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Adaptation of diet in a changed environment: Increased consumption of lobster krill *Munida gregaria* (Fabricius, 1793) by Argentine hake

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Abstract

A well-replicated decadal-term (2005–2014) stomach content data set was analysed in order to infer inter-annual fluctuations in the diet of the Argentine hake, *Merluccius hubbsi*, an opportunistic predator in the San Jorge Gulf (SJG) ecosystem in the Southwest Atlantic. Ten research cruises were carried out each year during January from 2005 to 2014. A total of 18,461 specimens of *Me. hubbsi* was analysed, of which 6,777 (36.71%) contained food in their stomachs. The diet of *Me. hubbsi* changed markedly from 2011 onwards, with much greater consumption of the lobster krill *Munida gregaria* compared to the years before 2011. The frequency of occurrence (%F) of *Mu. gregaria* in the stomach contents of Argentine hake increased from the year 2009 onwards, most noticeably since 2011, and mostly over the southern region of the SJG. The main predators of *Mu. gregaria* in the SJG are two species of teleost fish (pink cusk eel, *Genypterus blacodes*, Argentine seabass, *Acanthistius brasilianus*) and three Rajidae skates (*Zearaja chilensis*, *Psammobatis* spp. and *Sympterygia bonapartii*), which exhibited decreased catches in the years analysed. The increased consumption of *Mu. gregaria* by *Me. hubbsi*, coupled with decreased trends in abundance of the main predators of the lobster krill during the last decade, indicate that top-down trophic dynamic control occurs in the SJG ecosystem.

KEYWORDS
diet shift, Galatheidae, Merlucciidae, top-down, trophic ecology

1 | INTRODUCTION

Conditions change in marine environments at a wide range of scales, from minutes to thousands of years, and bring pronounced changes in communities of organisms (Valiela, 1984). The modification of one or several components of marine ecosystems can have strong effects on higher or lower trophic levels, depending on whether the food web is controlled by resources or predators by bottom-up or top-down controls, (Cury, Shannon, & Shin, 2003). These systems can also be controlled by a number of key species in the middle through wasp-waist control, which is most probable in upwelling ecosystems (Cury et al., 2000). It is difficult to identify concretely how such changes affect marine communities, but opportunistic predators take advantage of a source of food outside their usual diet, changing their preferred prey type in relation to local availability, moving towards the most abundant resource (Gerking, 1994). Changes in the diet of opportunistic predators can provide valuable insights on ecosystem dynamics (Link & Ford, 2006), physical variability (Tam, Purca, Duarte, Blaskovic, & Espinoza, 2006) and large structural changes of marine communities (Becker & Beissinger, 2006). However, an opportunistic species may appear to have a specialized diet as it feeds exclusively on an abundant prey species (Mahe, Amara, Bryckaert, Kacher, & Brylinski, 2007), but an opportunistic pattern may be recognized over a broad temporal scale (Gerking, 1994).

The subfamily Merlucciinae (family Merlucciidae) comprises one genus, *Merluccius*, with 13 currently recognized species worldwide (Cohen, Inada, Iwamoto, & Scialabba, 1990; Nelson, Grande, & Wilson, 2016), of which most are opportunistic, generalist feeders exhibiting broad diets (Buckley & Livingston, 1997; Du Buit, 1996; Garrison & Link, 2000; Payne, Rose, & Leslie, 1987; Tam et al., 2006). Hake fisheries are present in the Atlantic (both sides and including the Mediterranean Sea and Black Sea), Southwestern Indian and Eastern Pacific (from British Columbia to the tip of South America) Oceans, and in New Zealand (Cohen et al., 1990; Nelson et al., 2016), and are economically the most important fishery in all of these localities. The Argentine hake, *Merluccius hubbsi*, is a demersal species, widely distributed across the Southwestern Atlantic Ocean from Brazil (21°30′S) to Southern Patagonia (55°S) (Cousseau & Perrota, 2013). There are two main stocks of *Me. hubbsi* in Argentina, the Northern stock (NS, 34°S–41°S) and the Patagonian stock (PS, 41°S–55°S) (Bezzi et al., 2004). Each stock has different historical exploitation patterns and is managed independently (Aubone et al., 2004).

Owing to Argentine hake's commercial importance in the South Atlantic Ocean, its high abundance and the fact that it is an important predator in the Patagonian shelf waters (Laptikhovsky & Fetisov, 1999), many studies have examined its diet composition (Angelescu & Cousseau, 1969; Angelescu, Gneri, & Nani, 1958; Angelescu & Prenski, 1987; Belleggia, Figueroa, Irusta, & Bremec, 2014; Cordo, 1981; Ocampo Reinaldo, González, & Romero, 2011; Ruiz & Fondacaro, 1997; Sánchez, 2009; Sánchez & García De La Rosa, 1999; Sánchez & Prenski, 1996; Temperoni, Viñas, & Buratti, 2013). Although the feeding habits of Argentine hake have been studied in detail, there is no work analysing long-term variations in diet composition. In this context, this work analysed the stomach contents of Argentine hake collected between 2005 and 2014 in the San Jorge Gulf (SJG) region in the Southwestern Atlantic, aiming to find evidence of temporal variation in the diet. Based on this time series, the specific goals of our study were: (i) to provide a quantitative analysis of the diet composition of *Me. hubbsi* in the SJG in the Southwestern Atlantic, (ii) to examine temporal variability in the diet of *Me. hubbsi*, (iii) to identify which prey was the major contributor to the observed temporal differences in diet, and (iv) to explore the abundances of the known predators of the prey identified in (iii), to infer which type of trophic dynamics applies (bottom-up or top-down control).

2 | MATERIAL AND METHODS

2.1 | Study area

The study was focused on an area located between 45°S–47°S and 63.55°W–67.28°W in the Southwest Atlantic Ocean, from a depth of 60–109 m. This region includes the SJG, a major coastal embayment in the region (Acha, Mianzan, Guerrero, Favero, & Bava, 2004). The SJG is influenced in the north by a tidal mixing front during spring and summer, with stratified offshore waters and a vertically coastal mixed body of water (Acha et al., 2004). The tidal friction acts from the bottom upwards, providing efficient recirculation of nutrients and high

primary production to the productive layer of water (Rydberg, 2009). The south region is influenced by a Patagonian cold estuarine front, a diluted water mass that flows from the northern extreme of the Drake Passage (55°S) 800 km northward, reaching the southern limit of the SJG and meeting the tidal mixing front here located (Acha et al., 2004). These fronts make the SJG region of utmost ecological importance for several species, including the Argentine hake, *Merluccius hubbsi*, for feeding and spawning (Acha et al., 2004).

2.2 | Data sources

Our study was focused on repeated and systematic scientific surveys conducted during Januaries 2005–2014 by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). Argentine hake stomachs were collected during bottom trawl surveys following a stratified random design in order to assess the biomass and spawn abundance of this species. Fishing was conducted during daylight hours (07.00–19.00 hr) at 3–4 knots for 30 min in each sampling site, and employed an Engel bottom trawl net (200 mm mesh in the wings, 103 mm in the cod ends, 4 m vertical opening and 15 m horizontal aperture). A total of 125 trawls was analysed, from which catches were identified to species level and weighted. Skates were grouped as Rajidae due to the inaccuracy of species identification during the first surveys of the decadal series. At each trawl location, the *Merluccius hubbsi* specimens were measured to the nearest cm and sexed. Finally, stomachs were excised and each prey item was identified to the lowest taxonomic level and classified as present (1) or absent (0). This decadal (2005–2014) stomach content data set of *Me. hubbsi* allowed us to calculate the percentage of frequency of occurrence of each prey (%F, the total number of stomachs containing a given prey expressed as percentage of the total number of stomachs excised that contained food) for each year, giving a robust and interpretable measure for quantifying diet composition (Baker, Buckland, & Sheaves, 2014).

2.3 | Statistical analyses

The differences in size frequency distributions among years were evaluated by pairwise Kolmogorov–Smirnov tests (Crawley, 2005). In order to assess whether the number of stomachs analysed was sufficient to accurately describe the diet of each year considered (Cortés, 1997; Ferry & Cailliet, 1996), the stomachs sampled were randomized 100 times, and an accumulation prey curve was constructed as a function of stomach number. The cumulative prey curves with their confidence intervals (95%) were fitted and the sample sizes were considered sufficient to describe diets when curves reached an asymptote.

The stomachs containing food were grouped and averaged by sampling site. The average number of each prey by sampling site was used to build a Bray–Curtis dissimilarity matrix (Krebs, 1989; Zuur, Ieno, & Smith, 2007). An analysis of similarities (ANOSIM) was performed to evaluate Argentine hake diet differences among years, and pairwise comparisons were considered significant if pairwise R > Global R and $p < .05$ (Clarke, 1993). In addition, the degree of separation among years increases as the R value increases (Clarke,

1993). Similarity percentages (SIMPER) analyses were used to assess the contribution of each prey to the diet differences observed in the ANOSIM, and also to find the most erratic prey (Clarke, 1993; Zuur et al., 2007). Following SIMPER, the most erratic prey was defined as the prey item that contributed most to the dissimilarity among years in the diet of Argentine hake. Hereafter, the frequency of occurrence of the most erratic prey was calculated by sample site (%F_t), as the number of stomachs of Argentine hake in which the erratic prey was found, expressed as the percentage of stomachs with food, in each sampling site. The %F_t calculated were interpolated using the ordinary Kriging interpolation function to create a grid for each year and plotted.

Finally, the main predators of the most erratic prey were identified following previous studies focused on the SJG ecosystem (Sánchez & Prenski, 1996). The catches of the species considered predators of the erratic prey in the scientific surveys were analysed by year using the loess procedure, which fits smooth curves using non-parametric techniques to the relationship between variables (Crawley, 2005). The yearly averaged catch of the main known predators of the most erratic prey expressed in kilograms was used as the dependent variable to explore temporal variability in relative abundance of these species, and to identify an ecosystem control mechanism (bottom-up or top-down control) (Richardson & Schoeman, 2004). Statistical analyses were performed in the open R language using R 3.2.2 with the libraries MASS, stasts and vegan (R Core Team, 2014).

3 | RESULTS

A total of 18,461 specimens of the Argentine hake *Merluccius hubbsi* was analysed, of which 6,777 (36.71%) contained food in their stomachs. The cumulative prey curves indicated that the number of stomachs analysed in each year was adequate to study the diet of this species (Figure 1). Size frequency distributions of *Me. hubbsi* (Figure 2) were generally significantly different among years (Kolmogorov–Smirnov test, $p < .05$), with the exception of the years 2009 and 2011 ($D = 0.046$, $p = .14$), which did not differ. The mean total length did not show any differences when 2005 was compared with 2007 or 2013, 2006 with 2014, 2007 with 2009, 2012 or 2013, 2008 with 2013, and 2009 with 2012 (Student's t test, $p > .05$; Figure 2). The variances of the total length did not show differences for the comparisons of 2005 with 2006, 2007 with 2010, 2008 with 2010 and 2014, and 2009 with 2013 (variance F test, $p > .05$; Figure 2).

A total of 21 prey items was identified in the stomach contents of *Me. hubbsi* during 2005–2014: seven fishes, seven crustaceans, five cephalopods and two others (Table 1). Among fish, predation on *Engraulis anchoita* and cannibalism were present throughout the decade of this study (Table 1). The crustaceans *Themisto gaudichaudii*, *Euphausia* spp., *Munida gregaria* and *Peisos petrunkevitchi*, and the cephalopod *Illex argentinus* were also present during all years from 2005 to 2014 (Table 1). The %F of all crustaceans showed an increasing trend over time, whereas fish and cephalopods declined (Table 1).

There were significant differences in the diet of *Me. hubbsi* among years (ANOSIM, Global $R = .171$, $p < .001$). The pairwise comparisons indicated that the greatest change in the diet occurred since 2011 ($R_{2005–2011} = .86$, $p < .001$; $R_{2006–2011} = .46$, $p < .001$; $R_{2007–2011} = .66$, $p < .001$; $R_{2008–2011} = .43$, $p < .001$; $R_{2009–2011} = .26$, $p < .001$; $R_{2010–2011} = .50$, $p < .001$). The diet did not show any differences when 2011 was compared with 2012, 2013 and 2014 (pairwise $R <$ Global R, and $p > .05$). The SIMPER analysis revealed that the squat lobster, *Munida gregaria*, was the most erratic prey and thus contributed most to the differences observed among years [contribution to dissimilarity $(C)_{2005–2011}$: 41.0%; $C_{2006–2011}$: 48.9%; $C_{2007–2011}$: 42.5%; $C_{2008–2011}$: 46.8%; $C_{2009–2011}$: 43.9%; $C_{2010–2011}$: 43.9%].

Mapping the %F_t of *Mu. gregaria* by year revealed that the increased consumption by *Me. hubbsi* started during 2008 over the southern region of the SJG, and geographically spread in 2011–2014 (Figure 3). The shift in the diet of *Me. hubbsi* exhibited a pronounced pattern from 2011 to 2014, mainly in the southern region of the SJG, where 100% of the stomachs contained *Mu. gregaria* as prey (Figure 3).

In the SJG ecosystem, the lobster krill *Mu. gregaria* was mainly predated by two species of teleost fish [pink cusk eel, *Genypterus blacodes* (*Mu. gregaria* was 43% of its diet), Argentine seabass, *Acanthistius brasilianus* (54%)] and three Rajidae skates [*Zearaja chilensis* (30%), *Psammobatis* spp. (73%) and *Sympterygia bonapartii* (67%)]. The catches of these main predator species decreased through time from 2005 to 2014 (Figure 4).

4 | DISCUSSION

The diet of the Argentine hake, *Merluccius hubbsi*, changed during the decade of the study, with decreasing proportions of fish and cephalopods, and increasing proportions of crustaceans. The major increase among crustaceans occurred for the squat lobster, *Munida gregaria*. The benthic phase of this prey substantially increased its relative availability and abundance in the SJG ecosystem, from 1,779.2 to 1,483.3 kg nm^{-2} in 2009 and 2010, respectively, to 4,040 kg nm^{-2} in 2011 (Ravalli, De La Garza, & López-Greco, 2013). This shift in diet composition towards the most abundant resource confirms the extreme plasticity in the opportunistic foraging behavior of *Me. hubbsi*. This pattern has also been observed in other opportunistic hakes such as *Merluccius gayi peruanus*, which changed its diet due to the reduction in its preferred prey during El Niño events (Tam et al., 2006). Pinnegar, Trenkel, Tidd, Dawson, and Du Buit (2003) suggested that fish species exhibit some flexibility in their feeding preferences but they have a 'portfolio' of suitable prey types, and they respond to changes in relative abundance of prey within their particular portfolio.

The shifts observed in the feeding habits of *Me. hubbsi*, a generalist predator, provided interesting insights into the distribution, boom and availability of the prey *Mu. gregaria*. The genus *Munida* with 243 species (Baba et al., 2008) is the most specious genus of the family Munididae (Ahyong, Baba, Macpherson, & Poore, 2010). *Munida gregaria* is distributed in the Southern Hemisphere around New Zealand and Southern Australia, from 36°S to 51°S, and around Southern South America, from 41°S to 55°S in the Pacific and from 35°S to 55°S in the
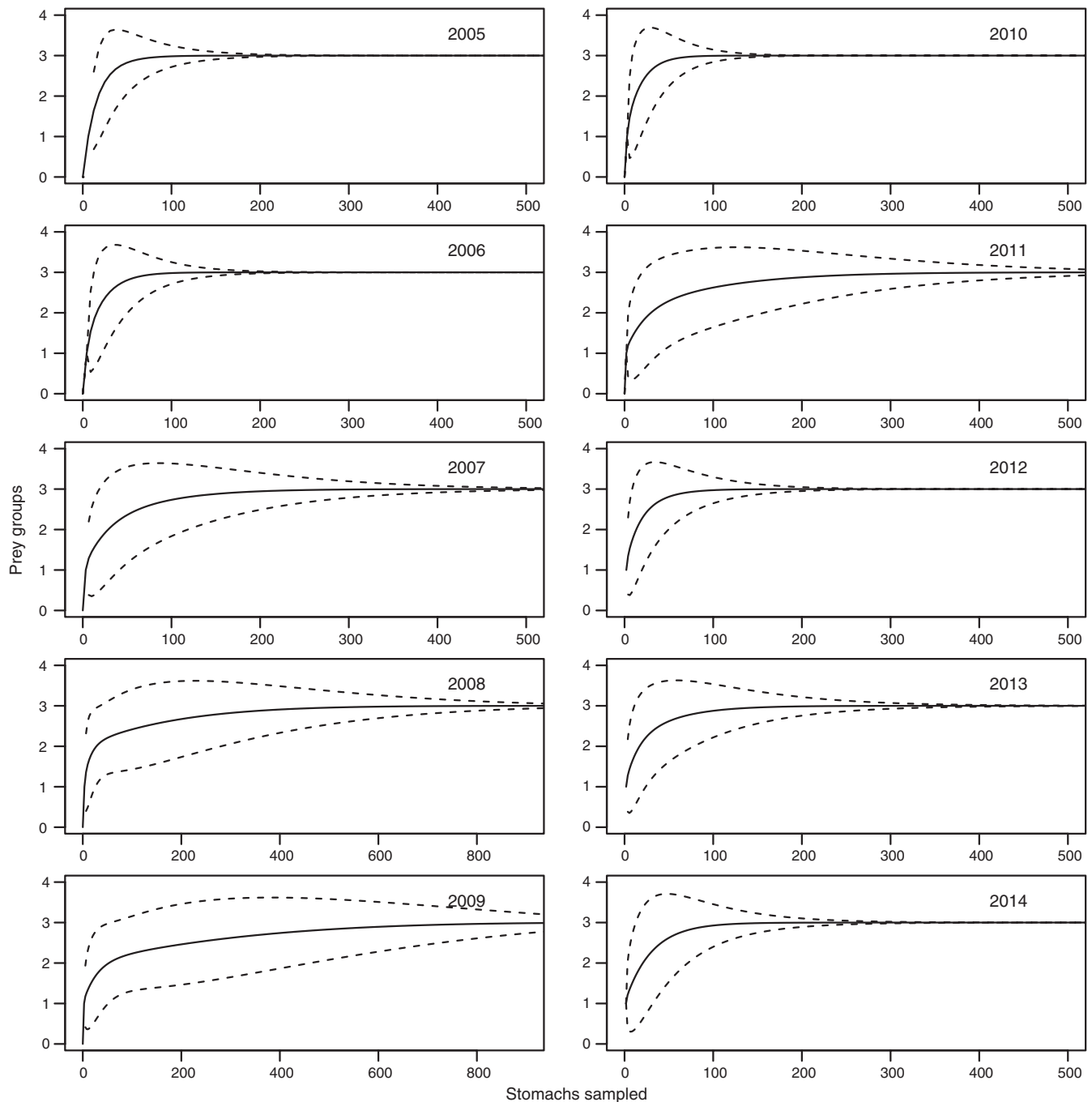
FIGURE 1 Randomized cumulative prey curves as a function of specimens of *Merluccius hubbsi* analysed for each year considered in the dietary analysis. Mean (continuous line) ± confidence intervals (dashed lines) are plotted

Atlantic (Ahyong & Poore, 2004; Baba et al., 2008; Boschi, Fischbach, & Iorio, 1992). *Munida gregaria* is one of the most abundant decapod species in the Southwestern Atlantic (Diez, Tapella, Romero, Madirolas, & Lovrich, 2016). It represents a direct trophic shortcut in this marine food web incorporating organic matter into the food web: it feeds at a low trophic level, upon algae, detritus and sediments, representing an important link between the particulate organic matter and many benthic and demersal top predators (Diez, Tapella, et al., 2016; Pérez-Barros, Romero, Calcagno, & Lovrich, 2010; Romero, Lovrich, Tapella, & Thatje, 2004; Vinuesa & Varisco, 2007).

Munida gregaria usually exhibits high abundances in Southern Chile and Argentina in the Drake Passage and Beagle Channel (Diez et al., 2012; Pérez-Barros, Tapella, Romero, Calcagno, & Lovrich, 2004). During the past decade scientists have started to examine the ecological role of these abundant organisms in an effort to take a more integrated ecosystem approach to fisheries management (Lovrich & Thiel, 2011). Diez, Cabreira, Madirolas, and Lovrich (2016) have more recently noted that between 2009 and 2014 pelagic swarms of *Mu. gregaria* increased their occurrence and abundance in both the Beagle Channel and on the
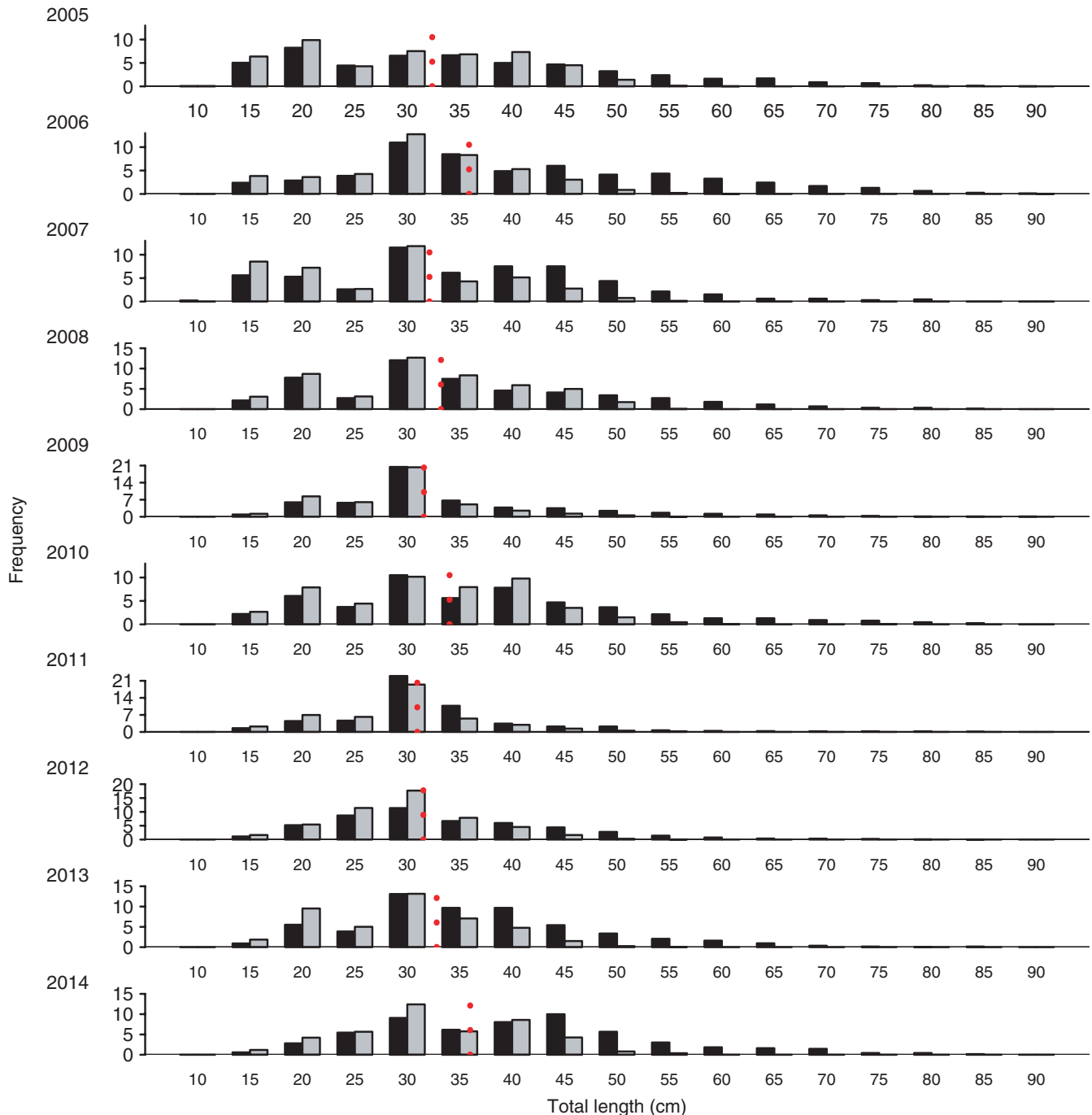
FIGURE 2 Size frequency distributions of the Argentine hake, *Merluccius hubbsi*, caught for the diet analysis from the year 2005–2014. Females (black bars), males (white bars) and the mean of total length (vertical red-dashed line) are represented

Argentine Patagonian Shelf. Moreover, *Mu. gregaria* is actually the most important crustacean in the by-catch of the Patagonian shrimp fishery (Varisco, Vinuesa, & Góngora, 2015). Its commercial potential was recognized, and it was even included in cookbooks from Argentina (Bigongiari, 2016). In accordance with our results, an increase in *Mu. gregaria* swarms and benthic aggregations occurred in southern areas of the SJG (Diez, Cabreira et al., 2016; Roux & Piñero, 2006), probably driven by natural population growth in the absence of high predation-related mortality,

coupled with oceanographic factors. Both aspects are discussed below.

The population expansion of *Mu. gregaria* agrees with our results, and can be explained by both oceanographic and biological factors. The former is supported by the Patagonian current, a diluted plume that occurs with an excess of rainfall in the Southeast Pacific and the continental discharge along the west coast of South America (Acha et al., 2004), which transports low salinity waters, mixed by tides and winds, 800 km northwards along the west coast of South America

TABLE 1 Diet composition of the Argentine hake *Merluccius hubbsi* from the year 2005 to 2014, in San Jorge Gulf from the Southwest Atlantic Ocean, expressed as the percentage of frequency of occurrence (%F)

	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Prey items	%F	%F	%F	%F	%F	%F	%F	%F	%F	%F
Crustaceans	44.13	64.38	84.16	77.59	91.42	70.97	89.95	80.66	84.94	89.37
Themisto gaudichaudii	6.68	5.68	31.69	13.79	22.57	18.16	6.70	11.00	9.61	10.54
Euphausia spp.	36.03	12.52	20.00	26.25	24.25	25.28	1.41	28.82	28.28	23.19
Munida gregaria	1.42	1.37	0.26	9.77	25.37	12.73	63.32	38.67	43.35	52.06
Peisos petrunkevitchi	0.81	45.60	37.40	30.46	22.76	14.98	19.93	4.17	3.97	4.12
Pleoticus muelleri	–	0.39	–	1.15	0.75	1.12	3.88	1.99	3.42	2.93
Pterigosquilla armata armata	–	–	0.26	–	0.56	0.37	0.18	–	0.09	0.09
Unidentified crustaceans	–	–	–	–	–	–	0.35	0.19	–	0.09
Fish	34.01	20.35	12.47	21.07	8.96	15.36	8.99	6.92	12.48	6.42
Engraulis anchoita	12.55	3.33	3.12	6.13	1.49	5.99	0.71	3.60	0.18	0.73
Merluccius hubbsi	12.75	11.55	6.23	9.96	4.66	8.05	6.00	2.65	11.18	4.22
Patagonotothen ramsayi	0.40	0.20	0.26	–	–	–	0.18	–	0.09	–
Genypterus blacodes	–	–	–	–	–	–	–	–	–	0.09
Stromateus brasiliensis	0.20	–	–	–	–	–	–	–	–	–
Raneya brasiliensis	0.00	0.20	–	–	0.19	–	–	–	–	–
Unidentified fish	8.10	5.28	2.86	4.79	2.61	1.31	2.12	0.66	1.02	1.37
Cephalopods	22.06	17.42	4.42	1.72	0.75	14.61	1.94	13.93	3.70	4.67
Illex argentinus	21.05	17.03	4.16	0.77	0.56	13.67	1.76	13.84	3.42	4.67
Doryteuthis gahi	0.81	0.20	–	0.57	0.19	0.94	–	–	–	–
Pulpo spp.	–	–	–	–	–	–	–	0.09	0.09	–
Semirossia tenera	0.20	0.20	0.26	0.38	–	–	0.18	–	0.09	–
Unidentified cephalopods	–	–	–	–	–	–	–	–	0.09	–
Others	1.01	0.00	0.52	–	–	0.19	–	0.19	0.65	0.64
Pleurobrachia sp.	0.81	–	–	–	–	–	–	–	–	–
Unidentified remains	0.20	–	0.52	–	–	0.19	–	0.19	0.65	0.64

from the Drake Passage to the southern limit of the SJG (Acha et al., 2004). *Munida gregaria* can remain pelagic after metamorphosis for up to 6 months; adults are benthic but can perform vertical migrations into the water layer (Diez et al., 2012; Zeldis, 1985), which would facilitate transport from the Beagle Channel to the frontal and highly productive region of the Southern SJG ecosystem. However, further studies considering oceanographic and environmental variables are necessary in order to explain the geographic expansion of *Mu. gregaria* and also to understand the fluctuations in its abundance.

The decrease in the abundance of the predators of *Mu. gregaria* can be considered among the biological factors explaining the population expansion. The time series herein analysed include both decreases in predator abundance and the corresponding increase in *Munida* spp. abundance. This may indicate that the absence of predators is the determinant of prey abundance when a linear predator–prey relationship is assumed. A similar pattern was identified for the Atlantic cod (*Gadus morhua*) and northern shrimp (*Pandalus borealis*) interaction across the North Atlantic Ocean, where shrimp

populations were strongly inversely related to predator abundance (Worm & Myers, 2003). Varisco et al. (2015) hypothesized that the lower abundance of *Me. hubbsi* could explain the demographic expansion of *Mu. gregaria*. However, other species exhibited decreasing trends and were the main predators of *Mu. gregaria* in the SJG ecosystem during the 1990s, for instance: the pink cusk eel, *Genypterus blacodes*, Argentine seabass, *Acanthistius brasilianus* and Rajidae skates (*Zearaja chilensis*, *Psammobatis* spp. and *Sympterygia bonapartii*) (Sánchez & Prenski, 1996).

The increased consumption of the lobster krill *Munida* spp. by the opportunistic *Me. hubbsi* combined with the decreased trends in abundance of the main predators of the lobster krill suggest a top-down trophic dynamic control in the SJG ecosystem. Bottom-up controls result in a positive correlation between predator and prey abundances, whereas top-down control should result in a negative correlation between predators and prey (Richardson & Schoeman, 2004). Similarly, in a neighboring area, a wasp-waist ecosystem control supported by the amphipod *Themisto gaudichaudii* was suggested (Padovani, Viñas,
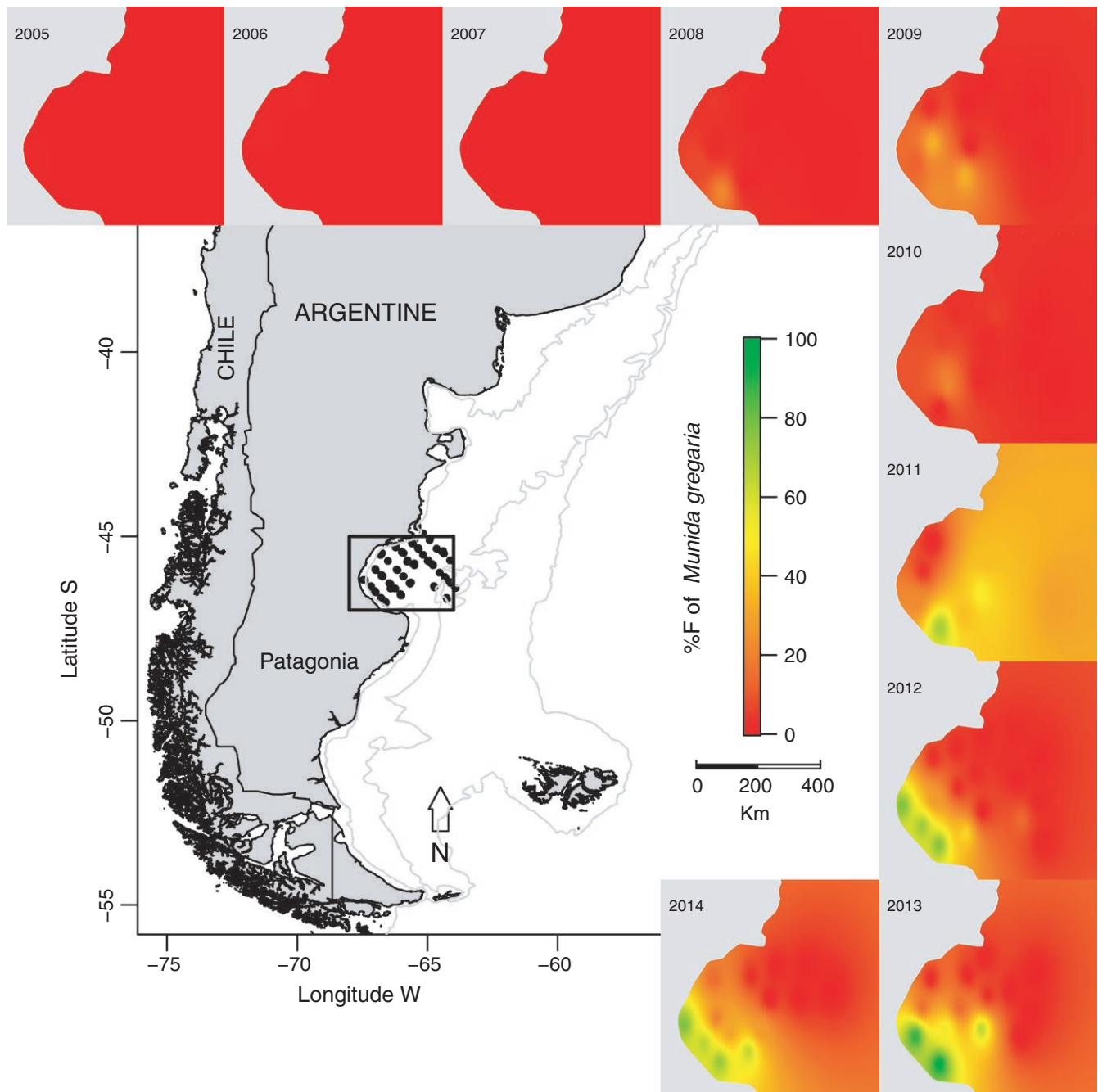
FIGURE 3 Map of the study area in the Southwestern Atlantic Ocean. The rectangle in San Jorge Gulf (SJG) region shows sample sites where specimens of *Merluccius hubbsi* were captured to study the diet composition from 2005 to 2014. The spatial distribution of the percentage of the frequency of occurrence of the most erratic prey (Munida gregaria) from 2005 to 2014 is color represented by ordinary Kriging interpolation in marginal maps

Sánchez, & Mianzan, 2012). The abundance and species composition in an environment are determined by a combination of competitive interactions among the species and the effect of predation on those species (Valiela, 1984). Our study suggests that the biological system was top-down controlled by several predators like the pink cusk eel, *G. blacodes*, the Argentine seabass *A. brasilianus* and Rajidae (*Z. chilensis*, *Psammobatis* spp. and *S. bonapartii*), which exhibited inverse correlations with their prey, the lobster krill *Mu. gregaria*, in the SJG ecosystem.

5 | CONCLUSIONS

Our results show that the diet of the Argentine hake, *Merluccius hubbsi*, changed during the decade of the study in the SJG ecosystem, with increased consumption of the lobster krill *Munida gregaria*.

Moreover, this work exhibited decreased catches for the main known predators of *Mu. gregaria* (pink cusk eel, *Genypterus blacodes*, the Argentine seabass, *Acanthistius brasilianus*, and three Rajidae
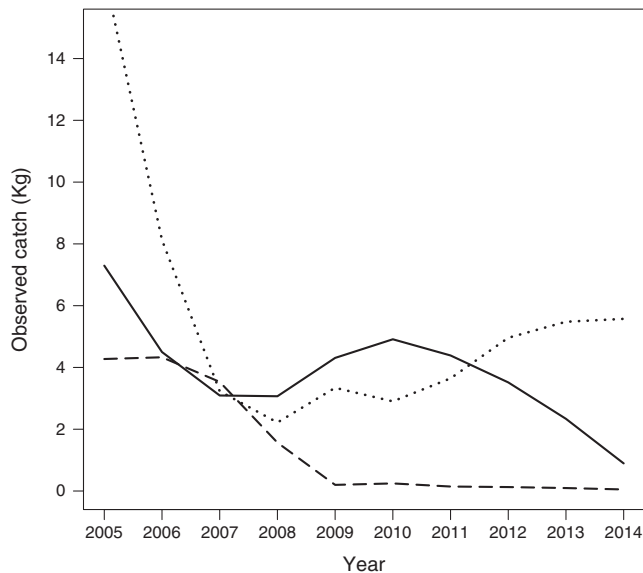
FIGURE 4 Catch trends for the pink cusk eel *Genypterus blacodes* (solid line), the Argentine seabass *Acanthistius brasilianus* (dashed line) and the Rajidae skates (*Zearaja chilensis*, *Psammobatis* spp., and *Sympterygia bonapartii* combined) (dotted line) observed on the scientific surveys from 2005 to 2014

species), which could be one of the biological factors that contributed to the lobster krill bloom. These results suggest a top-down trophic dynamic system controlled by predators in the SJG ecosystem.

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REFERENCES

Acha, E. M., Mianzan, H. W., Guerrero, R. A., Favero, M., & Bava, J. (2004). Marine fronts at the continental shelves of austral South America. Physical and ecological processes. *Journal of Marine Systems*, *44*, 83–105.

Ahyong, S. T., Baba, K. J., Macpherson, E., & Poore, G. C. B. (2010). A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura). *Zootaxa*, *2676*, 57–68.

Ahyong, S. T., & Poore, G. C. B. (2004). Deep-water Galatheidae (Crustacea: Decapoda: Anomura) from southern and eastern Australia. *Zootaxa*, *472*, 3–76.

Angelescu, V., & Cousseau, M. B. (1969). Alimentación de la merluza en la región del talud continental Argentino, época invernal (Merluccidae *Merluccius hubbsi*). *Boletín del Instituto de Biología Marina*, *19*, 5–84.

Angelescu, V., Gneri, F. S., & Nani, A. (1958). *La merluza del mar Argentino (biología y taxonomía)*. Argentina: Secretaría Marina, Servicio de Hidrografía Naval, Buenos Aires. 246.

Angelescu, V., & Prenski, L. B. (1987). Ecología trófica de la merluza común del mar Argentino (Merluccidae, *Merluccius hubbsi*). Parte 2. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y las evaluaciones de los efectivos en su área de distribución. *Contribución INIDEP*, *561*, 1–205.

Aubone, A., Bezzi, S. I., Cañete, G., Castrucci, R., Dato, C., Irusta, G., ... Villarino, M. F. (2004). Evaluación y sugerencias de manejo del recurso merluza (*Merluccius hubbsi*). La situación hasta 1999. In: R. Sánchez & S. I. Bezzi (Eds.), *El Mar Argentino y sus recursos pesqueros. Tomo IV. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación* (pp. 207–235). INIDEP, Argentina: Mar del Plata.

Baba, K., Macpherson, E., Poore, G. C. B., Ahyong, S. T., Bermudez, A., Cabezas, P., ... Schnabel, K. E. (2008). Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura—families Chirostylidae, Galatheidae and Kiwaidae). *Zootaxa*, *1905*, 1–220.

Baker, R., Buckland, A., & Sheaves, M. (2014). Fish gut analysis: Robust measures of diet composition. *Fish and Fisheries*, *15*, 170–177.

Becker, B. H., & Beissinger, S. R. (2006). Centennial decline in the trophic level of an endangered seabird after fisheries declines. *Conservation Biology*, *20*, 470–479.

Belleggia, M., Figueroa, D. E., Irusta, G., & Bremec, C. (2014). Spatio-temporal and ontogenetic changes on the diet of the Argentine hake *Merluccius hubbsi* (Marini, 1933). *Journal Marine Biological Association of the United Kingdom*, *94*, 1701–1710.

Bezzi, S. I., Renzi, M., Irusta, G., Santos, B., Tringali, L. S., Ehrlich, M. D., ... Castrucci, R. (2004). Caracterización biológica y pesquera de la merluza (*Merluccius hubbsi*). In: R. Sánchez & S. I. Bezzi (Eds.), *El Mar Argentino y sus recursos pesqueros. Tomo IV. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado del estado de explotación* (pp. 157–205). INIDEP, Argentina: Mar del Plata.

Bigongiari, D. (2016). *Teoría y práctica de pescados de mar & mariscos de Argentina*. Planeta, Argentina: Buenos Aires, 144.

Boschi, E. E., Fischbach, C. E., & Iorio, M. I. (1992). Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marítimo*, *10*, 7–94.

Buckley, T. W., & Livingston, P. A. (1997). Geographic variation in the diet of Pacific hake with a note on cannibalism. *California Cooperative Oceanic Fisheries Investigations*, *38*, 53–62.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143.

Cohen, D. M., Inada, T., Iwamoto, T., & Scialabba, N. (1990). *FAO species catalogue. Vol 10. Gadiform fishes of the world (Order Gadiformes)*. Roma: FAO Fisheries Synopsis. 442.

Cordo, H. D. (1981). Resultados sobre la alimentación de la merluza del mar epicontinental Argentino (*Merluccius hubbsi*). Análisis biológico y estadístico de los datos obtenidos de las campañas de B/I "Shinkai Maru" y "Walther Herwig" (1978–1979). In: V. Angelescu (Ed.), *Campañas de investigación pesquera realizadas en el mar Argentino por los B/I "Shinkai Maru" y "Walther Herwig", años 1978 y 1979. Resultados de la parte argentina* (pp. 299–312). INIDEP, Argentina: Mar del Plata.

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 726–738.

Cousseau, M. B., & Perrota, R. G. (2013). *Peces Marinos de Argentina: Biología, Distribución y Pesca*. INIDEP, Argentina: Mar del Plata. 193.

Crawley, M. J. (2005). *Statistics: An introduction using R*. Chichester: Wiley. 327.

Cury, P. M., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, *57*, 603–618.

Cury, P. M., Shannon, L. J., & Shin, Y. J. (2003). The functioning of marine ecosystems: A fisheries perspective. In M. Sinclair, & G. Valdimarsson (Eds.), *Responsible Fisheries in the marine ecosystem* (pp. 103–123). Wallingford: CAB International.

Diez, M. J., Cabreira, A. G., Madirolas, A., & Lovrich, G. A. (2016). Hydroacoustical evidence of the expansion of pelagic swarms of *Munida gregaria* (Decapoda, Munididae) in the Beagle Channel and the Argentine Patagonian Shelf, and its relationship with habitat features. *Journal of Sea Research*, 114, 1–12.

Diez, M. J., Pérez-Barros, P., Romero, M. C., Scioscia, G., Tapella, F., Cabreira, A. G., ... Lovrich, G. A. (2012). Pelagic swarms and beach strandings of the squat lobster *Munida gregaria* (Anomura: Munididae) in the Beagle Channel, Tierra del Fuego. *Polar Biology*, 35, 973–983.

Diez, M. J., Tapella, F., Romero, M. C., Madirolas, A., & Lovrich, G. A. (2016). La langostilla Munida gregaria en el Mar Argentino: Biología e interés económico. In E. E. Boschi (Ed.), *El Mar Argentino y sus recursos pesqueros. Tomo VI. Los crustáceos de interés pesquero y otras especies relevantes en los ecosistemas marinos* (pp. 213–228). INIDEP, Argentina: Mar del Plata.

Du Buit, M. H. (1996). Diet of hake (*Merluccius merluccius*) in the Celtic Sea. *Fisheries Research*, 28, 381–394.

Ferry, L. A., & Cailliet, G. M. (1996). Sample size and data analysis: Are we characterizing and comparing diet properly? In: D. Mackinlay & K. Shearer (Eds.), *Feeding Ecology and Nutrition in Fish: Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish. International Congress on the Biology of Fishes, 14–18 July 1996* (pp. 71–80). San Francisco: American Fisheries Society.

Garrison, L. P., & Link, J. (2000). Diets of five hake species in the northeast United States continental shelf ecosystem. *Marine Ecology Progress Series*, 204, 243–255.

Gerking, S. D. (1994). *Feeding ecology of Fish*. San Diego: Academic Press. 416.

Krebs, C. J. (1989). *Ecological Methodology*. New York: Harper Collins. 654.

Laptikhovsky, V., & Fetisov, A. (1999). Scavenging by fish of discards from the Patagonian squid fishery. *Fisheries Research*, 41, 93–97.

Link, J. S., & Ford, M. D. (2006). Widespread and persistent increase in Ctenophora in the Northeast U.S. Shelf ecosystem. *Marine Ecology Progress Series*, 320, 153–159.

Lovrich, G. A., & Thiel, M. (2011). Ecology, physiology, feeding and trophic role of squat lobsters. In G. C. B. Poore, S. T. Ahyong, & J. Taylor (Eds.), *The biology of squat lobsters* (pp. 183–222). Melbourne: CSIRO Publishing.

Mahe, K., Amara, R., Bryckaert, T., Kacher, M., & Brylinski, J. M. (2007). Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES Journal of Marine Science*, 64, 1210–1219.

Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the world*. 5th edn. Hoboken: John Wiley and Sons. 707.

Ocampo Reinaldo, M., González, R., & Romero, M. A. (2011). Feeding strategy and cannibalism of the Argentine hake *Merluccius hubbsi*. *Journal of Fish Biology*, 79, 1795–1814.

Padovani, L. N., Viñas, M. D., Sánchez, F., & Mianzan, H. (2012). Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. *Journal of Sea Research*, 67, 85–90.

Payne, A. I. L., Rose, B., & Leslie, R. W. (1987). Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. *South African Journal of Marine Science*, 5, 471–501.

Pérez-Barros, P., Romero, M. C., Calcagno, J. A., & Lovrich, G. A. (2010). Similar feeding habits of two morphs of *Munida gregaria* (Decapoda) evidence the lack of trophic polymorphism. *Revista de Biología Marina y Oceanografía*, 45, 461–470.

Pérez-Barros, P., Tapella, F., Romero, M. C., Calcagno, J. A., & Lovrich, G. A. (2004). Benthic decapod crustaceans associated with captures of *Munida* spp. (Decapoda: Anomura) in the Beagle Channel, Argentina. *Scientia Marina*, 68, 237–246.

Pinnegar, J. K., Trenkel, V. M., Tidd, A. N., Dawson, W. A., & Du Buit, M. H. (2003). Does diet in Celtic Sea fishes reflect prey availability? *Journal of Fish Biology*, 63, 197–212.

R Core Team (2014). *R: A Language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ravalli, C., De La Garza, J., & López-Greco, L. (2013). Distribución de los morfotipos gregaria y subrugosa de la langostilla *Munida gregaria* (Decapoda, Galatheidae) en el Golfo San Jorge en la campaña de verano AE-01/2011. Integración de resultados con las campañas 2009 y 2010. *Revista de Investigación y Desarrollo Pesquero*, 22, 29–41.

Richardson, A. J., & Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305, 1609–1612.

Romero, M. C., Lovrich, G. A., Tapella, F., & Thatje, S. (2004). Feeding ecology of the crab *Munida subrugosa* (Decapoda: Anomura: Galatheidae) in the Beagle Channel, Argentina. *Journal of the Marine Biological Association of the United Kingdom*, 84, 359–365.

Roux, A., & Piñero, R. (2006). Crustáceos decápodos y Estomatópodos asociados a la pesquería del langostino patagónico *Pleoticus muelleri* (Bate, 1888) en el Golfo San Jorge, Argentina. *Revista de Investigaciones y Desarrollo Pesquero*, 18, 33–43.

Ruiz, A. E., & Fondacaro, R. R. (1997). Diet of hake (*Merluccius hubbsi* Marini) in a spawning and nursery area within Patagonian shelf waters. *Fisheries Research*, 30, 157–160.

Rydberg, L. (2009). Oceanography and global fish production. In P. Wramner, M. Cullberg, & H. Ackefors (Eds.), *Fisheries, sustainability and development* (pp. 9–20). Stockholm: The Royal Swedish Academy of Agriculture and Forestry.

Sánchez, F. (2009). Alimentación de la merluza (*Merluccius hubbsi*) en el Golfo San Jorge y aguas adyacentes. *Informe Técnico INIDEP*, 75, 1–21.

Sánchez, F., & García De La Rosa, S. B. (1999). Alimentación de *Merluccius hubbsi* e impacto del canibalismo en la región comprendida entre 34°50′ S–47°S del Atlántico Sudoccidental. *Revista de Investigación y Desarrollo Pesquero*, 12, 77–93.

Sánchez, F., & Prenski, L. B. (1996). Ecología trófica de peces demersales en el Golfo San Jorge. *Revista de Investigación y Desarrollo Pesquero*, 10, 57–71.

Tam, J., Purca, S., Duarte, L. O., Blaskovic, V., & Espinoza, P. (2006). Changes in the diet of hake associated with El Niño 1997-1998 in the northern Humboldt Current ecosystem. *Advances in Geosciences*, 6, 63–67.

Temperoni, B., Viñas, M. D., & Buratti, C. C. (2013). Feeding strategy of juvenile (age-0 + year) Argentine hake *Merluccius hubbsi* in the Patagonian nursery ground. *Journal of Fish Biology*, 83, 1354–1370.

Valiela, I. (1984). *Marine Ecological Processes*. New York: Springer-Verlag. 546.

Varisco, M., Vinuesa, J. H., & Góngora, M. E. (2015). Bycatch of the squat lobster *Munida gregaria* in bottom trawl fisheries in San Jorge Gulf, Patagonia Argentina. *Revista de Biologia Marina y Oceanografia*, 50, 249–259.

Vinuesa, J. H., & Varisco, M. (2007). Trophic ecology of the lobster krill *Munida gregaria* in San Jorge Gulf, Argentina. *Investigaciones Marinas*, 35(2), 25–34.

Worm, B., & Myers, R. A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84, 162–173.

Zeldis, J. R. (1985). Ecology of *Munida gregaria* (Decapoda, Anomura): Distribution and abundance, population dynamics and fisheries. *Marine Ecology Progress Series*, 22, 77–99.

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analysing Ecological Data*. New York: Springer. 672.