

Marine fronts as preferred habitats for young Patagonian hoki *Macruronus magellanicus* on the southern Patagonian shelf

Daniela Alemany^{1,*}, Oscar O. Iribarne¹, Eduardo M. Acha^{1,2}

¹Instituto de Investigaciones Marinas y Costeras (IIMyC, CONICET-UNMdP), CC 1260 Correo Central Mar del Plata, Argentina

²Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paeso Victoria Ocampo N°1, Esollera Norte, Mar del Plata, Argentina

ABSTRACT: Due to strong seasonality and spatial variation in ecosystem productivity, fish can show ontogenetic and/or seasonal changes in habitat use and move between different habitats to exploit the richest food resources. Here, we evaluate the spatial patterns of the size distribution of Patagonian hoki *Macruronus magellanicus* in relation to the highly productive frontal systems of the southern Patagonian shelf. Additionally, we assessed diet composition in relation to size. Fish data came from 10 scientific cruises that were carried out between April 1978 and March 1979 during cold and warm seasons of the year. Samples were collected using demersal hauls that for the purposes of this study were ascribed to frontal or non-frontal zones. Based on the analysis of the total length of 3660 Patagonian hoki individuals, a generalized linear model was constructed to evaluate the association between fish size and fronts. Moreover, prey items consumed by fish grouped into 4 size classes were evaluated by analysing the contents of 1067 stomachs. Our results showed that smaller fish (juveniles) were more frequently located along frontal areas and preyed upon zooplankton. In contrast, larger fish (adults) preyed on larger items and showed no spatial relationship with fronts. The positive relationship observed between small-sized fish and fronts may be related to the low trophic level of these fish and the abundance of small-sized prey in frontal zones.

KEY WORDS: Fish size · Trophic level · Diet · Southwestern Atlantic

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INTRODUCTION

The environment influences the dynamics of marine fish populations by affecting their life history and ecological traits such as body size, age at maturity, mobility, habitat type and home range (Claudet et al. 2010). These life-history traits determine how populations respond to changes in the marine environment (King & McFarlane 2003), and finding suitable habitat for feeding, growth and/or reproduction is a critical step at each life stage. Multiple factors, including abiotic conditions, food availability, and competition and predation, influence habitat selection by

fishes. Because fish show ontogenetic changes in their response to these factors, species exhibit ontogenetic habitat shifts and movements between and within habitats (Craig & Crowder 2002, Huijbers et al. 2013).

Oceanographic variability causes fluctuations in the supply of nutrients and light to phytoplankton (e.g. Gargett & Marra 2002, Mann & Lazier 2006), and physical processes such as upwellings, currents and fronts act as barriers and/or discontinuities that directly or indirectly influence patterns of diversity, abundance, and the body size and geographic range of organisms (Leichter & Witman 2009). Frontal sys-

tems are narrow regions with high horizontal gradients in temperature and/or salinity, and they are sites associated with high phytoplankton abundance (e.g. Lutz et al. 2010, Acha et al. 2015). This high production is transferred to higher trophic levels within the regional food web, and fronts thus affect the reproduction, foraging and migration of fish. In addition, fronts provide food resources and act as a mechanism to carry planktonic larvae into feeding grounds (Olson 2002). Thus, frontal systems can potentially influence the biology and ecology of fish.

Marine bony fishes have complex life cycles, and the diets of the fishes change as the organisms grow (Moloney et al. 2011). In most cases, larvae and juveniles feed on organisms in lower trophic levels, mainly zooplankton, while larger fish tend to feed at higher trophic levels. As many species show ontogenetic shifts in their diet (i.e. they change their prey over the course of their lifetime), a species can occupy different trophic levels during its life history (Link et al. 2005). There is a strong spatial coupling between fronts and organisms of lower trophic levels (i.e. phytoplankton and zooplankton), but the association becomes more diffuse and complex when moving up in the food web to higher trophic levels (see Olson 2002) where behaviour and swimming abilities may determine distributional patterns (McManus & Woodson 2012). Thus, since the responses of organisms to productive frontal systems differ depending on their trophic level (Olson 2002), we expect the spatial distribution of small fishes to show greater coupling to frontal zones than the spatial distribution of larger fishes.

In the southern Patagonian shelf (southwest Atlantic), there are 2 major frontal systems: the shelf-break front (SBF) and the Patagonian Current Front (PCF). Both are associated with high primary productivity (e.g. Acha et al. 2004). There is a strong coupling between the fronts and the distribution of organisms of lower trophic levels in this area, affecting groups of organisms such as phytoplankton and zooplankton (e.g. Lutz et al. 2010, Sabatini et al. 2012). Moreover, the distribution (e.g. Podesta 1990, Wang et al. 2007), diet (e.g. Podesta 1990, Ruiz & Fondacaro 1997) and reproduction (e.g. Alvarez Colombo et al. 2011, Marrari et al. 2013) of fishes are positively correlated with fronts. However, large-scale studies assessing the possible effects of fronts on the spatial patterns of fish size are scarce.

The gadiform fish Patagonian hoki *Macruronus magellanicus* (also known as Patagonian grenadier; hereafter hoki) is a highly migratory, pelagic-demersal species that is distributed in the southeast

Pacific and southwest Atlantic (Schuchert et al. 2010). It is the most abundant species south of 45° S on the Argentine shelf (biomass $>1 \times 10^6$ t), and hoki sustain an important trawl fishery (Prenski et al. 2012). However, several features of this species' life cycle remain unclear, particularly the timing and location of spawning in the southern Atlantic, for which a number of hypotheses have been proposed (Giussi et al. 2016a). Hoki is an opportunistic feeder, changing prey items at different times in its life cycle (Giussi et al. 2004). Larval and juvenile fish feed on euphausiids, amphipods, small cephalopods and fish, while adults eat larger fish and cephalopods in addition to the aforementioned groups (Giussi et al. 2016a, Ciancio et al. 2008). Juveniles are concentrated in the southern part of the SBF (Scarlato et al. 2000). Given that the association of hoki with fronts may be mediated by intermediate trophic links (see McManus & Woodson 2012), we expect hoki of different sizes to show differential associations with fronts based on their position in the food web throughout their ontogeny.

Against this background, we evaluated the spatial pattern of the size distribution of hoki in relation to the highly productive Patagonian frontal systems and we analysed diet composition in relation to size. We hypothesized that small fish would be distributed along frontal areas, given that they feed on zooplankton and small prey species that are more abundant in fronts than in adjacent zones. We also hypothesized that larger fish would show weaker associations with fronts as individuals move up through the food web to higher trophic levels. Thus, we expected to observe a spatial and temporal decoupling between the secondary and tertiary consumers and the high primary production at fronts.

MATERIALS AND METHODS

Study site

The study area (Fig. 1) is located in the Patagonian Shelf large marine ecosystem (PSLME; Sherman 2005). The PSLME is one of the largest shelves in any ocean basin (Belkin et al. 2009), and is a very productive region that sustains important fisheries (e.g. Acha et al. 2004). The area includes, among others, 2 highly productive fronts: the SBF and the PCF (the latter is called the 'Southern Patagonia Front' in Acha et al. 2004).

The SBF, located at the edge of the Argentine shelf, results from the convergence of the Malvinas

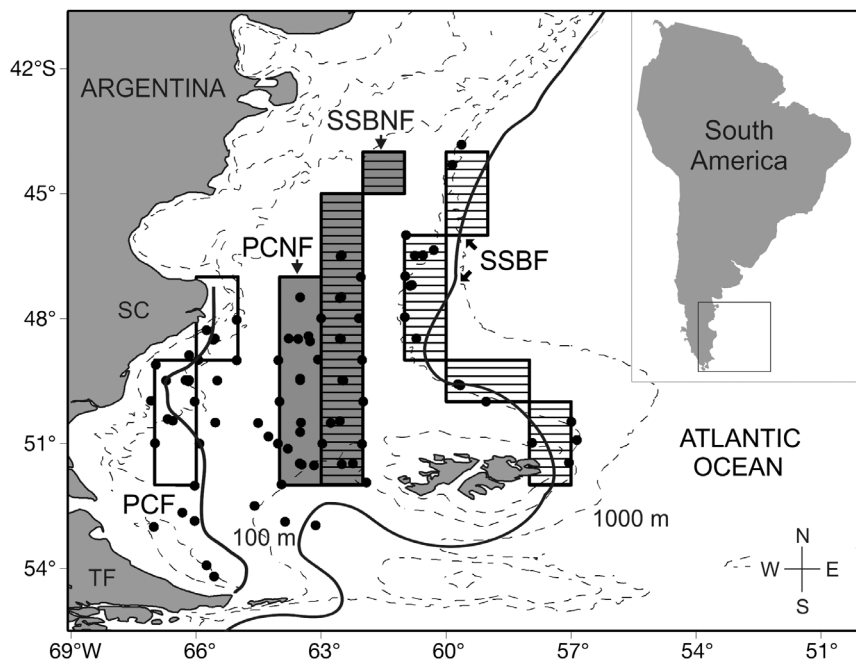


Fig. 1. Study area in the Patagonian Shelf large marine ecosystem showing demersal hauls (black dots) taken by scientific cruises between April 1978 and March 1979. Black lines represent both frontal systems in a schematic way; dashed lines are isobaths. Rectangles represent frontal (white background) and non-frontal (grey background) zones from which data for this study were obtained. SSBF: southern shelf-break front; SSBNF: southern shelf-break non-front; PCF: Patagonian Current Front; PCNF: Patagonian Current non-front (adapted from Alemany et al. 2009). Tierra del Fuego (TF) and Santa Cruz (SC) provinces on the Argentinian mainland are also shown

Current and the shelf water masses. It is a permanent thermohaline front that is wider and more intense during the austral spring and summer than during the cold season (Rivas & Pisoni 2010). The SBF is associated with high surface chlorophyll concentrations, which are linked to the primary production in the region (Rivas 2006, Romero et al. 2006). The PCF is located in Argentinian Patagonia and extends southward from 46° 30' S (south of the San Jorge Gulf) to 54° 30' S. The northern part of the PCF is characterized by a thermohaline front that has a strong salinity gradient to the south, caused by the discharge of fresher waters from the Magellan Strait and the Cape Horn Current (Acha et al. 2004). In the austral winter, this frontal system is less intense than during the warm season (Rivas & Pisoni 2010).

Following Alemany et al. (2009), both frontal systems were defined schematically, and the study area was divided into 1° × 1° cells, each with an area, at 48° S, of ca. 74.5 × 111.3 km (Fig. 1). The areas to be compared included the southern shelf-break front (SSBF), the PCF, and their non-frontal counterparts,

the southern shelf-break non-front (SSBNF) and the Patagonian Current non-front (PCNF). To avoid border effects, each frontal system and its non-frontal counterpart were separated by a longitudinal interval of at least 1° (Fig. 1).

Given that the intensities of the fronts change throughout the year, data collected at the shelf break and in the Patagonian Current frontal systems were divided into the cold season (May to September) and the warm season (October to April).

Fish sampling

Fish data were obtained from demersal hauls taken during 10 scientific cruises on the RV 'Shinkai Maru' (from April 1978 to March 1979, encompassing approximately 30 d per cruise), covering nearly all of the Patagonian shelf. This information was gathered before the large increase in fishing pressure in the

Argentine continental shelf occurred (Bezzi et al. 1995, Thorpe et al. 2000); thus, these data represent a system with relatively low levels of fishing exploitation. Stations were selected based on an *a priori* sampling scheme with a spatial resolution of approximately 1° × 1° (see Cousseau et al. 1979 for more details). At each station, the depth and the bottom and surface temperatures were recorded. A bottom trawl (vertical opening 5 m, horizontal aperture 30 m, cod-end mesh size 2.4 cm) was employed for demersal fish catches. At each station, trawls were performed at approximately 4 knots (7.4 km h⁻¹) for 30 min (depth ranged from 87 to 382 m). At several stations, the number of individuals and the total length (TL, cm) of hoki were recorded, and a random sample from the total catch was used for the analysis of stomach contents. Hoki individuals were considered small fish or juvenile fish when TL was <56 cm (Bezzi 1984).

To evaluate the relationship between the frontal systems and the spatial pattern of fish size, 27 demersal hauls were used to represent the 4 frontal/non-frontal zones described above.

Relationship between fronts and the spatial pattern of fish size

From 27 demersal hauls, data on 3660 hoki were analysed (Table 1). To evaluate the spatial pattern of fish size, a generalized linear model (GLM; McCullagh & Nelder 1989) was constructed with hoki TL as the response variable; the data were normalized with a Box-Cox data transformation. Statistical analysis was performed on TL data grouped at 1 cm intervals. Two fixed categorical factors, area (4 levels: SSBF, SSBNF, PCF, PCNF) and season (2 levels: cold, warm), and 3 environmental covariates (depth, bottom and surface temperature) were evaluated. The interaction between factors was also considered (area \times season). In an exploratory analysis, the relationship between covariates was evaluated using a scatterplot matrix, and collinearity was not a problem. Then, the most parsimonious model was selected using a forward stepwise method, in which effects can be entered or removed. The best and most simple model explaining hoki TL included the following variables: area, season, interaction (area \times season) and bottom temperature. Model fit and performance were assessed through multiple R^2 and global Fisher tests with a significance level of 0.05, and the conformity of the model residuals to the linear model assumptions was checked from normal probability plots and plots of the residuals versus the predicted values plots. Pairwise *a priori* comparisons were used when significant differences were detected (Zar 2010).

Hoki diet composition

A total of 1067 hoki stomachs were collected during the cruises (see Cousseau et al. 1979 for more details). Fish were dissected on board, and their stomach con-

Table 1. Sample data for study of spatial distribution of Patagonian hoki *Macruronus magellanicus* in frontal (SSBF, PCF) and non-frontal (SSBNF, PCNF) zones of the Patagonian Shelf large marine ecosystem, between April 1978 and March 1979, showing number of trawling stations and, in parentheses, number of hoki measured per zone and season. Cold season: May to September; warm season: October to April. See Fig. 1 for locations and key to abbreviations of zones

Season	Zone			
	SSBF	SSBNF	PCF	PCNF
Cold	2 (267)	4 (166)	5 (311)	2 (63)
Warm	1 (110)	4 (508)	4 (1368)	5 (867)

tents were analysed. Fish TL ranged between 10 and 114 cm. Recognizable prey items were identified to the lowest possible taxonomic level. Unfortunately, information on prey abundance in stomach contents was not available; thus, diet information was only semi-quantitative based on presence/absence data. Empty stomach and digested or regurgitated stomach contents were excluded from the analysis.

To study the relationship between fish size and diet composition, size groups and their range were identified by K-means analysis: this widely used method is a clustering technique that seeks to minimize the average squared distance between points within the same cluster (Arthur & Vassilvitskii 2007). Then, the diet information from each stomach was assigned to each of the identified size groups. To evaluate differences in diet composition between the different size groups of hoki, we used permutational multivariate analysis of variance (PERMANOVA) performed by PRIMER 6 software (Clarke & Gorley 2006). To test the multivariate null hypothesis of no differences in diet composition among groups, a Bray-Curtis similarity resemblance matrix was constructed using presence/absence data (Clarke & Warwick 2001). To obtain p-values, the permutation tests relied on 999 unrestricted permutations of the raw data. This permutation method is more appropriate because it provides an exact test for 1-way cases (Anderson et al. 2008).

Prey items most responsible for the multivariate pattern were identified using a similarity percentage (SIMPER) analysis. This method examines the contribution of each prey item to similarities within a group or dissimilarities between groups (Clarke & Warwick 2001).

RESULTS

Hoki TL was related to area, season and bottom temperature, and the model that included these 2 explanatory variables and an environmental covariate accounted for 73% of the variation in hoki size ($R^2 = 0.73$, $p < 0.001$). GLM results showed that the interaction effect of area \times season (first-order interaction) was significant ($p < 0.001$; Table 2).

Relationship between fronts and the spatial pattern of fish size

Southern shelf-break front. A total of 1051 hoki (TL 15 to 114 cm; Fig. 2) were caught in this region. During the cold season, smaller fish (21.7 ± 5.1 cm,

Table 2. Summary statistics of generalized linear model results comparing Patagonian hoki *Macruronus magellanicus* total length (response variable) between zones (SSBF, SSBNF, PCF, PCNF) and seasons (cold, warm) in the Patagonian Shelf large marine ecosystem. See Fig. 1 for locations and key to abbreviations of zones. Data were Box-Cox transformed

	MS	df	F	p
Area	5.50	3	812	<0.001
Season	12.97	1	1914	<0.001
Area × Season	4.25	3	627	<0.001
Bottom temperature	5.53	1	815	<0.001
Error	0.007	3651		

mean \pm SD) were distributed along the front, while larger fish (89.5 ± 8.5 cm) were distributed in the non-frontal area of the southern shelf-break system (Fig. 2a, Table 3). The same pattern was observed during the warm season, although the difference in mean TL between the front and the non-frontal area was not as high as the difference during the cold season; specifically, smaller fish (26.1 ± 5.2 cm) were distributed at the front and larger fish (35.4 ± 4.8 cm) were observed in the non-frontal area (Fig. 2b, Table 3).

Patagonian Current Front. A total of 2609 hoki (10 to 102 cm TL) were caught in the Patagonian Current frontal system. During the cold season, larger fish (77.3 ± 11.7 cm) were recorded in the frontal area of the Patagonian Current system, while smaller fish (32.9 ± 6.6 cm) were distributed along the non-frontal area, (Fig. 2c, Table 3). The opposite pattern was detected during the warm season, with smaller hoki (22.6 ± 6.8 cm) distributed along the front and larger fish (33.1 ± 6.8 cm) recorded in the non-frontal area of the system (Fig. 2d, Table 3).

Hoki diet composition

Using K-means analysis hoki were classed into 4 size groups (SGs; Fig. 3). Based on length at first maturity (Bezzi 1984), in this study SG1 (10 to 28 cm TL) and SG2 (29 to 54 cm) correspond to hoki juveniles; SG3 (55 to 81 cm) and SG4 (82 to 114 cm) correspond to adults. Fig. 3 shows the absolute frequency distribution of TL of hoki considered in this study and, for each size class, the number of stomach contents analysed.

Regarding the contents of the 1067 collected stomachs, 39% were empty, 9% were regurgitated and 4% were digested. Thus, we analysed 512 sets of stomach contents with recognizable prey items

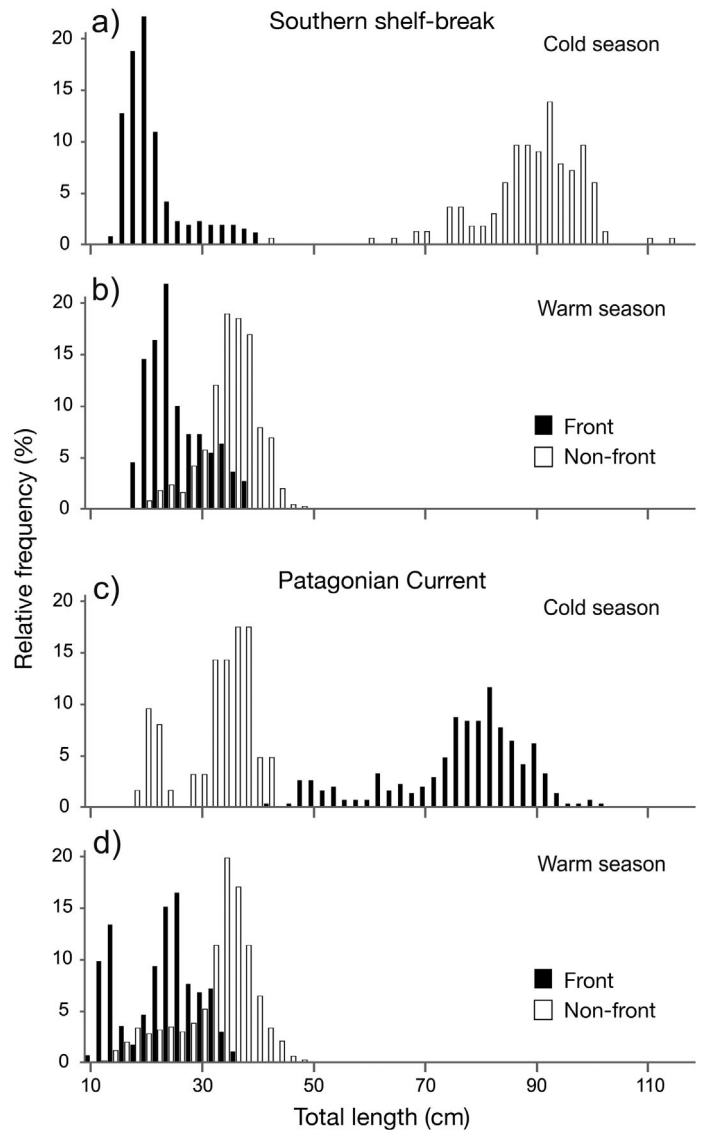


Fig. 2. Size frequency distributions (%) of total length (cm) of Patagonian hoki *Macruronus magellanicus* during (a,c) cold and (b,d) warm seasons in frontal and non-frontal zones in the (a,b) southern shelf-break and (c,d) Patagonian Current frontal systems. For graphical purposes, the figure was constructed using total length intervals of 2 cm

Table 3. Summary statistics of pairwise *a priori* comparisons (df = 1; residual df = 3651) of Patagonian hoki *Macruronus magellanicus* total length between frontal (SSBF, PCF) and non-frontal (SSBNF, PCNF) zones in the Patagonian Shelf large marine ecosystem, in cold and warm seasons. See Fig. 1 for locations and key to abbreviations of zones

Pairwise comparisons	MS	F	p
SSBF vs. SSBNF (cold)	9.81	1447	<0.001
SSBF vs. SSBNF (warm)	0.32	47	<0.001
PCF vs. PCNF (cold)	0.03	5	0.03
PCF vs. PCNF (warm)	14.83	2189	<0.001

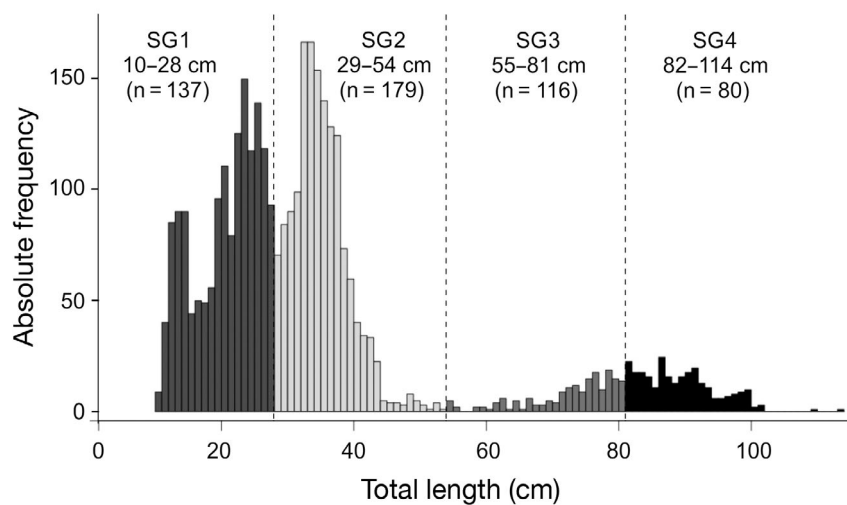


Fig. 3. Absolute frequency distribution of total lengths of Patagonian hoki *Macruronus magellanicus* taken by scientific cruises in the Patagonian Shelf large marine ecosystem between April 1978 and March 1979. Hoki were classed into 4 size groups (SG) identified by the K-means method. SG1 and SG2 correspond to hoki juveniles; SG3 and SG4 correspond to adults. For each SG, the size range (total length) and number of stomach contents analysed (n) are shown

Table 4. Prey items of Patagonian hoki *Macruronus magellanicus* in the Patagonian Shelf large marine ecosystem, showing percentage of occurrence (%) in stomach contents of different hoki size groups (SG). SG1 (10 to 28 cm total length) and SG2 (29 to 54 cm) correspond to hoki juveniles; SG3 (55 to 81 cm) and SG4 (82 to 114 cm) correspond to adults

Prey item	Size group			
	1	2	3	4
Copepods	75	25	0	0
Amphipods	51	27	15	8
Euphausiids	55	22	22	2
Decapods	0	0	0	100
Isopods	0	0	0	100
Shrimps	0	0	48	52
<i>Munida gregaria</i>	58	21	21	0
Crustaceans	0	0	0	100
Ctenophores	0	0	50	50
Chaetognaths	0	100	0	0
Bobtail squid	0	100	0	0
<i>Loligo</i> squid	50	50	0	0
<i>Illex</i> squid	0	28	34	38
Cuttlefish	0	0	100	0
Octopus	0	0	33	67
Fish juveniles	5	35	36	24
Notothenia juveniles	0	75	0	25
Notothenia adults	0	67	6	28
Myctophids	0	100	0	0
<i>Micromesistius australis</i>	2	98	0	0
<i>Macruronus magellanicus</i>	0	0	100	0
<i>Sprattus fueguensis</i> juveniles	0	0	53	47

(hoki size ranged between 11 and 100 cm). A total of 22 different types of prey item were identified in the stomach contents of hoki, with amphipods, euphausiids, and juvenile fish being amongst the most important. Copepods, amphipods, euphausiids and the squat lobster *Munida gregaria* were the most abundant prey item in the stomach contents of SG1; 4 prey types (chaetognaths, bobtail squid, myctophids and the Southern blue whiting *Micromesistius australis*) appeared exclusively in SG2; cuttlefish and hoki were only present in the stomach contents of SG3; and decapods, isopods and crustaceans were exclusively identified in SG4 (Table 4). SG3 and SG4 shared several prey items (e.g. shrimps, ctenophores, octopus and juveniles of the Patagonian sprat, *Sprattus fueguensis*) that differentiated them from SG1 and SG2.

PERMANOVA showed differences in prey items among all hoki SGs ($p < 0.05$). The results of the SIMPER analysis of prey items showed that the presence of amphipods and euphausiids in the stomach contents of SG1 was more than twice as high as in the other groups. As fish size increased, from SG2 to SG4, other prey items were identified and/or incorporated into the diet. The presence of juvenile fish and squids was twice as high in the stomach contents of SG3 than in those of SG2. Juveniles of Patagonian sprat were only present in the stomach contents of larger fish (SG3 and SG4) and were more abundant in the stomach contents of SG4. Almost twice as many *Illex* squid and shrimps, and about 30% more juvenile fish, were present in SG4 than in SG3.

DISCUSSION

We evaluated the size distribution pattern of hoki *Macruronus magellanicus* in relation to 2 frontal systems on the southern Patagonian shelf and assessed the relationship between diet composition and fish body size. Our results indicate a habitat selection with ontogenetic variation by hoki. While small (juvenile) fish were more frequently located in frontal areas, larger (adult) fish did not show a preference for a specific area. Moreover, the analysis of stomach contents showed that prey items differed

between the 4 SGs identified, with smaller fish feeding mainly on small zooplankton and larger fish preying on larger items, such as fish, squids and shrimps.

Free-swimming organisms that feed at or near the base of the food web are more likely to be associated with marine fronts, where plankton is abundant. In this study, we also detected a close relationship between small-sized hoki and fronts. Other studies have reported close relationships between smaller fish and fronts in the Benguela system (Macpherson & Gordo 1996) and in the Ross Sea (La Mesa et al. 2010); in both cases, favourable food conditions were hypothesized to explain this pattern. In the southwest Atlantic, during austral spring and summer, phytoplankton and zooplankton blooms are concentrated in Patagonian frontal areas (Sabatini et al. 2004, Lutz et al. 2010), and these food-rich surroundings may attract juvenile fish, which feed on smaller prey items than adults. Small-sized hoki were closely coupled to the SSBF throughout the year and they were coupled to the PCF during the warm season. Hoki schools move based on oceanographic conditions and according to their needs and preferences (Giussi et al. 2016a). Small-sized hoki are pelagic and feed on mesozooplankton, such as euphausiids (eggs, larvae, juveniles and adults) and large-sized copepods that are abundant in the shelf-break frontal system (Carreto et al. 1981, Ciechomski & Sanchez 1983, Sabatini et al. 2012). The PCF is also a highly productive area, and the amphipod *Themisto gaudichaudii* is a key component of the local food web and an important food resource for hoki and other fish (Ciancio et al. 2007, Padovani et al. 2012). The high biomass of several prey items (e.g. copepods, amphipods, euphausiids) eaten by small-sized hoki is also associated with the frontal region in southern Patagonia (Sabatini et al. 2004). Consistent with our results, the feeding areas and nursery grounds of juvenile hoki have been described as occurring mainly on the Tierra del Fuego and Santa Cruz shelves (Machinandiarena & Ehrlich 1999), where the front develops (Fig. 1). Also in agreement with our results, in southern Patagonia the size of prey items of hoki increases with fish size, with adult fish feeding on fish, squid and planktonic prey (Brickle et al. 2009), while juveniles take advantage of suitable and abundant food at the Patagonian fronts. Altogether, this evidence indicates a strong coupling between hoki and frontal areas that varies with ontogenetic changes.

Many species show ontogenetic and/or seasonal changes in habitat use, migrating across regional boundaries and moving between different habitats

to improve survival and reproductive success (e.g. Breen et al. 2015). The larval and juvenile stages are times in the life history of fish when they need to find high concentrations of food to maintain growth and, in turn, to reduce predation pressure (Houde 2008). In that context, we found that during the warm season and in both frontal systems only small-sized fish that were classified as juveniles were caught. Hoki juveniles occupy different habitats than those of adults (Prenski et al. 2012), which is a typical behaviour of cannibalistic species (e.g. Angelescu & Prenski 1987, Prenski & Angelescu 1993). Although the incidence of cannibalism is not very high in hoki, small-sized individuals were found in the stomach contents of adults (Giussi et al. 2004). Moreover, in Tasmania and New Zealand, the different distributions of hoki adults and juveniles have been interpreted as a mechanism to reduce cannibalism (Bulman & Blaber 1986). Thus, in this study we found a spatial segregation between juvenile and adult hoki, not only because small fish find suitable food at southern fronts but also because it is a strategy to reduce cannibalism.

However, the 2 fronts showed opposite patterns regarding the distribution of hoki sizes during winter. Along the southern shelf break, juvenile hoki were associated with the front and adults with the non-frontal region, while the Patagonian Current frontal system showed the opposite pattern. Both Patagonian fronts exist even in winter; this is due to bathymetry and the convergence of different water masses in the case of the SBF and to a permanent plume of diluted waters originating in the Pacific in the case of the PCF (named the Atlantic Patagonian cold estuarine zone; Acha et al. 2004). However, in this region, primary production declines significantly during the cold season (austral autumn and winter; Rivas 2006, Romero et al. 2006), suggesting a decrease in food for juveniles in the area and thus explaining their lack of association with this system. Regarding large fish, adult hoki feed on macrozooplankton (hyperiid amphipods) in a coastal sector (50 to 52° S) of the PCF even in the cold season (Padovani et al. 2012). During the warm season, no hoki adults were caught; larger fish were only present during the cold season and they did not show a preference for a specific area. The absence of adult fish in the study area could be due to migratory movements, although hoki movements are currently not well understood (Giussi et al. 2016a). To date, no important breeding areas have been found in the southwest Atlantic that could sustain the observed stock biomass; the only known reproduction area for this species is in the South

Pacific, in Chilean waters between 41 and 46° S (Giussi et al. 2016b). Therefore, in late winter and spring, hoki adults may be migrating to the Chilean coasts in the Pacific (Prenski et al. 2012), where spawning grounds for the species have been described (Ernst et al. 2005). However, the existence of a pelagic spawning ground in the southwest Atlantic was proposed by Gorini & Pájaro (2014), who postulated that, during spring, hoki may spawn in small areas in the Argentine Sea, at 51 to 57° S and at depths greater than 200 m. If this were the case, since our sampling scheme did not cover that region, it would provide an alternative explanation for the absence of hoki adults in the samples collected during the warm season. In any case, uncertainties remain regarding population structure, distribution of early stages, spawning grounds, and stock identification of this species, highlighting the complex spatial dynamics of its life history.

In summary, our results show that hoki juveniles are positively associated with Patagonian fronts, likely because they feed on small prey items that are highly abundant at these oceanographic features. Moreover, this pattern indicates that due to the suitable feeding conditions, the lower the trophic level, the more closely organisms are coupled to the fronts.

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LITERATURE CITED

- Acha EM, Mianzan H, Guerrero R, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *J Mar Syst* 44:83–105
- Acha EM, Piola AR, Iribarne O, Mianzan H (2015) Ecological processes at marine fronts. *Oases in the ocean*. Springer International Publishing, Cham
- Aleman D, Acha EM, Iribarne O (2009) The relationship between marine fronts and fish diversity in the Patagonian shelf large marine ecosystem. *J Biogeogr* 36: 2111–2124
- Alvarez-Colombo GL, Dato C, Macchi GJ, Palma ED and others (2011) Distribution and behavior of Argentine hake larvae: evidences of a biophysical mechanism for self-recruitment at the North Patagonian shelf waters. *Cienc Mar* 37:633–657
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Angelescu V, Prenski LB (1987) Ecología trófica de la merluza común del Mar Argentino (Merlucciidae, *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 561, Instituto Nacional de Investigación y Desarrollo Pequero, Mar del Plata
- Arthur D, Vassilvitskii S (2007) k-means++: the advantages of careful seeding In: Gabow H (ed) Proc 18th Annual ACM-SIAM Symposium on Discrete Algorithms. Society for Industrial and Applied Mathematics, New Orleans, LA, p 1027–1035
- Belkin IM, Cornillon PC, Sherman K (2009) Fronts in large marine ecosystems. *Prog Oceanogr* 81:223–236
- Bezzi SI (1984) Aspectos biológico-pesqueros de la merluza de cola (*Macruronus magellanicus*) del Atlántico Sudoccidental. *Rev Invest Des Pesq* 4:63–80
- Bezzi SI, Verazay GA, Dato CV (1995) Biology and fisheries of Argentine hakes. In: Alheit J, Pitcher TJ (eds) Hake: biology, fisheries and markets. Chapman & Hall, London, p 241–267
- Breen P, Posen P, Righton D (2015) Temperate Marine Protected Areas and highly mobile fish: a review. *Ocean Coast Manage* 105:75–83
- Brickle P, Arkhipkin AI, Laptikhovskiy V, Stocks A, Taylor A (2009) Resource partitioning by two large planktivorous fishes *Micromesistius australis* and *Macruronus magellanicus* in the Southwest Atlantic. *Estuar Coast Shelf Sci* 84:91–98
- Bulman C, Blaber S (1986) Feeding ecology of *Macruronus novaezelandiae* (Hector) (Teleostei: Merlucciidae) in south-eastern Australia. *Mar Freshw Res* 37:621–639
- Carreto JI, Ramírez F, Dato C (1981) Zooplankton y producción secundaria. Parte II. Distribución y variación estacional de la biomasa zooplanctónica. In: Angelescu V (ed) Campañas de investigación en el Mar Argentino por los BI 'Shinkai Maru' y 'Walter Herwig' y el BIP 'Marburg', años 1978 y 1979. Resultados de la parte argentina. Contribución 383, Instituto Nacional de Investigación y Desarrollo Pequero, Mar del Plata, p 213–232
- Ciancio JE, Pascual MA, Beauchamp DA (2007) Energy density of Patagonian aquatic organisms and empirical predictions based on water content. *Trans Am Fish Soc* 136: 1415–1422
- Ciancio JE, Pascual MA, Botto F, Frere E, Iribarne O (2008) Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. *Limnol Oceanogr* 53:788–798
- Ciechowski JD, Sanchez RP (1983) Relationship between ichthyoplankton abundance and associated zooplankton biomass in the shelf waters off Argentina. *Biol Oceanogr* 3:77–101
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial, PRIMER-E, Plymouth
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- Claudet J, Osenberg CW, Domenici P, Badalamenti F and others (2010) Marine reserves: Fish life history and ecological traits matter. *Ecol Appl* 20:830–839
- Cousseau MB, Hansen JE, Gru DL (1979) Campañas realizadas por el buque de investigación 'Shinkai Maru' en el Mar Argentino desde abril de 1978 hasta abril de 1979. Organización y reseña de datos básicos obtenidos.

- Contribución 373, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata
- Craig JK, Crowder L (2002) Factors influencing habitat selection in fishes with a review of marsh ecosystems. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Springer Netherlands, Dordrecht, p 241–266
- Ernst B, Aedo G, Roa R, Cubillos L and others (2005) Evaluación del reclutamiento de merluza de cola entre la V y X Regiones: revisión metodológica. Informe Final. Proyecto del Fondo de Investigación Pesquera N° 2004-12. Departamento de Oceanografía, Universidad de Concepción
- Gargett AE, Marra J (2002) Effects of upper ocean physical processes (turbulence, advection, and air-sea interaction) on oceanic primary production. In: Robinson AR, Rothschild BJ, McCarthy JJ (eds) The sea, Vol 12: biological–physical interactions in the sea. John Wiley & Sons, New York, NY, p 19–49
- Giussi AR, Hansen JE, Wöhler OC (2004) Biología y pesquería de la merluza de cola (*Macruronus magellanicus*). In: Boschi EE (ed) El Mar Argentino y sus recursos pesqueros, Vol 4. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, p 321–346
- Giussi AR, Zavatteri A, Di Marco E, Gorini FL, Bernardele JC, Mari NR (2016a) Biology and fishery of long tail hake (*Macruronus magellanicus*) in the Southwest Atlantic Ocean. *Rev Invest Des Pesq* 28:55–82. <http://marabierto.inidep.edu.ar/handle/inidep/1667>
- Giussi AR, Zavatteri A, Di Marco EJ, Wöhler OC (2016b) Evaluación de abundancia de la merluza de cola (*Macruronus magellanicus*) del Atlántico Sudoccidental. Período 1985–2015. INIDEP Informe Técnico Oficial 40, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata
- Gorini FL, Pájaro M (2014) Características reproductivas y longitud de primera madurez de la merluza de cola (*Macruronus magellanicus*) en el Atlántico sudoccidental. Período 2003–2010. *Rev Invest Des Pesq* 24:5–19. <http://hdl.handle.net/1834/6772>
- Houde ED (2008) Emerging from Hjort's shadow. *J Northwest Atl Fish Sci* 41:53–70
- Huijbers CM, Nagelkerken I, Debrot AO, Jongejans E (2013) Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. *Ecology* 94:1859–1870
- King JR, McFarlane GA (2003) Marine fish life history strategies: applications to fishery management. *Fish Manag Ecol* 10:249–264
- La Mesa M, Catalano B, Russo A, Greco S, Vacchi M, Azzali M (2010) Influence of environmental conditions on spatial distribution and abundance of early life stages of Antarctic silverfish, *Pleuragramma antarcticum* (Nototheniidae), in the Ross Sea. *Antarct Sci* 22:243–254
- Leichter JJ, Witman JD (2009) Basin-scale oceanographic influences on marine macroecological patterns. In: Witman JD, Kaustuv R (eds) Marine macroecology. University of Chicago Press, Chicago, IL, p 205–226
- Link JS, Stockhausen WT, Methratta ET (2005) Food-web theory in marine ecosystems. In: Belgrano A, Scharler UM, Dunne J, Ulanowicz RE (eds) Aquatic food webs: an ecosystem approach. Oxford University Press, Oxford, p 98–114
- Lutz VA, Segura V, Dogliotti AI, Gagliardini DA, Bianchi AA, Balestrini CF (2010) Primary production in the Argentine Sea during spring estimated by field and satellite models. *J Plankton Res* 32:181–195
- Machinandiarena L, Ehrlich MD (1999) Detection of a long tail hake *Macruronus magellanicus* nursery ground in the Argentine sea. *Rev Invest Des Pesq* 12:45–50. <http://hdl.handle.net/1834/1877>
- Macpherson E, Gordo A (1996) Biomass spectra in benthic fish assemblages in the Benguela System. *Mar Ecol Prog Ser* 138:27–32
- Mann KH, Lazier JRN (2006) Dynamics of marine ecosystems. Biological–physical interactions in the oceans. Blackwell Publishing, Malden, MA
- Marrari M, Signorini SR, McClain CR, Pájaro M, and others (2013) Reproductive success of the Argentine anchovy, *Engraulis anchoita*, in relation to environmental variability at a mid-shelf front (Southwestern Atlantic Ocean). *Fish Oceanogr* 22:247–261
- McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman & Hall, London
- McManus MA, Woodson CB (2012) Plankton distribution and ocean dispersal. *J Exp Biol* 215:1008–1016
- Moloney CL, St John MA, Denman KL, Karl DM, Köster FW, Sundby S, Wilson RP (2011) Weaving marine food webs from end to end under global change. *J Mar Syst* 84:106–116
- Olson DB (2002) Biophysical dynamics of ocean fronts. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) The sea, Vol 12: biological–physical interactions in the sea. John Wiley & Sons, New York, NY, p 187–218
- Padovani LN, Viñas MD, Sánchez F, Mianzan H (2012) Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. *J Sea Res* 67:85–90
- Podesta GP (1990) Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fish Bull* 88:167–177
- Prenski LB, Angelescu V (1993) Trophic ecology of the common hake (*Merluccius hubbsi*) in the continental shelf. Part 3. Annual food consumption by stocks and its relation to exploitation of multispecific fisheries. INIDEP Documento Científico 1, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata (in Spanish with summary in English). <http://hdl.handle.net/1834/2557>
- Prenski LB, Morales-Yokobori ML, Minte Vera CV, Bridi J, Landa P, Di Giacomo EE, Perier M (2012) Assessment against MSC principles and criteria for Argentine hoki (*Macruronus magellanicus*) bottom and semi pelagic trawl net fishery. Public Certification Report. Organización Internacional Agropecuaria (OIA), Buenos Aires
- Rivas AL (2006) Quantitative estimation of the influence of surface thermal fronts over chlorophyll concentration at the Patagonian shelf. *J Mar Syst* 63:183–190
- Rivas AL, Pisoni JP (2010) Identification, characteristics and seasonal evolution of surface thermal fronts in the Argentinean Continental Shelf. *J Mar Syst* 79:134–143
- Romero SI, Piola AR, Charo M, Eiras Garcia CA (2006) Chlorophyll-*a* variability off Patagonia based on SeaWiFS data. *J Geophys Res* 111:C05021
- Ruiz AE, Fondacaro RR (1997) Diet of hake (*Merluccius hubbsi* Marini) in a spawning and nursery area within Patagonian shelf waters. *Fish Res* 30:157–160
- Sabatini M, Reta R, Matano R (2004) Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer. *Cont Shelf Res* 24:1359–1373

- ✦ Sabatini ME, Akselman R, Reta R, Negri RM and others (2012) Spring plankton communities in the southern Patagonian shelf: hydrography, mesozooplankton patterns and trophic relationships. *J Mar Syst* 94: 33–51
- Scarlato N, Remaggi CA, Hansen JE, Wöhler OC (2000) Pesca exploratoria de merluza de cola (*Macruronus magellanicus*) en el talud continental y sector adyacente al norte de 48° S. INIDEP Informe Técnico Interno 88, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata
- ✦ Schuchert PC, Arkhipkin AI, Koenig AE (2010) Traveling around Cape Horn: Otolith chemistry reveals a mixed stock of Patagonian hoki with separate Atlantic and Pacific spawning grounds. *Fish Res* 102:80–86
- Sherman K (2005) The large marine ecosystem approach for assessment and management of ocean coastal waters. In: Hennessey TM, Sutinen JG (eds) *Sustaining large marine ecosystems: the human dimension*, Vol 13. Elsevier, Amsterdam, p 3–16
- ✦ Thorpe A, Ibarra AA, Reid C (2000) The new economic model and marine fisheries development in Latin America. *World Dev* 28:1689–1702
- ✦ Wang J, Pierce GJ, Sacau M, Portela J, Santos MB, Cardoso X, Bellido JM (2007) Remotely sensed local oceanic thermal features and their influence on the distribution of hake (*Merluccius hubbsi*) at the Patagonian shelf edge in the SW Atlantic. *Fish Res* 83:133–144
- Zar JH (2010) *Biostatistical analysis*, 5th edn. Prentice Hall, Englewood Cliffs, NJ

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