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Food habits of South Pacific hake (*Merluccius gayi*) in Ecuadorian waters

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Abstract

The food habits of the South Pacific hake (*Merluccius gayi*) from Ecuadorian waters were studied by analysing 232 stomachs of specimens ranging from 23.4–83.1 cm in total length (TL). Fish was the most important prey group (Alimentary Index, %AI = 94), *Ctenosciaena peruviana* being the most represented prey species (%AI = 62.17). PERMANOVA analysis showed dietary differences between the smallest individuals (class I < 30 cm TL) and the largest (class IV 40–45 cm TL; class V ≥ 45 cm TL). In addition, spatial differences in dietary composition were found between the three sampled regions (Manabí, Santa Elena and Guayas). The results of this study indicate that the South Pacific hake is an opportunistic predator feeding on a wide variety of vertebrate and invertebrate organisms.

Introduction

The South Pacific hake (*Merluccius gayi*) is a demersal species found off the Ecuadorian, Peruvian and Chilean coasts (from 01°N to 47°S) in depths between 50 and 800 m (Aguayo, 1995; Guevara-Carrasco & Lleonart, 2008; García-Domínguez *et al.*, 2014). In Ecuador, this species represents an important fishery resource for bottom trawls, with a total landing of 13,000 tons in 2013 (García-Domínguez *et al.*, 2014). However, despite its economic importance, information on the feeding habits of the South Pacific hake in Ecuador is lacking. Feeding ecology investigations based on stomach content analysis (SCA) are an ideal tool to investigate such habits and to implement ecosystem analysis based on food web models (i.e. Ecopath-Ecosim) (Pauly *et al.*, 2000).

The South Pacific hake is a voracious predator with a large mouth and prominent rows of sharp teeth well suited to seizing prey. Previous studies carried out in Peruvian and Chilean waters suggested that this species is a non-selective predator that feeds on a wide variety of fish and invertebrate species (Fuentes, 1983; Alamo & Espinoza, 1996, 1997; Castillo *et al.*, 1997; Vidal *et al.*, 1997; Orrego & Mendo, 2012). At the same time, *M. gayi* represents an important prey source for large pelagic fishes in Ecuadorian waters, such as billfishes, dolphinfishes and sharks (Polo-Silva *et al.*, 2007, 2009, 2013; Rosas-Luis *et al.*, 2016; Loor-Andrade *et al.*, 2017*a*, 2017*b*; Varela *et al.*, 2017; Zambrano-Zambrano *et al.*, 2019). Therefore, this species may play a crucial ecological role in demersal food webs both as predator and prey.

The Ecuadorian coast, located at the confluence of the Pacific Central American Coastal and the Humboldt ecosystems, is characterized by a marked spatial variability of the physical-oceanographic conditions (Sonnenholzner *et al.*, 2013). Thus, the northernmost regions (Esmeraldas and Manabí provinces) are influenced by the Panama current (warm and nutrient-poor water), whereas the southernmost region (Guayas province) is affected by the Peruvian coastal current (cold and nutrient-rich water) (Sonnenholzner *et al.*, 2013; Martínez-Ortiz *et al.*, 2015). These singular oceanographic features may cause geographic variation in the abundance and distribution of prey.

New information regarding the trophic biology of the South Pacific hake in Ecuadorian waters may provide useful data to understand the trophic role of this species in the south-eastern Pacific Ocean. The present study was conducted to describe and quantify the feeding habits of the South Pacific hake in Ecuadorian waters assessing spatial and size-related variation in feeding habits.

Materials and methods

Sampling and stomach-content analysis

Stomachs of South Pacific hake (N = 232), ranging from 23.4–83 cm in total length (TL) and from 98–1200 g in body mass, were collected aboard bottom trawlers operating off the Ecuador coast (Figure 1) in January–June 2015. Whole stomachs were collected and stored at −20 °C until analysis. In the laboratory, they were cut open for prey identification to the lowest possible taxonomic level, and their wet weight was recorded to the nearest 0.01 g. Partially digested fish items were identified from otoliths (Harvey *et al.*, 2000; García-Godos Naveda, 2001), whereas cephalopod species were identified from mandibles using the key of

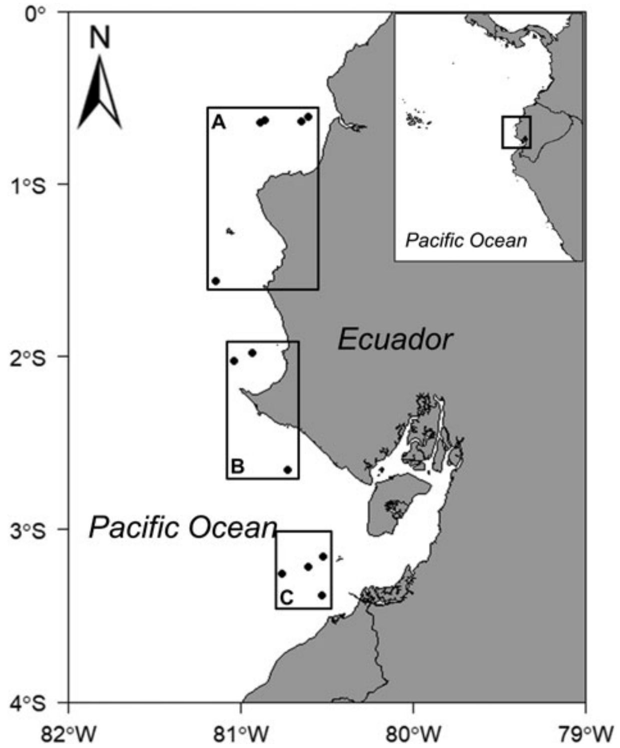

Fig. 1. Map of the study area. (A) Manabí; (B) Santa Elena, (C) Guayas.

Clarke (1986). Stomachs containing only hard parts were not taken into consideration for analysis.

Data analysis

To determine the relative importance of different prey in the diet of the South Pacific hake, three indices were calculated: (1) per cent composition by weight ($\%W_i$ = weight of prey item $i \times 100$/total weight of all prey items), (2) frequency of occurrence ($\%O_i$ = number of stomachs containing prey item $i \times 100$/total number of non-empty stomachs), and (3) alimentary index expressed as percentage ($\%AI_i = [(\%O_i \times \%W_i)/(\sum \%W_i \times \%O_i)] \times 100$) (Kawakami & Vazzoler, 1980).

To determine sampling thoroughness, a cumulative prey curve was generated by the vegan package (Oksanen *et al*., 2010) in R (R Development Core Team, 2019). To determine whether the curve reached an asymptote, the slope of the linear regression estimated from the last four stomachs was compared with a line of zero slope (horizontal asymptote) by a *t*-test (Preti *et al*., 2012).

A Pearson's chi-square test (χ^2) was applied to test for significant differences in the frequency of empty stomachs among areas and size classes. A level of $\alpha = 0.05$ was considered significant. Statistical analyses were performed using Statgraphics Centurion v16.2.04.

Permutational multivariate analysis of variance (PERMANOVA) was used to detect size-related and spatial variations in diet composition (Anderson, 2001; McArdle & Anderson, 2001). The experimental design included two factors: 'Size class' (with six levels, class I (<30 cm in TL), class II (30–35 cm in TL), class III (35–40 cm in TL), class IV (40–45 cm in TL) and class V (≥45 cm in TL)), and 'Regions' (with three levels, Manabí Province, Santa Elena Province and Guayas Province). The analysis was based on the Bray–Curtis dissimilarity matrix calculated on the prey weight values after performing a *fourth-root transformation* (Bray & Curtis, 1957). Significant terms were investigated using *a posteriori* pairwise comparisons with the PERMANOVA test. The homogeneity of multivariate dispersion was tested by PERMDISP (Anderson, 2006). Multivariate analyses were performed using the software PRIMER v6.1.13 & PERMANOVA + v1.0.3 statistical package (PRIMER-E Ltd, Plymouth, UK).

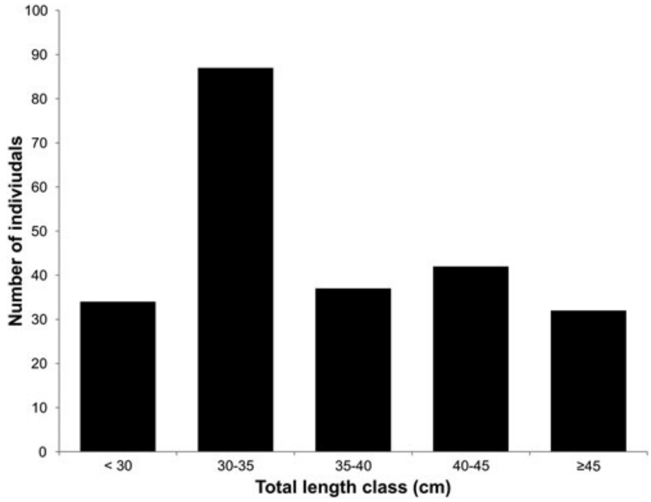

Fig. 2. Length frequency distribution of the sampled South Pacific hake.

Prey importance and feeding strategy were analysed with a modification of the Costello graphical method (Costello, 1990; Amundsen *et al*., 1996). In this method, prey-specific abundance ($\%P_i$) is plotted against $\%O_i$, with $\%P_i = (\sum$ prey i weight/$\sum$ weight of all prey in the stomach containing prey $i) \times 100$. As in Varela *et al*. (2017), prey categories that only appear in one stomach were not considered in the analysis.

Results

Figure 2 shows the size frequency distribution of the sampled fish. The cumulative prey curve did not reach the asymptote (*t*-test, $P = 0.01$) (Figure 3); therefore, the number of samples may not be enough to describe the diet. While regional differences were not found in the frequency of empty stomachs (χ^2, $P = 0.43$), differences were detected among size classes (χ^2, $P = 0.02$). Of the 232 stomachs analysed, 155 (66.81%) contained prey and 77 (33.10%) were empty. The diet was made up of 12 prey categories, including 6 fishes, 4 crustaceans, 1 cephalopod and unidentified remains. Fish was the most important prey group in terms of *W*, *O* and AI (87.76, 51.61 and 94.29%, respectively), followed by crustaceans ($\%W = 2$ .35, $\%O = 31.61$ and $\%AI = 4.13$) and cephalopods ($\%W = 0.64$, $\%O = 4.52$ and $\%AI = 0.06$). The teleost Peruvian barbel drum (*Ctenosciaena peruviana*) was the most important taxon in terms of *W* and AI (42.50% and 61.58%, respectively), while krill (*Nyctiphanes simplex*) was the most frequent prey species ($\%O = 25.81$) (Table 1).

Feeding strategy, based on the Amundsen graphical method, is shown in Figure 4. Most prey species were located close to the y-axis, indicating that the prey consumed by *M. gayi* were rarely seen in the stomachs (low occurrence). However, krill and Peruvian barbel drum, which were located in the upper central area of the graph, can be considered as the most important prey species in the diet of the South Pacific hake.

The PERMANOVA analysis detected significant differences in dietary composition among regions (PERMANOVA, $P = 0.001$) and size classes (PERMANOVA, $P = 0.003$). There was, furthermore, a significant interaction between both factors, indicating that differences in size classes were not homogeneous across regions (PERMANOVA, $P = 0.0047$).

The PERMDISP analysis did not show significant differences (PERMDISP, $P > 0.05$), suggesting that the differences obtained with PERMANOVA were not due to multivariate dispersion.

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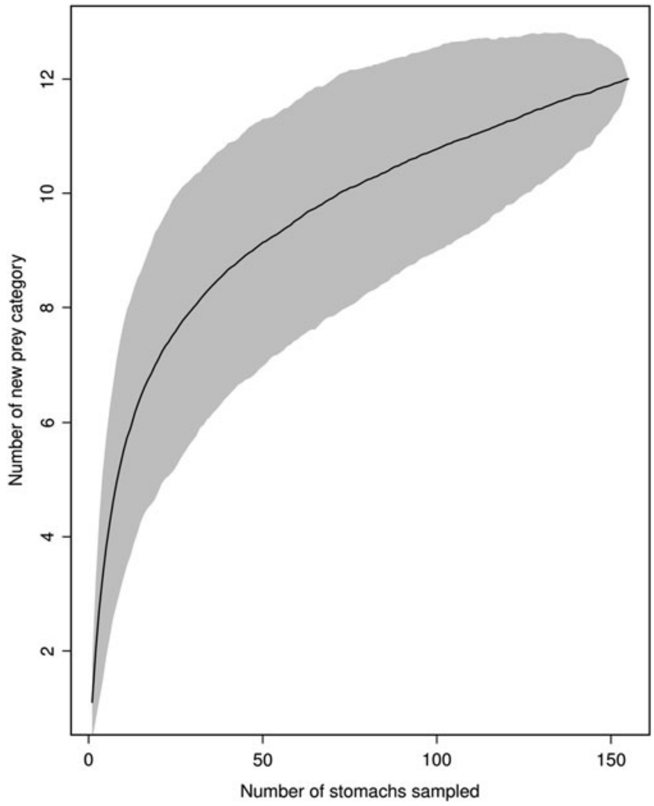

Fig. 3. Cumulative prey curve.

Table 1. Dietary composition of South Pacific hake caught off Ecuador. Percentage of weight (%*W*), occurrence (%*O*) and alimentary index (%AI)

Prey	%*W*	%*O*	%AI
Fishes	87.76	51.61	94.29
Ctenosciaena peruviana	42.50	25.16	61.58
Peprilus medius	18.60	16.77	17.97
Larimus effulgens	12.26	5.81	4.10
Merluccius gayi	11.62	3.23	2.16
Diplectrum maximum	2.72	0.65	0.10
Paralichthys sp.	0.05	0.65	< 0.01
Crustaceans	**2.35**	**31.61**	**1.55**
Nyctiphanes simplex	1.71	25.81	2.53
Protrachypene precipua	0.06	4.52	0.02
Hemisquilla sp.	0.07	0.65	< 0.01
Unidentified crustaceans	0.51	1.29	0.04
Cephalopods	**0.64**	**4.52**	**0.06**
Loliolopsis diomedeae	0.64	4.52	0.17
Others	**9.25**	**21.29**	**4.10**
Unidentified remains	9.25	21.29	11.34

The pair-wise PERMANOVA test revealed significant differences in the dietary composition between classes I and IV ($P = 0.001$), and I and V ($P = 0.001$). Significant dietary differences were also found between Manabí and Santa Elena (PERMANOVA, $P = 0.013$), Manabí and Guayas (PERMANOVA, $P = 0.001$), and between Santa Elena and Guayas (PERMANOVA, $P = 0.001$).

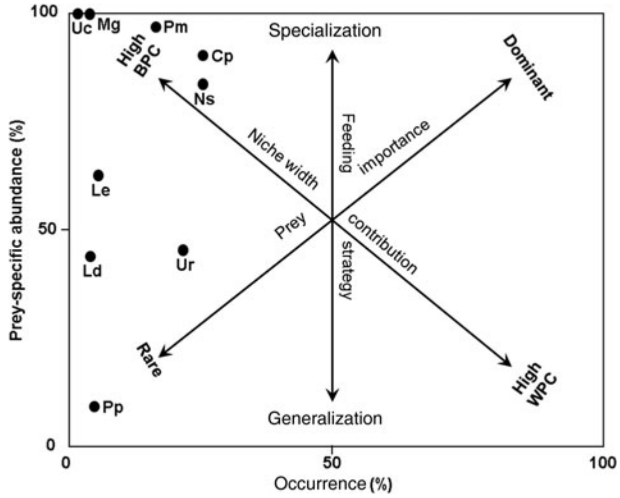

Fig. 4. Plot of the feeding strategy. The two diagonal axes represent the importance of prey (dominant *vs* rare) and the contribution to the niche width (high between-phenotype *vs* high within-phenotype contribution); the vertical axis defines the predator feeding strategy (specialist *vs* generalist). Cp, *Ctenosciaena peruviana*; Ld, *Loliolopsis diomedeae*; Le, *Larimus effulgens*; Mg, *Merluccius gayi*; Ns, *Nyctiphanes simplex*; Pm, *Peprilus medius*, Pp, *Protrachypene precipua*, Uc; Unidentified crustacean, Ur, Unidentified remains.

Figure 5 shows the contribution of each prey (%AI) to the diet of the South Pacific hake by size class and region. While class I fed mainly on krill (%AI = 57.64), the principal dietary component in the remaining size classes were fish species. That is, class II and class III consumed primarily Pacific harvestfish (*Peprilus medius*) (%AI = 56.26 and 68.53, respectively); while class IV and class V fed almost exclusively on Peruvian barbel drum (%AI = 88.12 and 76.92, respectively). In Manabí and Santa Elena, Peruvian barbel drum was the most important prey (%AI = 45.33 and 98.02, respectively), whereas krill was the major food item in Guayas (%AI = 90.84).

Discussion

The feeding behaviour of the South Pacific hake has been widely examined along the coasts of Peru and Chile (Stobberup, 1992; Castillo *et al*., 1995, 1997; Alamo & Espinoza, 1997; Vidal *et al*., 1997; Orrego & Mendo, 2012); thus far, however, no information is available on the food habits of this species in Ecuadorian waters. The present study, therefore, provides the first information about the trophic biology of the South Pacific hake in the area.

The results of this study show that the diet of South Pacific hake in Ecuadorian waters is mainly composed by fish. This finding is consistent with previous studies carried out in the northern coast of Chile (Alamo & Espinoza, 1997; Orrego & Mendo, 2012). For instance, Alamo & Espinoza (1997) found that myctophids and sardine were the most important food prey, whereas Orrego & Mendo (2012) reported that hakes and engraulids were the groups that most contributed to the diet (%W = 60). Stobberup (1992), however, observed that the South Pacific hake fed mainly on euphausiids off the central coast of Chile. These marked geographic differences in the dietary composition of the South Pacific hake indicate that this species exhibits an extensive plasticity in its food habits.

Multivariate analysis showed size-related shifts in the feeding habits. The smallest South Pacific hake fed mainly on euphausiids, which have been reported to be an important prey species not only for small South Pacific hake (Alamo & Espinoza, 1997; Vidal *et al*., 1997), but also for small individuals of the co-generic hake *Merluccius merluccius* from the Mediterranean and Celtic seas, and from the Bay of Biscay (Carpentieri *et al*., 2005;

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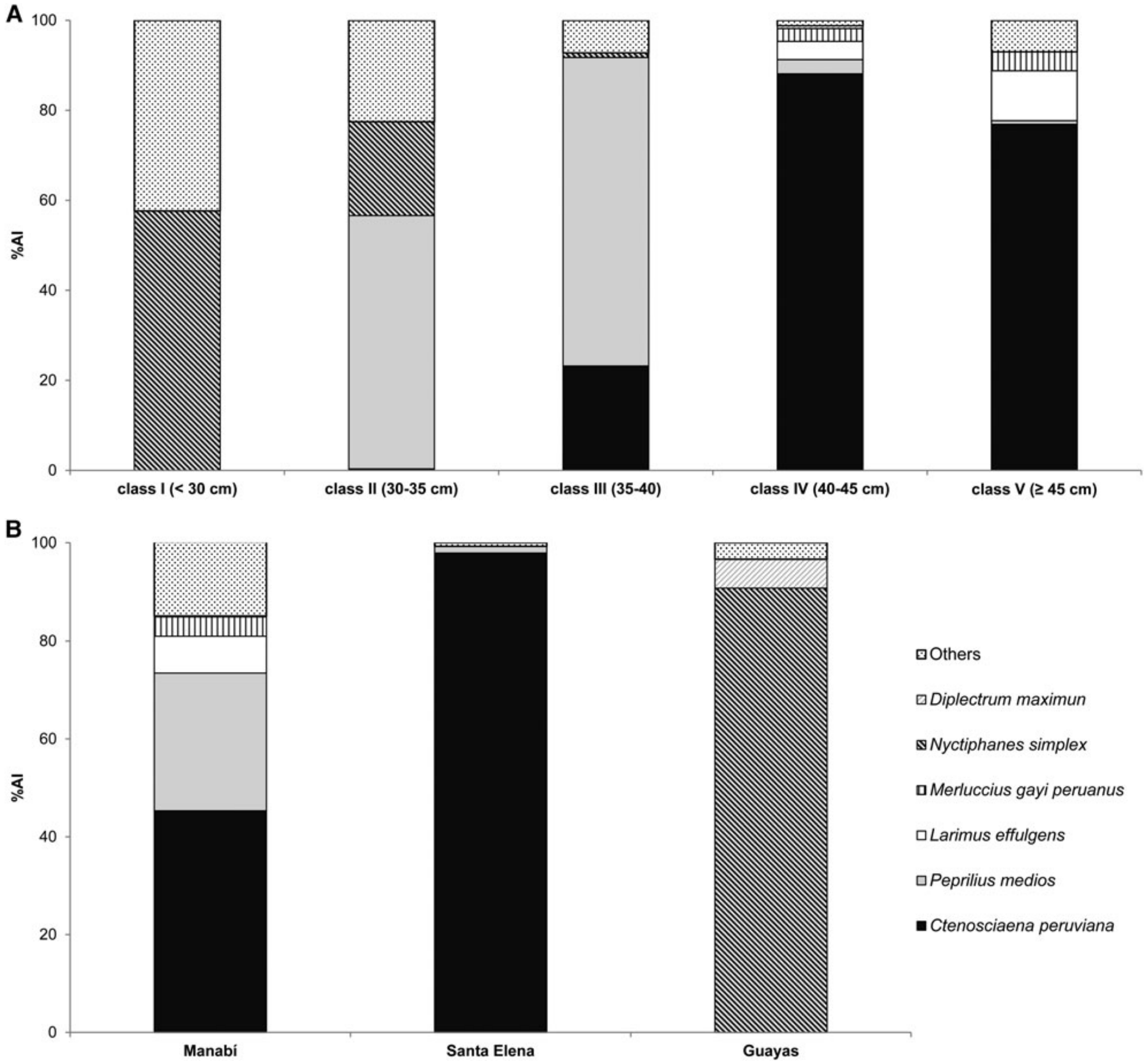

Fig. 5. Dietary composition by (A) size class and (B) region. Data are presented in %AI.

Mahe *et al.*, 2007; Sinopoli *et al.*, 2012). For instance, Alamo & Espinoza (1997) observed that Euphausiacea was the most important food source for South Pacific hake <30 cm (TL, total length) from northern Peru, whereas Vidal *et al.* (1997) reported that South Pacific hake >42 cm TL fed primarily on *Euphausia mucronata* off the northern coast of Chile. Carpentieri *et al.* (2005), on the other hand, found that the diet of 5.0–11.9 cm TL *M. merluccius* was dominated by the euphausiid *Nyctiphanes couchi* in the Mediterranean Sea. Sinopoli *et al.* (2012) also reported euphasiids to be the most important prey for *M. merluccius* collected in the central Mediterranean Sea. It is worth noting that the ingestion of crustaceans decreased with size in our analyses. The largest specimens (≥45 cm), in fact, showed a fully piscivorous feeding behaviour. A similar pattern was reported for *M. capensis* and *M. merluccius* from the Celtic Sea and western coast of South Africa, respectively (Payne *et al.*, 1987; Mahe *et al.*, 2007). Mahe *et al.* (2007) stated that this size-dietary shift is caused by an increasing energy demand. This hypothesis, however, does not explain our observations in South Pacific hake, as euphausiids show a high caloric content in comparison to fish (Cartes *et al.*, 2008), representing an important energetic resource for predators (Sorell *et al.*, 2017). PERMANOVA analysis also detected regional differences in dietary composition, which probably are related to geographic variations in the abundance and distribution of prey.

The presence of conspecifics in the stomachs was not unexpected, since cannibalism has been widely reported in many hake species such as South Pacific hake (Orrego & Mendo, 2012), Cape hake (*M. capensis* and *M. paradoxus*) (Payne *et al.*, 1987; Punt *et al.*, 1992), European hake (*M. merluccius*) (Velasco & Olaso, 1998; Cabral & Murta, 2002; Mahe *et al.*, 2007), and silver hake (*M. bilinearis*) (Link *et al.*, 2012). In agreement with most of these studies, we found that cannibalism increases with increasing body size. This may be explained by the fact that hakes live in large aggregations, generally composed of different size classes, which make small specimens readily accessible and/or available to conspecific predation (Juanes, 2003).

The results of this study suggest that the South Pacific hake is a generalist feeder as it preys on a wide variety of invertebrates and vertebrates. Future investigations of a higher number of stomachs are however needed to confirm the robustness of our results. To complement the information provided by gut analysis, stable

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isotope analyses, which give information at longer timescales, should be carried out to improve the understanding of the trophic biology of this species.

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