas-Chacoff, L. & Valdivia, N. 2019. Sharks in the forest: relationships between kelp physical-complexity attributes and egg deposition sites of the red-spotted catshark. Marine Ecology Progress Series, 610: 125-135. doi: 10.3354/meps12818

Vásquez, J.A., Veliz, D. & Pardo, L.M. 2001. Biodiversidad de macroinvertebrados bajo las grandes algas. In: Alveal, K. & Antezana, T. (Eds.). Sustentabilidad de la biodiversidad. Universidad de Concepción, Concepción, pp. 293-308.

Velasco-Charpentier, C., Pizarro-Mora, F., Navarro, N.P. & Valdivia, N. 2021. Disentangling the links between habitat complexity and biodiversity in a kelp-dominated subantarctic community. Ecology and Evolution, 11: 1214-1224. doi: 10.1002/ece3.7100

Vélez, J.A., Watson, W., Sandknop, E.M. & Arntz, W. 2003. Larval development of the Pacific sandperch (*Prolatilus jugularis*) (Pisces: Pinguipedidae) from the Independencia Bight, Pisco, Peru. Journal of the Marine Biological Association of the United Kingdom, 83: 1137-1142. doi: 10.1017/S0025315403008397h

Vera-Duarte, J.A. & Landaeta, M.F. 2017. Feeding habits and dietary overlap during the larval development of two sandperches (Pisces: Pinguipedidae). Scientia Marina, 81: 195-204. doi: 10.3989/scimar.04544.06A

Witman, J.D. & Lamb, R.W. 2018. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. Plos One, 13: e0189388. doi: 10.1371/journal.pone.0189388

Zagal, C.J., Hermosilla, C. & Riedemann, A. 2007. Guide to marine invertebrates of southern Chile. Fantastico Sur Birding Ltda., Puerto Natales.