

ORIGINAL RESEARCH

Trophic ecology of hairy conger eel *Bassanago albescens* in the Southwest Atlantic and its implications for the ecosystem-based fishery management

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ABSTRACT. This study aimed to determine the diet composition and feeding strategies of the hairy conger eel *Bassanago albescens* in the Southwest Atlantic (35° S-45° S), from stomach contents analysis of 222 specimens. The diet consisted mainly of cephalopods, followed by isopods, amphipods, ophiuroids, brachyurous and polychaetes. Results showed significant differences in the composition of the diet between sexes, regions and size classes that were reflected in the changes in the foraging strategy. The consumption of squid *Illex argentinus* progressively increased with a growing predator size, where the largest individuals showed specialization in the consumption of this particular prey. We propose these dietary changes would be related to morphological limitations and abilities associated with the body size of *B. albescens*, with larger individuals having access to larger prey. Our results help to understand the biology of a species that has a sympatric distribution with two key species in the Argentine fisheries: hake *Merluccius hubbsi* and *I. argentinus*, with evidence of a strong trophic interaction between them. This new information on the resources involved would allow an optimization of the fisheries management under an ecosystem-based criterion.

Key words: Anguilliformes, ecosystem-based fishery management, feeding habits, ontogenetic changes.



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Ecología trófica del congrio de profundidad *Bassanago albescens* en el Atlántico Sudoccidental y sus implicancias para el manejo ecosistémico de las pesquerías

RESUMEN. En el presente estudio se determina la composición de la dieta y estrategia alimentaria del congrio de profundidad *Bassanago albescens* en el Atlántico Sudoccidental (35° S-45° S), a partir del análisis del contenido estomacal de 222 individuos. La dieta consistió de cefalópodos, seguidos por isópodos, anfípodos, ofiuroideos, braquiuros y poliquetos. Los resultados mostraron diferencias significativas en la composición de la dieta entre sexos, zonas y clases de tallas que se vieron reflejadas en los cambios de la estrategia de forrajeo. Se registró un aumento progresivo en el consumo de *Illex argentinus* con el aumento del tamaño de *B. albescens*, donde los individuos más grandes mostraron una especialización en el consumo de esta presa. Estos cambios alimentarios estarían relacionados a limitaciones morfológicas y habilidades asociadas al tamaño corporal de *B. albescens*, teniendo los individuos más grandes acceso a presas de mayor tamaño. Nuestros resultados ayudan a comprender la biología de una especie que tiene una distribución simpátrica con dos especies clave en las pesquerías de la Argentina: *Merluccius hubbsi* e *I. argentinus*, con

evidencias de una fuerte interacción trófica entre ellas. Esta nueva información sobre los recursos involucrados permitiría una optimización del manejo pesquero bajo un criterio ecosistémico.

Palabras clave: Anguilliformes, manejo ecosistémico de las pesquerías, hábitos alimentarios, cambios ontogenéticos.

INTRODUCTION

The hairy conger eel *Bassanago albescens* (Barnard, 1923) is an endemic species of the Southern Hemisphere (Figueroa 1992; Anderson 2005; Buratti et al. 2020). It lives between 81 and 600 m deep (Reyes 2007) and presents a sympatric distribution with two key species in Argentine fisheries, the Argentine hake (*Merluccius hubbsi*) and Argentine squid (*Illex argentinus*) (Haimovici et al. 1998; Arkhipkin et al. 2015). *B. albescens* is an iteroparous species with a leptocephalus larva (Figueroa and Ehrlich 2006), marked sexual dimorphism (Blasina et al. 2018), and benthic trophic habits (Figueroa 1999). In the Argentine shelf, a large biomass has been recorded (García et al. 2010) as part of the bycatch of the Patagonian scallop (*Zygochlamys patagonica*) fishery (Bremec et al. 2003) and commercial catches of *M. hubbsi* (Renzi and Castrucci 1998).

Aquatic ecosystems are suffering alterations due to the development of the fishing industry, and these have been the focus of copious investigations (Craig et al. 2009; FAO 2018). The propagation of such impacts on ecosystems differs according to whether the food web is controlled by apex predators (top-down control), by lower levels (bottom-up control) or by dominant species in medium trophic level (wasp-waist control) (Hill et al. 2020). Therefore, in recent decades, a consensus has been reached on the need to implement ecosystem-based fisheries management (Pikitch et al. 2004; FAO 2018). In this context, the complex interactions occurring in an ecosystem must be considered to evaluate the effects of fishing activities in an integrated way (Branch et al. 2010). Such interactions are

key factors in the functioning, structure, composition and abundance of the species involved, and in ecological processes such as predation and competition for resources (Lercari et al. 2014). Therefore, trophic ecology studies are essential to understand the interrelationships and community dynamics within an ecosystem (Amundsen and Sánchez-Hernández 2019).

To understand the role that a species plays in a biotope, it is necessary to describe the trophic behaviour of the constituent species that compose it, even those that have not been investigated due to their lack of commercial importance (Stephens et al. 2007; Brown et al. 2012). In this sense, stomach content analysis is essential (Amundsen and Sánchez-Hernández 2019). Few studies have been conducted on the diet of *B. albescens* to date, noting that its prey is represented mostly by benthic invertebrates (Meyer and Smale 1991; Figueroa 1999; Anderson 2005). The breadth of a consumer's trophic niche is determined by a variety of biological and environmental characteristics (Hayden et al. 2019). Hayden et al. (2019) have shown a latitudinal variation in the mean trophic niche breadth of fish species, evidencing that near the Equator they present a broader trophic niche than those of the Arctic or Antarctic seas. However, diet is also determined by a predator's morphology, especially size, mobility, and dentition that will determine what types of prey it can capture (Stuart-Smith et al. 2013). Many species show ontogenetic changes in habitat, which are related to the type of prey and its size (Griffiths 2020). Understanding these changes in resource use is particularly important from an ecological perspective because they can help illustrate the integral functioning of the ecosystem (Hooper et al. 2005; Brose et al. 2019). The present work aims to: (1) quantify the composi-

tion of the diet of *B. albescens*, (2) determine the feeding strategy through stomach content analysis, and (3) investigate possible ontogenetic changes in diet.

MATERIALS AND METHODS

The study area covered part of the Argentine shelf between 36° S and 46° S and between 100 and 170 m deep. *B. albescens* specimens were

caught in two research surveys (EH-02/2009 and EH-04/2009) carried out by the fisheries research vessel 'Dr. Eduardo L. Holmberg' from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Argentina (Figure 1). In both surveys, a bottom trawl gear was used for sampling, and individuals were kept at -20 °C for posterior analysis. Samples were thawed in the laboratory at room temperature, and total length (L_T), weight without stomach (W) and sex were recorded in each specimen. Prey found inside stomachs were separated and identified to the lowest possi-

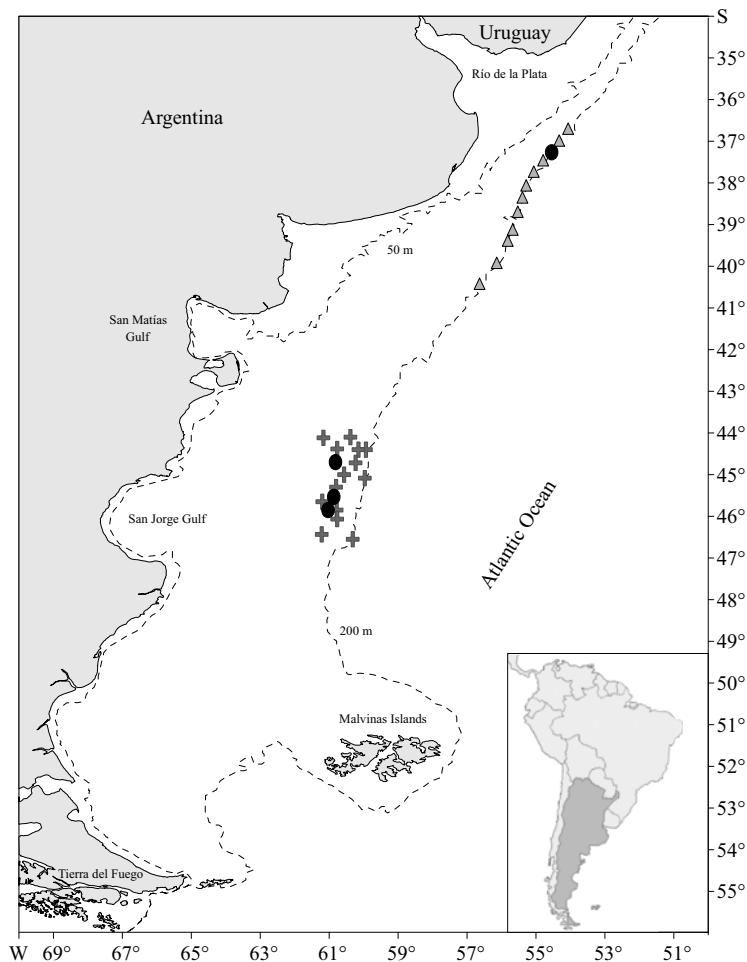


Figure 1. Map of the study area showing fishing trawls where specimens of *Bassanago albescens* were caught. Black circles indicate positive trawls for *B. albescens* from which diet samples were obtained. Grey triangles and crosses correspond to the northern and southern region trawls.

ble taxonomic level using taxonomic keys and field guides (Bastida and Torti 1973; Boschi et al. 1992). The number, length (mm) and wet weight (± 0.01 g) of each prey were also recorded.

To determine the most important prey in the diet of *B. albescens*, the Prey-Specific Index of Relative Importance (%PSIRI, Brown et al. 2012) was estimated as follows:

$$\text{PSIRI} = 0.5 \times \%FO \times (\%N_i + \%M_i)$$

where %FO is the percent frequency of occurrence of a particular prey (i.e. the number of times a given prey is found in the total number of stomachs with content, expressed as a percentage), %N_i is the specific numerical abundance of each prey (i.e. the percent numerical abundance of a given prey found among the stomach samples), and %M_i is the abundance of the specific wet weight of the prey calculated for each prey. PSIRI values were relativized to 100% (%PSIRI). Cumulative prey curves were used to determine whether an adequate number of stomachs had been examined to describe the diet accurately. The order in which stomachs were analysed was randomized 100 times to minimize bias resulting from the order of sampling. The asymptote of the curve indicated the minimum sample size required to adequately describe the diet (Ferry and Cailliet 1996). To construct these curves, six prey groups were considered: ophiuroids, amphipods, isopods, polychaetes, cephalopods and brachyurous, which together represented more than 95% of the %PSIRI.

The variation in diet composition between sexes, size classes (SC 1: ≤ 540 mm L_T, SC 2: 540-650 mm L_T, and SC 3: > 650 mm L_T) and regions (north: 36° S-41° S, and south: 44° S-47° S, corresponding to campaigns EH-04/2009 and EH-02/2009, respectively) were analysed. The interaction between SC and regions were also analysed through a non-parametric multivariate analysis of variance (NP-MANOVA, Anderson 2001), using the number of prey and the Bray Cur-

tis distance measure with 10.000 permutations (Zuur et al. 2007). All statistical analyses were performed using R Software version 3.6.0 (R Core Team 2019), with a significance level of 0.05.

To evaluate the feeding strategy of *B. albescens* (as a generalist or specialist) and the importance of prey (dominant or rare), we used the graphic method proposed by Amundsen et al. (1996). The method consists of plotting the specific abundance of the prey (P_i) against its frequency of occurrence (%FO). P_i is defined as the percentage of the total number of prey *i* divided by the number of all prey present in those individuals that contained prey *i*. The analysis of the feeding strategy was carried out considering the main prey categories outlined above.

The relationship between the total length of *B. albescens* and prey size was evaluated using the width of the crabs' shell, total length of amphipods and isopods, disk width of echinoderms, and standard length of teleosts. The increase in the minimum, average and maximum size of the prey consumed with the increase in the total length of the predator was calculated, testing the significance ($P = 0.05$) of the slope of the quantile regressions of 5, 50 and 95%, respectively (Griffiths 2020).

The trophic position of *B. albescens* was determined by its trophic level (TL) for each size class and area, applying the method proposed by Cortés (1999) expressed as:

$$\text{TL} = 1 + (\sum P_j \times \text{TL}_j)$$

where TL_j is the trophic level of each prey item (taken from Ebert and Bizarro 2007) and P_j is the proportion of each prey item in the diet of *B. albescens*.

To evaluate whether differences in the diet composition and TL between regions were reflected in the L_T-W relationship of the individuals, an estimation of it was carried out according to the equation $W = a L_T^b$ using linear regression after a logarithmic transformation of the vari-

ables: $\log W = \log a + b \log L_T$ (Froese 2006). The degree of association between L_T and W was determined using the coefficient of determination (r^2). The hypothetical isometry values ($b = 3$) were tested by Student's t-test with a 95% confidence limit level (Zar 1999). An analysis of covariance (ANCOVA, Zuur et al. 2007) was performed to test for significant differences in regression gradients between sexes ($P = 0.05$).

RESULTS

Of the 222 stomachs analysed, 186 (83.78%) presented some type of content. The sample from the southern region consisted of 131 females rang-

ing 543-772 mm L_T . No males were recorded. The northern region was represented by 52 females ranging 498-640 mm L_T , and 39 males ranging 400-537 mm L_T , which represented 16% of the total sample and were all grouped within the SC 1. A total of 34 prey items were identified. %PSIRI values indicated that the main prey category in the diet of *B. albescens* was cephalopods, followed by isopods, amphipods, ophiuroids, brachyurous and polychaetes (Table 1). The rest of the prey items presented less than 5% of the %PSIRI (Table 1). The most frequently consumed prey was the squid *I. argentinus*, followed by the isopod *Cirolana* spp., and the ophiuroid *Ophiuroglypha lymani* (Table 1). Cumulative curves of the number of prey as a function of the sample size revealed that the number of stomachs considered

Table 1. Frequency of occurrence (%FO), prey-specific number abundance (% N_i), prey-specific weight abundance (% M_i), Prey-Specific Index of relative Importance (PSIRI), and percentage of PSIRI (%PSIRI) for the total sample of *Bassanago albescens*.

Prey item	%FO	% N_i	% M_i	PSIRI	%PSIRI
Teleostei					4.48
<i>Patagonotothem</i> sp.	2.19	30.77	37.52	74.78	
<i>Sebastes oculatus</i>	0.54	33.33	20.48	14.53	
<i>Iluocoetes fimbriatus</i>	0.54	50.00	99.83	40.45	
No identificados	7.65	32.65	21.39	206.70	
Chondrichthyes					0.16
<i>Psammobatis</i> sp.	0.55	33.33	9.73	11.84	
Polychaeta					6.95
Questidae	0.54	50.00	79.31	34.91	
Flabelligeridae	0.55	66.66	88.88	42.77	
Eunicidae	1.09	45.45	79.68	68.20	
Ophelidae	1.63	37.50	2.66	32.73	
Lumbrineridae	3.28	3.28	6.63	16.25	
Onuphidae	1.64	42.86	0.76	35.77	
Capitellidae	0.55	20.00	6.85	7.38	
Gliceridae	1.64	50.00	0.62	41.51	
Not identified	12.02	31.82	8.48	242.20	

Table 1. Continued

Prey item	%FO	%N _i	%M _i	PSIRI	%PSIRI
Mollusca					
Cephalopoda					37.74
<i>Illex argentinus</i>	38.80	50.74	95.29	2,832.98	
Gasteropoda					0.73
<i>Marginella warrenii</i>	0.54	50.00	42.86	25.07	
<i>Natica isabelleana</i>	0.55	50.00	57.5	29.56	
Bivalvia					0.78
<i>Amiantis purpurata</i>	1.09	7.41	8.22	8.52	
<i>Atrina seminude</i>	0.54	96.97	87.62	49.84	
Crustacea					
Amphipoda					11.02
Gammaridae	13.66	57.00	2.83	408.64	
Hyperiididae	7.10	80.7	37.14	418.33	
Isopoda					15.16
<i>Cirolana</i> sp.	29.51	44.27	5.84	739.37	
<i>Serolis schythei</i>	13.66	37.36	10.12	324.29	
<i>Serolis</i> sp.	2.18	60.00	8.47	74.63	
Brachyura					10.35
<i>Sympagurus dimorphus</i>	10.93	35.61	93.34	704.71	
Not identified	2.73	11.36	41.45	72.09	
Echinodermata					
Ophiuroidea					10.91
<i>Ophiuroglypha lymani</i>	16.39	64.63	35.34	819.25	
Cnidaria					1.41
<i>Actinostola crassicornis</i>	0.55	100.00	100.00	55.00	
Tubo Hidrozoa indet.	3.28	25.8	5.23	50.89	
Thaliacea					0.13
<i>Iasis zonaria</i>	0.54	7.14	28.09	9.51	
Algae					0.18
Not identified	0.54	25.00	25.00	13.50	

to describe and analyse the diet of *B. albescens* were sufficient since the asymptote was reached as a function of the number of samples for all the groups considered (Figure 2).

Comparison of the composition of the diet between the SC 1 individuals of both sexes did not show significant differences ($F = 0.77$; $P = 0.5405$) and were grouped for subsequent analyses. Results of the two-way NP-MANOVA indicated that there were significant differences in the composition of

the diet between SCs ($F = 15.29$; $P = 0.0009$) and regions ($F = 47.27$; $P = 0.0011$), and also interaction between the effects of both factors ($F = 3.89$; $P = 0.0001$). Subsequent one-way NP-MANOVA indicated significant differences between SC 2 and SC 3 in the southern region, and between all SCs in the northern region *versus* those of the southern region. On the contrary, no significant differences were found in the composition of the diet between the specimens of both SCs from the

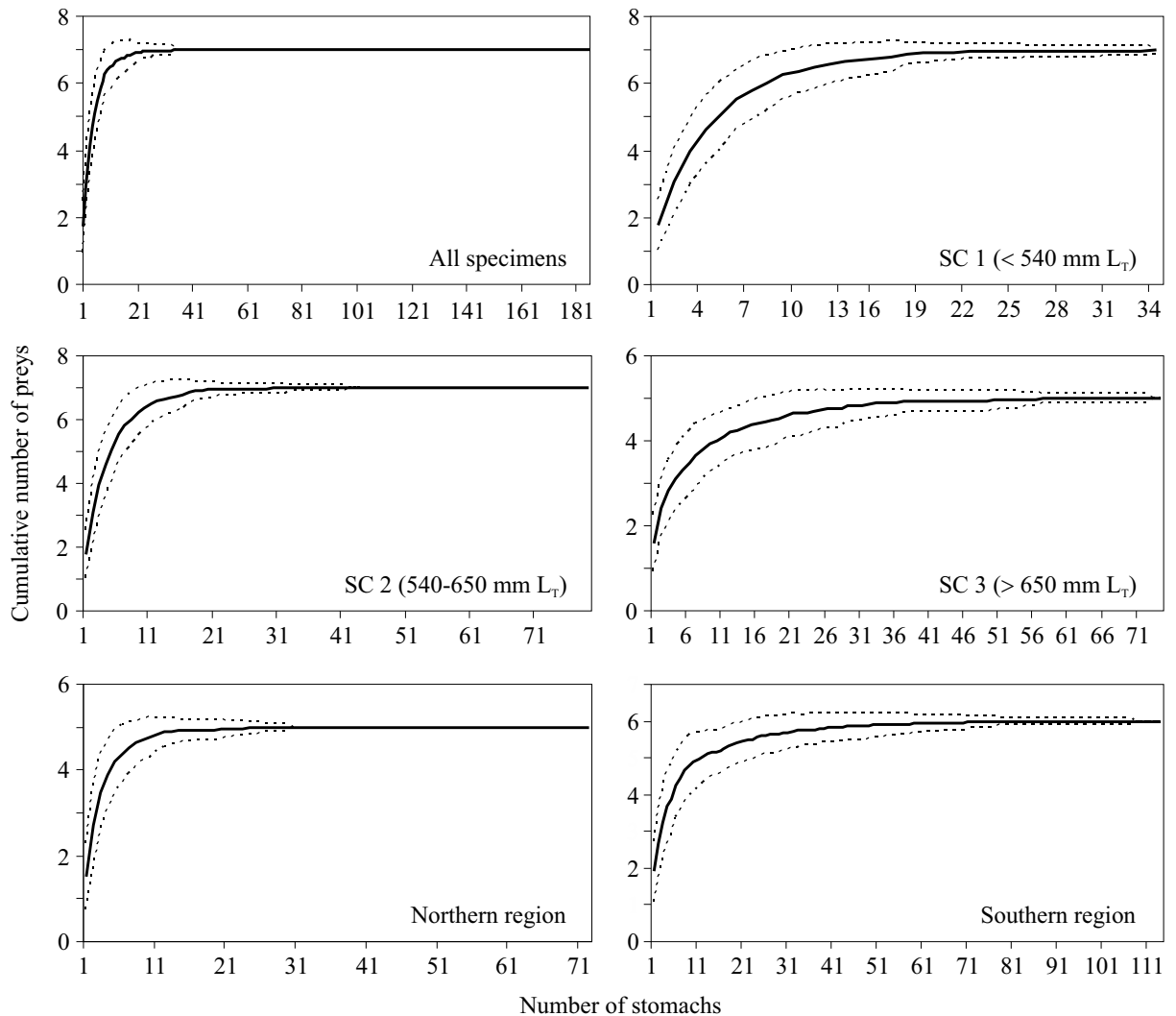


Figure 2. Cumulative prey curves for *Bassanago albescens* as a function of stomach number (mean \pm SD) from all specimens, three size classes (SC) and both regions.

northern region (Table 2). Therefore, all the individuals from the northern region were grouped for the following analyses. The specimens from the northern region fed predominantly on amphipods and ophiuroids, completing their trophic spectrum with brachyurous and polychaetes. As for the southern region, SC 2 specimens consumed a higher proportion of isopods and amphipods, while those corresponding to SC 3 consumed a higher proportion of cephalopods, followed by isopods (Figure 3).

Taking into account the diet variation, the feeding strategy was evaluated in general and for each size class. The relationship between P_i and %FO indicated that the feeding strategy of *B. albescens* tended towards generalist (Figure 4 A), but presented variations according to the size of the individuals. SC 1 specimens tended to specialize in amphipods and those belonging to SC 2 presented a generalist feeding strategy (Figures 4 B and C). SC 3 individuals presented a specialization towards cephalopods and isopods (Figure 4 D).

When analysing the relationship between sizes of predator and prey, we see that the size of the prey increases linearly with the size of the predator. However, the minimum prey size remained

constant, indicating that the largest *B. albescens* individuals fed on both large and small prey, while those with a smaller length fed only on small prey (Table 3; Figure 5).

The TL of *B. albescens* varied by region and between southern region size classes. Individuals captured in the northern region presented an TL of 3.78, whereas the specimens of classes SC 2 and SC 3 captured in the southern region showed an TL of 3.89 and 4.11, respectively.

The L_T -W relationship of *B. albescens* did not differ significantly between regions (ANCOVA; $F = 2.203$; $df = 1$; $P = 0.139$), presenting positive allometric growth in both (Table 4; joint Student's t-test: $t = 8.671$; $P = 0.0002$).

DISCUSSION

The study of the feeding habits of *B. albescens* in the Argentine shelf indicated that the species is a demersal-benthic predator. Its main prey is cephalopods, followed by isopods, amphipods, ophiuroids, brachyurous and polychaetes. The percentage of empty stomachs was low (16.22%),

Table 2. Non-parametric MANOVA testing differences in sex, size classes (SC) and region on the number and weight of main prey items of *Bassanago albescens*. df: degrees of freedom.

	df	Factor			
		Number		Weight	
		F	P	F	P
North-SC 1 versus North-SC 2	1	0.50	0.7715	0.46	0.8537
North-SC 1 versus South-SC 2	1	19.01	*0.0001	8.51	*0.0001
North-SC 1 versus South-SC 3	1	24.59	*0.0001	15.60	*0.0001
North-SC 2 versus South-SC 2	1	20.93	*0.0001	10.50	*0.0001
North-SC 2 versus South-SC 3	1	24.59	*0.0001	19.90	*0.0001
South-SC 2 versus South-SC 3	1	7.17	*0.0002	3.84	*0.0036

*Significant differences.

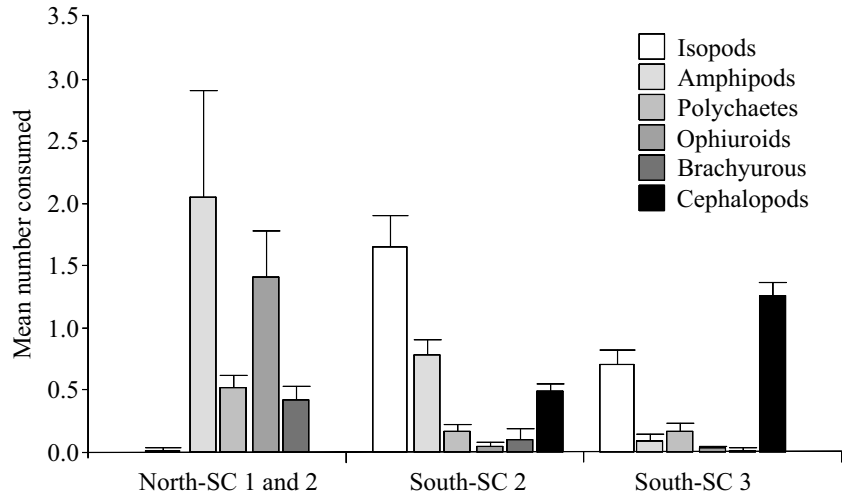


Figure 3. Mean number (\pm SD) of prey consumed by *Bassanago albescens* grouped by size class (SC) and region.

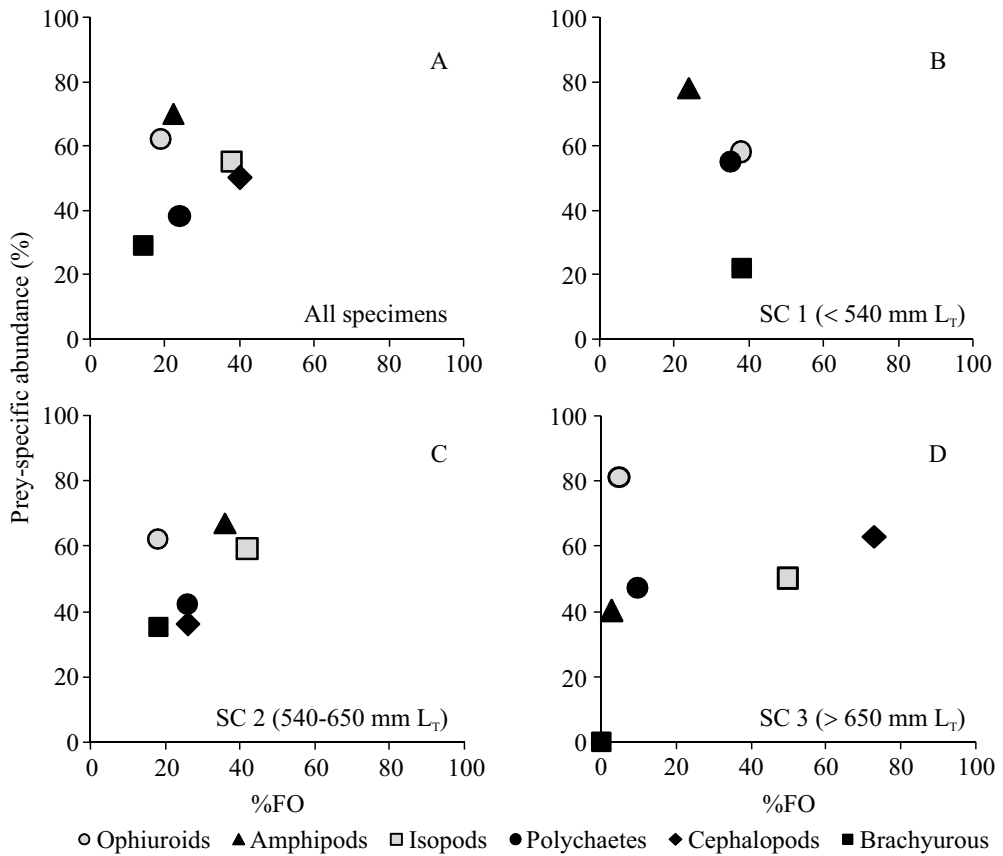


Figure 4. Relationship between percent prey-specific abundance and frequency of occurrence (%FO) of *Bassanago albescens* prey from all specimens and size classes (SC) considered.

Table 3. Predator length-prey length relationship using the total length of *Bassanago albescens* and maximum size of prey. Minimum (5% quantile regressions), mean (50% quantile regressions) and maximum (95% quantile regressions).

Regression	Maximum size of prey		P
	Intersection	Slope	
Minimum	-17.06	0.038	0.004
Mean	-59.47	0.126	< 0.001
Maximum	-361.90	0.853	< 0.001

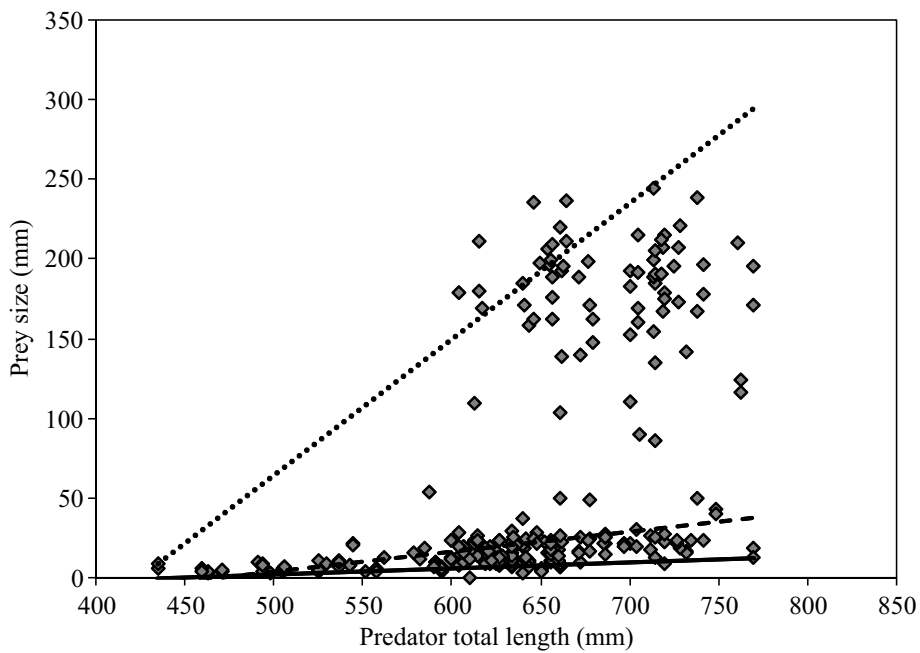


Figure 5. Relationship between *Bassanago albescens* (predator) size and prey size. Dotted, dashed, and solid lines indicate regression quartiles 5, 50, and 95%, respectively.

Table 4. Estimated parameters of length (L_T)-weight (W) relationship and determination coefficient (r^2) for *Bassanago albescens* in the Southwest Atlantic shelf. N: number of individuals, min: minimum, max: maximum, a: intersection, b: slope.

Region	N	L_T (mm)		W (g)		a	b	r^2
		Min	Max	Min	Max			
North	91	371	661	50	510	2×10^{-8}	3.654	0.910
South	131	543	772	208	905	2×10^{-7}	3.363	0.883

with similar values reported by Meyer and Smale (1991) and Figueroa (1999). On the contrary, in related species that feed mainly on teleosts such as the coastal conger eel, *Conger orbignianus*, the proportion of empty stomachs is higher (71%, Figueroa 1999). This is because the species that feed mainly on small and medium invertebrates, such as *B. albescens*, have a more frequent consumption of prey than those species with a diet based on fish (San Martín et al. 2007).

Results from diet composition in the present work are in part consistent with previous studies. In the coasts of Argentina, Figueroa (1999) observed a diet consisting of ophiuroids with the presence of crustaceans and polychaetes. In the coasts of South Africa, Meyer and Smale (1991) found sea pen cnidarians and brachyurous *Chaceon* sp. as dominant and more numerous preys over the ophiuroid *Ophiura trimeni*; many of the prey were small crustaceans that included isopods, tanaidaceans, and *Macrura* decapods. Studies carried out by Anderson (2005) indicated hagfish *Myxine capensis* and different species of mesopelagic teleosts as dominant prey; the most abundant fish in the diet were juveniles of hake *Merluccius* spp. and other conger eels; the second most important category consisted of at least six species of ophiuroids. The rest of the prey were benthic or benthopelagic species, except squid. The differences found in the results of Meyer and Smale (1991), Figueroa (1999) and Anderson (2005) with respect to the present work, could be related to the area from where the samples were obtained in each study.

The diet of *B. albescens* varied according to the study area. In the southern region, the most important prey was *I. argentinus*, which would be explained by a concentration of the South Patagonian subpopulation of this prey that coincided spatiotemporally with the southern sampling survey (Ré 2007). Furthermore, the fact that the survey is directed to the evaluation of squid could generate a bias in the composition of the diet of the SC 3 individuals. The SC 2 class,

the only class present in both areas, fed mainly on isopods in the south, and wide-distributed amphipods and ophiuroids in the north (Boschi et al. 1992; Bremec et al. 2003). Differences in the diet composition of *B. albescens* between different regions would be attributed to differences in the availability of prey species, and the size and sex of the specimens captured in each one, possibly driven by energy requirements of each sex and ontogenetic stage (Livingston 2003). To analyse the selective characteristics of this species in detail, complementary studies should be carried out in which the relative abundance of prey is determined in these two regions of the Argentine shelf.

The analysis indicated that the feeding strategy changed during growth. SC 1 individuals (all males are included here) showed a tendency to specialize in the consumption of amphipods, SC 2 individuals had a generalist feeding strategy, and SC 3 individuals (all mature females) presented a specialization towards cephalopods and isopods. Transitions from one feeding stage to another are generally related to the ontogenetic development of the species (Livingston 2003). Stuart-Smith et al. (2013) highlighted that feeding progressions are associated with ontogenetic changes regarding body morphology and correlated with movement, teething and dimensions of the mouth and guts. Figueroa (1999) mentioned that in *C. orbignianus*, smaller specimens feed on crustaceans and fish while older fish are exclusively piscivorous, with prey of demersal-benthic origin (sciaenids and flounder). On the contrary, Anderson (2005) observed in the coasts of South Africa that there was no relationship between the predator size and the type of diet of *B. albescens* and the southern conger *Gnathophis capensis*. The ontogenetic and regional differences recorded in the present study, both in the diet composition and feeding strategy, suggested that a variation in the abundance of *B. albescens* in the Southwest Atlantic has the potential to impact various levels of the trophic chain of the region.

This observation is supported by the results of the TL analysis, which varies according to the SC and the distribution range of predators.

The relationship between *B. albescens* size and the maximum prey size increased linearly, which is consistent with the maximization of energy intake, although the minimum prey size remained constant. Small prey provides low benefits, while relatively large prey has higher energy content, but is potentially dangerous to attack (Griffiths 1980). Although the probability of an individual prey being encountered by a predator may increase with the body size of that prey (Mihalitsis and Bellwood 2017), predators could also increase energy potential with ingestion as they grow larger if they continue to eat small and easy-to-catch prey (Griffiths 2020). This is why the maximum prey size is roughly proportional to the size of the predator in all habitats, but the minimum prey size slopes may differ between habitats since predators can change the type of prey they ingest to keep elevated encounter rates (Floeter and Temming 2003; Killen et al. 2007). The combination of a high frequency of encounter, due to a greater relative abundance, and a high probability of capture could explain the continued inclusion of small prey in the diet of *B. albescens*.

Blasina et al. (2018) found a sexual dimorphism in the size of *B. albescens*, where males reached smaller size than females. This conclusion is reflected in the ranges of SCs used in the present work, in which all males were included in SC 1 and located in the northern region. The feeding strategy determined for this class indicated a tendency to specialize in amphipods. The situation of SC 3 is different because is comprised of larger female individuals distributed in the southern region, and specialized in cephalopods and isopods. Energy requirements for sperm production are not the same as those required for the production of oocytes, which after fertilization results in leptocephali larvae that can exceed 200 mm (Figueroa and Ehrlich, 2006). This could explain the greater size of females and their

southern distribution to access these resources. Macchi et al. (2010) argued that large mature female hake could travel long distances to deep Patagonian waters in search of *I. argentinus*, where it is found in large concentrations. This cephalopod would be chosen for its high concentration of fatty acids.

In the Argentine shelf, *B. albescens* presents important biomass, recording catches of up to 12 t per trawl (Figueroa 1992, 1999). In the present study, it was determined that one of the most important prey items in the diet of *B. albescens* is the squid *I. argentinus*. This species is also an important trophic resource in the diet of the Argentine hake, *M. hubbsi* (Belleggia et al. 2014), which could suggest a possible trophic niche overlap that would be pertinent to assess in the future. When two or more species coexist, interspecific competitive interactions can develop by exploiting a common resource that is scarce or predated each other. These interactions can affect the abundance and distribution of species in a community (Hayden et al. 2019). Argentine hake *M. hubbsi* represents one of the main species of fish caught in Argentine trawl fisheries (Irusta et al. 2016) and, together with squid *I. argentinus*, are among the most important species in terms of exportable quota from Argentina (MAGyP 2019). Given the complexity of the interactions that can occur in a marine community, the study of individual trophic behaviour and the relationships of the organisms that comprise it become essential for the implementation of adequate management of fishing resources under an ecosystem-based approach (FAO 2018).

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REFERENCES

- AMUNDSEN PA, GABLER H, STALDVIK F. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data modification of the Costello (1990) method. *J Fish Biol.* 48: 607-614.
- AMUNDSEN PA, SÁNCHEZ-HERNÁNDEZ J. 2019. Feeding studies take guts - critical review and recommendations of methods for stomach contents analysis in fish. *J Fish Biol.* 95: 1364-1373.
- ANDERSON ME. 2005. Food habits of some deep-sea fish off South Africa's west coast. 2. Eels and spiny eels. *Afr J Mar Sci.* 27: 557-566.
- ANDERSON MJ. 2001. Permutation test for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci.* 58: 629-639.
- ARKHIPKIN AI, LAPTIKHOVSKY VV, BARTON AJ. 2015. Biology and fishery of common hake (*Merluccius hubbsi*) and southern hake (*Merluccius australis*) around the Falkland/Malvinas Islands on the Patagonian shelf of the Southwest Atlantic Ocean. In: ARANCIBIA H, editor. Hakes, biology and exploitation. Oxford: Wiley. p. 154-184.
- BASTIDA R, TORTI M. 1973. Los isópodos Serolidae en la Argentina. Clave para su reconocimiento. *Physis A.* 32 (84): 19-46.
- BELLEGGIA M, FIGUEROA DE, IRUSTA G, BREMEC C. 2014. Spatio-temporal and ontogenetic changes in the diet of the Argentine hake *Merluccius hubbsi*. *J Mar Biol Assoc UK.* 94: 1701-1710.
- BLASINA GE, IZZO L, FIGUEROA D. 2018. Sexual dimorphism and length-weight relationship of the hairy conger eel *Bassanago albescens* (Anguilliformes: Congridae). *J Ichthyol.* 58 (3): 396-400.
- BOSCHI E, FISCHBACH C, IORIO M. 1992. Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marít.* 10: 7-94.
- BRANCH TA, WATSON R, FULTON EA, JENNINGS S, MCGILLIARD RC, PABLICO GT, RICARD D, TRACEY SR. 2010. The trophic fingerprint of marine fisheries. *Nature.* 468: 431-435.
- BREMEC C, MARECOS A, SCHEJTER L, LASTA M. 2003. Guía técnica para la identificación de invertebrados epibentónicos asociados a los bancos de vieira patagónica (*Zygochlamys patagonica*) en el Mar Argentino. Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). 28 p.
- BROSE U, ARCHAMBAULT P, BARNES AD, BERSIER LF, BOY T, CANNING-CLODE J, CONTI E, DIAS M, DIGEL C, DISSANAYAKE A, et al. 2019. Predator traits determine food-web architecture across ecosystems. *Nat Ecol Evol.* 3: 919-927.
- BROWN SC, BIZZARRO JJ, CAILLIET GM, EBERT DA. 2012. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environ Biol Fish.* 95 (1): 3-20.
- BURATTI C, DÍAZ DE ASTARLOA JM, FALABELLA V, HÜNE M, IRIGOYEN A, LANDAETA M, LINARDICH C, RIESTRA C, VIEIRA J, CAMPAGNA C. 2020. Informe del Taller Regional de Evaluación del Estado de Conservación de Especies para el Mar Patagónico según criterios de la Lista Roja de UICN: Peces óseos. Foro para la Conservación del Mar Patagónico y áreas de influencia. 117 p.
- CORTÉS E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES J Mar Sci.* 56 (5): 707-717.
- CRAING CM, HALPERN BS, BECK MW, KAPPEL CV. 2009. Understanding and managing human threats to the coastal marine environment. *Ann NY Acad Sci.* 1162 (1): 39-62.

- EBERT DA, BIZZARRO JJ. 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environ Biol Fishes*. 80: 115-131.
- [FAO] FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATION. 2018. The state of world fisheries and aquaculture. Rome: FAO. 227 p.
- FERRY L, CAILLIET G. 1996. Sample size and data analysis: are we characterizing and comparing diet properly? In: MAC KINLAY D, SHEARER K, editors. *Feeding ecology and nutrition in fish*. San Francisco: American Fisheries Society. p. 71-80.
- FIGUEROA D. 1992. Distribución geográfica y estadísticas pesqueras de los congrios *Conger orbignyanus* y *Pseudoxenomystax albescens*. *Frente Marít*. 11 (A): 33-36.
- FIGUEROA D. 1999. Estudio sobre la anatomía y algunos aspectos de la biología de los congrios que habitan el Mar Argentino y adyacencias [PhD thesis]. Mar del Plata: Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. 108 p.
- FIGUEROA DE, EHRLICH M. 2006. Systematics and distribution of leptocephali in the western south Atlantic. *Bull Mar Sci*. 78 (2): 227-242.
- FLOETER J, TEMMING A. 2003. Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preference vs. prey availability. *Can J Fish Aquat Sci*. 60: 140-150.
- FROESE R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J Appl Ichthyol*. 22: 241-253.
- GARCÍA M, JAUREGUIZAR A, PROTOGINO L. 2010. Fish community ecology from Río de la Plata to shelf slope. *Lat Am J Aquat Res*. 38 (1): 81-94.
- GRIFFITHS D. 1980. Foraging costs and relative prey size. *Am Nat*. 116: 743-752.
- GRIFFITHS D. 2020. Foraging habitat determines predator-prey size relationships in marine fishes. *J Fish Biol*. 97 (4): 964-973.
- HAIMOVICI M, BRUNETTI NE, RODHOUSE PG, CSIRKE J, LETA RH. 1998. *Illex argentinus*. In: RODHOUSE PG, DAWE EG, DOR RKO, editors. *Squid recruitment dynamics. The genus Illex as a model, the commercial Illex species and influence on variability*. FAO Fish Tech Pap. 376. p. 27-58
- HAYDEN B, PALOMARES MLD, SMITH BE, POELEN JH. 2019. Biological and environmental drivers of trophic ecology in marine fishes- a global perspective. *Nat Sci Rep*. 9: 11415.
- HILL S, HINKE J, BERTRAND S, FRITZ L, FURNESS R, IANELLI J, MURPHY M, OLIVEROS-RAMOS R, PICHEGRU L, SHARP R, STILLMAN R, WRIGHT P, RATCLIFFE N. 2020. Reference points for predators will progress ecosystem-based management of fisheries. *Fish Fish*. 21 (2): 368-378.
- HOOPER D, CHAPIN F, EWEL J, HECTOR A, INCHAUSTI P, LAVOREL S, LAWTON J, LODGE D, LOREAU M, NAEEM S, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr*. 75 (1): 3-35.
- IRUSTA C, MACCHI G, LOUGE E, RODRIGUES K, D'ATRI L, VILLARINO M, SANTOS B, SIMONAZZI M. 2016. Biology and fishery of the Argentine hake (*Merluccius hubbsi*). *Rev Invest Desarr Pesq*. 28: 9-36.
- KILLEN S, BROWN J, GAMPERL A. 2007. The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. *J Anim Ecol*. 76: 814-825.
- LERCARI D, VÖGLER R, VELASCO G. 2014. Trophic models in the Southwestern Atlantic Ocean: evaluating. *Fish Cent Res Rep*. 22 (3): 75 p.
- LIVINGSTON R. 2003. *Trophic organization in coastal systems*. Tallahassee: CRC. Florida University. 388 p.
- MACCHI G, LEONARDUZZI E, DIAZ M, RENZI M, RODRIGUES K. 2013. Maternal effects on fecundity and egg quality of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish Bull*. 111 (4): 325-336.

- MACCHI G, MARTOS P, RETA R, DATO C. 2010. Offshore spawning of the Argentine hake (*Merluccius hubbsi*) Patagonian stock. *Pan Am J Aquat Sci.* 5: 22-35.
- MEYER M, SMALE M. 1991. Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 2. Benthic and epibenthic predators. *S Afr J Mar Sci.* 11: 409-442.
- MIHALITSIS M, BELLWOOD D. 2017. A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS ONE:* e0184679.
- [MAGYP] MINISTERIO DE AGRICULTURA, GANADERÍA Y PESCA. 2019. [accessed 2021 February]. <https://www.magyp.gob.ar/>.
- PIKITCH E, SANTORA C, BABCOCK E, BAKUN A, BONFIL R, CONOVER D, DAYTON P, DOUKAKIS P, FLUHARTY D, HENEMAN B, HOUE E. 2004. Ecosystem-based fishery management. *Science.* 305 (5682): 346-347.
- R CORE TEAM. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing. [accessed 2020 December]. <http://www.r-project.org/index.html>.
- RÉ ME. 2007. Cefalópodos. *Illex argentinus*. In: BOLTOVSKOY D, editor. Atlas de sensibilidad ambiental de la costa y el Mar Argentino. Ciudad Autónoma de Buenos Aires: Secretaría de Ambiente y Desarrollo Sustentable. 5 p.
- RENZI M, CASTRUCCI R. 1998. Análisis cualitativo de la fauna acompañante en la pesquería de merluza (*Merluccius hubbsi*) al norte de 41° S. *Inf Téc Int DNI-INIDEP.* 24/1998. 20 p.
- REYES P. 2007. Peces abisales de la 'Triple Unión', lugar de contacto de las placas Antártica, Sudamericana y de Nazca (archipiélago patagónico noroccidental). *Rev Biol Mar Oceanogr.* 42 (1): 37-47.
- SAN MARTÍN M, BRACCINI L, CHIARAMONTE G, PÉREZ J. 2007. Temporal and sexual effects in the feeding ecology of the marbled sand skate *Psammobatis bergi* Marini, 1932. *Mar Biol.* 151: 505-513.
- STEPHENS D, BROWN J, YDENBERG R. 2007. Foraging. Behavior and ecology. Chicago: The University of Chicago Press. 608 p.
- STUART-SMITH R, BATES A, LEFCHECK J, DUFFY J, BAKER S, THOMSON R, STUART-SMITH J, HILL N, KININMONTH S, AIROLDI L, et al. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature.* 501: 539-542.
- ZAR JH. 1999. Biostatistical Analysis, 4th ed. New York: Prentice Hall. 663 p.
- ZUUR A, IENO E, SMITH G. 2007. Analysing ecological data. New York: Springer. 672 p.

