

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

Mauro Belleggia^{1,2}  | Diego Giberto^{1,2} | Claudia Bremec²

¹Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

Correspondence

Mauro Belleggia, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina.

Email: belleggia@inidep.edu.ar

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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 brasiliensis*) 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 (Laptikhovskiy & 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 Januarys 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 $R > \text{Global } R$ 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 & Prenske, 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 $R < \text{Global } R$, 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 brasiliensis* (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 speciose 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

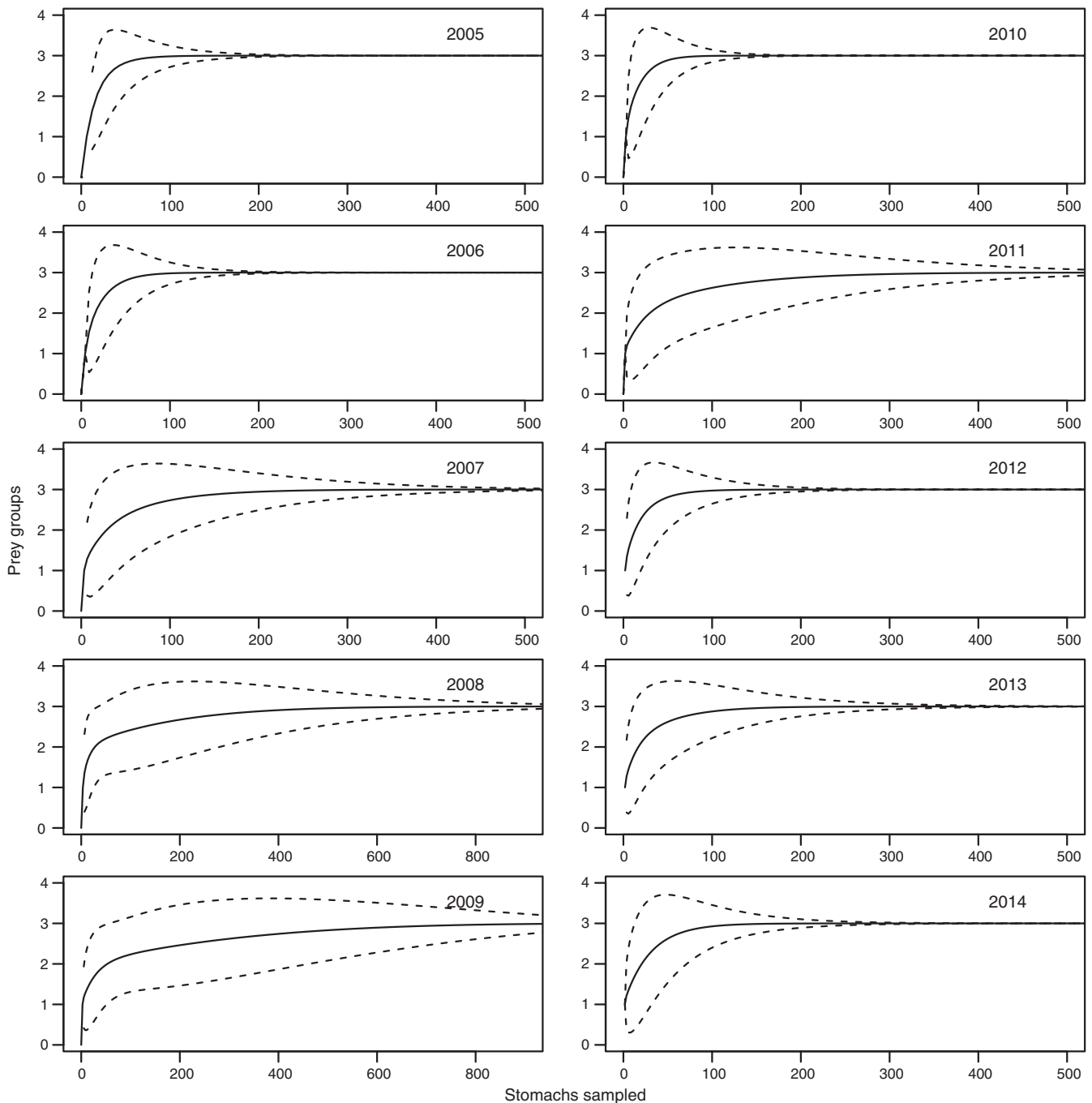


FIGURE 1 Randomized cumulative prey curves as a function of specimens of *Merluccius hubbsi* analysed for each year considered in the dietary analysis. Mean (continuous line) \pm confidence intervals (dashed lines) are plotted

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

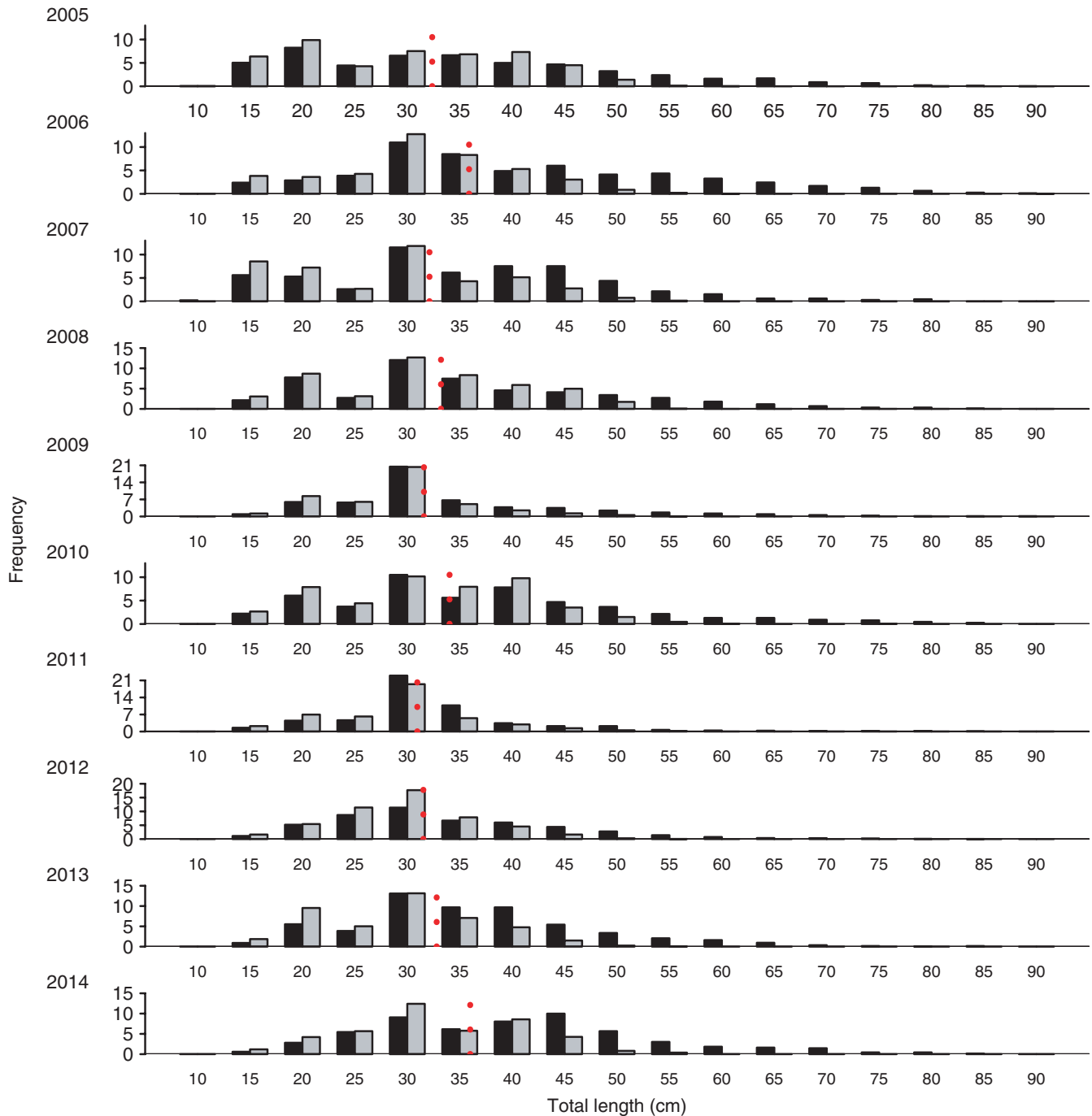


FIGURE 2 Size frequency distributions of the Argentine hake, *Merluccius hubbsi*, caught for the diet analysis from the year 2005–2014. Females (black bars), males (white bars) and the mean of total length (vertical red-dashed line) are represented

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
<i>Themisto gaudichaudii</i>	6.68	5.68	31.69	13.79	22.57	18.16	6.70	11.00	9.61	10.54
<i>Euphausia</i> spp.	36.03	12.52	20.00	26.25	24.25	25.28	1.41	28.82	28.28	23.19
<i>Munida gregaria</i>	1.42	1.37	0.26	9.77	25.37	12.73	63.32	38.67	43.35	52.06
<i>Peisos petrunkevitchi</i>	0.81	45.60	37.40	30.46	22.76	14.98	19.93	4.17	3.97	4.12
<i>Pleoticus muelleri</i>	-	0.39	-	1.15	0.75	1.12	3.88	1.99	3.42	2.93
<i>Pterigosquilla armata armata</i>	-	-	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
<i>Engraulis anchoita</i>	12.55	3.33	3.12	6.13	1.49	5.99	0.71	3.60	0.18	0.73
<i>Merluccius hubbsi</i>	12.75	11.55	6.23	9.96	4.66	8.05	6.00	2.65	11.18	4.22
<i>Patagonotothen ramsayi</i>	0.40	0.20	0.26	-	-	-	0.18	-	0.09	-
<i>Genypterus blacodes</i>	-	-	-	-	-	-	-	-	-	0.09
<i>Stromateus brasiliensis</i>	0.20	-	-	-	-	-	-	-	-	-
<i>Raneya brasiliensis</i>	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
<i>Illex argentinus</i>	21.05	17.03	4.16	0.77	0.56	13.67	1.76	13.84	3.42	4.67
<i>Doryteuthis gahi</i>	0.81	0.20	-	0.57	0.19	0.94	-	-	-	-
<i>Pulpo</i> spp.	-	-	-	-	-	-	-	0.09	0.09	-
<i>Semirossia tenera</i>	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
<i>Pleurobrachia</i> 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 brasiliensis* and Rajidae skates (*Zearaja chilensis*, *Psammobatis* spp. and *Sympterygia bonapartii*) (Sánchez & Prenske, 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,

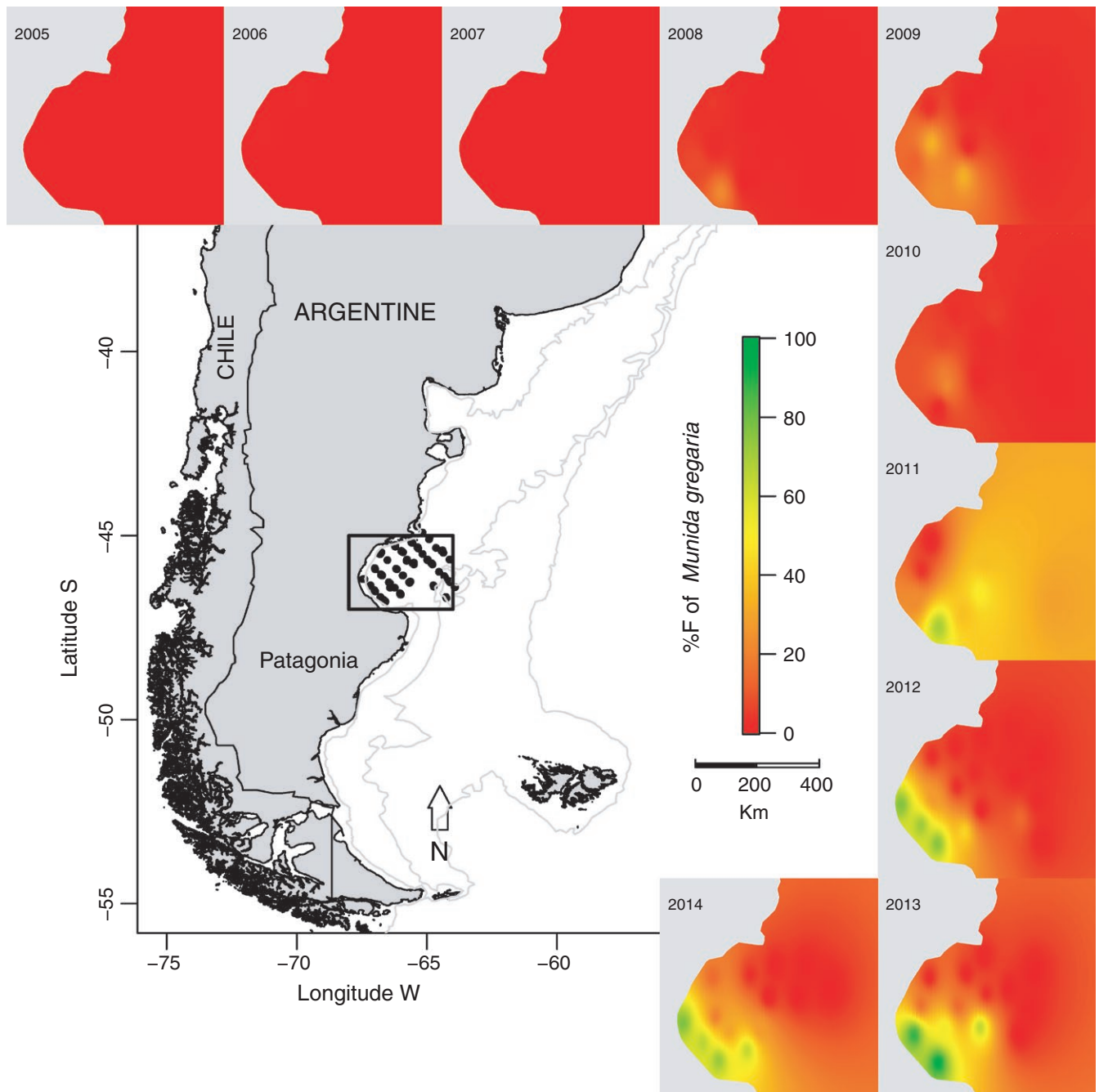


FIGURE 3 Map of the study area in the Southwestern Atlantic Ocean. The rectangle in San Jorge Gulf (SJG) region shows sample sites where specimens of *Merluccius hubbsi* were captured to study the diet composition from 2005 to 2014. The spatial distribution of the percentage of the frequency of occurrence 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. brasiliensis* 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 brasiliensis*, and three Rajidae

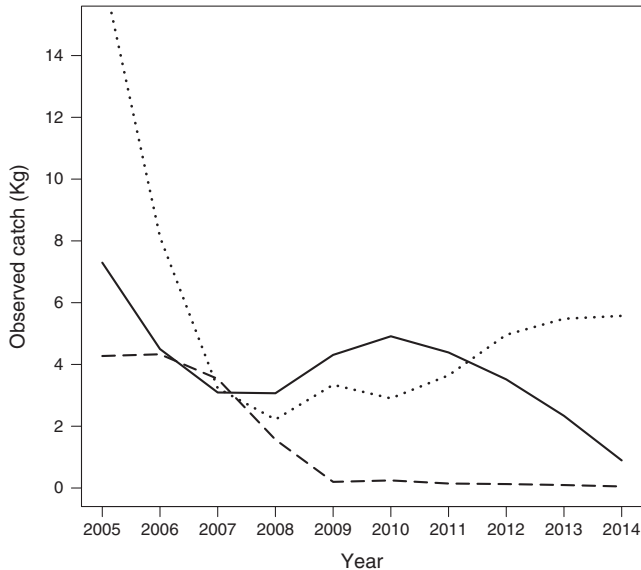


FIGURE 4 Catch trends for the pink cusk eel *Genypterus blacodes* (solid line), the Argentine seabass *Acanthistius brasilianus* (dashed line) and the Rajidae skates (*Zearaja chilensis*, *Psammobatis* spp., and *Sympterygia bonapartii* combined) (dotted line) observed on the scientific surveys from 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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