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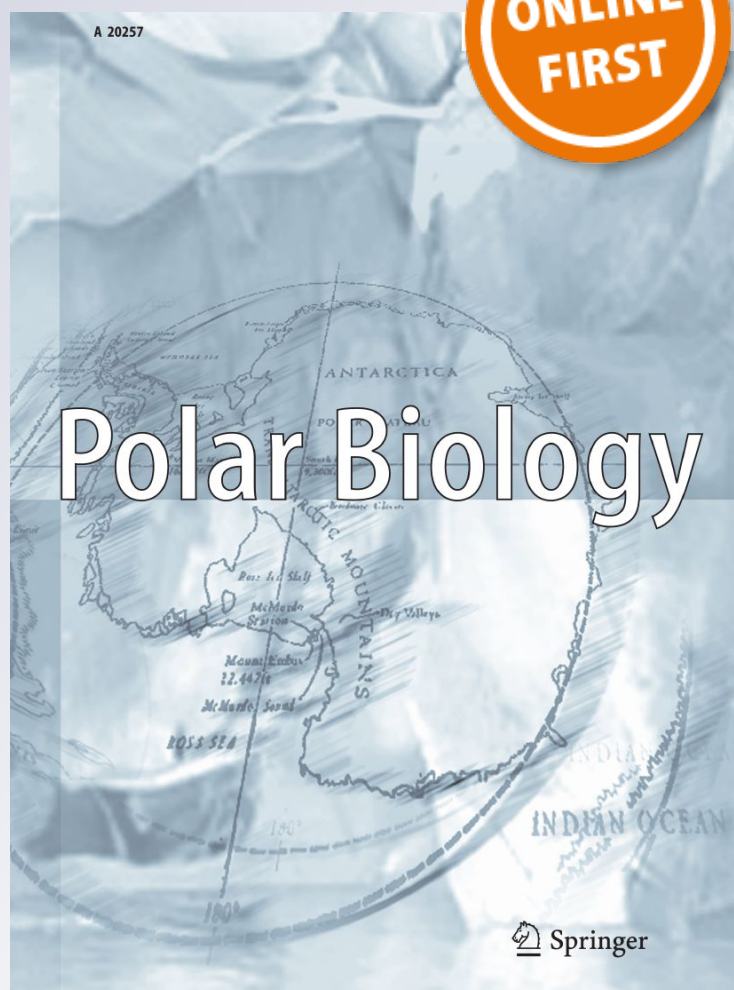
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Diet and food consumption of the Patagonian toothfish (*Dissostichus eleginoides*) in South Pacific Antarctic waters

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Abstract

The Patagonian toothfish, *Dissostichus eleginoides*, is a fish with high commercial value in all countries bordering the southern cone of Pacific and Atlantic waters. Like most fishing landings, the fishing status of the toothfish has collapsed, and thus ecosystem-based fisheries management is needed in Antarctic waters. Therefore, the stomach contents, stable isotopes, and gastric evacuation and food consumption rates were analyzed to describe the diet and infer possible prey species of individuals of *Dissostichus eleginoides* in the Antarctic Pacific Ocean. The results show that rattails and hakes were the most important prey in the diet of the Patagonian toothfish, composing 54.1 and 33.3% of the diet, respectively. The gastric evacuation rate was 1.8 g h⁻¹, and the rate of food consumption was 2.1% of the body weight, which indicates that *D. eleginoides* is a predator with frequent feeding behavior and a high predation rate in the deep waters above the continental platform.

Keywords Stable isotopes · Evacuation rate · Daily ration · Chilean sea bass

Introduction

The deep-water Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898, inhabits deep waters (700–1500 m) in the Southern Hemisphere in most of the world's oceans. In the Pacific Ocean, its range is from the southern extreme of continental Chile to around the sub-Antarctic islands, and it reaches a maximum size of 200 cm (Young et al. 1996; Lap-tikhovsky et al. 2006). This species represents an important economic resource for those countries whose economy is

centered in the south Atlantic and austral Pacific Oceans; it is frequently caught in these areas as a result of deep-water longline fishing (Young et al. 1996; Koslow et al. 2000; Norse et al. 2012; Drazen and Sutton 2017). Although the toothfish is abundant in Pacific fishing operations, there is little knowledge about its biology; there have only been efforts to study its diet relations and reproductive aspects (Movillo and Bahamonde 1971; Arrizaga et al. 1996; Muri-llo et al. 2008). Earlier reports on the diet of the genus *Dissostichus* in the Atlantic have found that it is based mainly on fish obtained from different environments (Xavier et al. 2002; Arkhipkin et al. 2003; van den Hoff 2004; Roberts et al. 2011). It is believed that in deeper waters *D. eleginoides* tends to show more opportunistic behavior, since remains of deep-water shrimp and onychoteuthid squid have been found in the stomachs of this species (Xavier et al. 2002; Arkhipkin et al. 2003; Collins et al. 2010).

The deep-water toothfish plays an important ecologic role in deep-water environments because of its position as a top predator; through predation, it may potentially regulate the size and population dynamics of its prey species (Drazen and Sutton 2017). The understanding of trophic dynamics is useful because it contributes to ecosystem analysis and the consequent inference of biologic processes and how they interact with fisheries. Trophic dynamics

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may also be used to estimate the food consumption and biomass of different species, quantify predator-prey relations and analyze the energy flow between different elements of the ecosystem, thus allowing the evaluation of the impacts on community structure, the understanding of which is then used to inform the integral management of marine ecosystems (Melnychuk et al. 2017).

Stomach content analysis is one of the methods most used in the study of trophic dynamics; however, these analyses are biased as a result of the opportunistic capacity of the predator and the different digestion rates of their prey. A very large number of stomachs must be analyzed in studies conducted in different aspects of predator's biology (e.g., ontogeny, fishing area) to obtain a general overview of the diet of the predator. On the other hand, stable isotopes, such as those of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), offer a robust approximation of the parameters of diet assimilation; they are used to establish the parameters of energy flow through trophic chains (Lopez et al. 2013). Comparative analysis of the $\delta^{15}\text{N}$ of a predator with that of a primary consumer provides a general and integrated view of the predator's trophic positions but does not give specific information on the diet of this predator (Phillips et al. 2014). However, the analysis of only isotope stability is not sufficient to determine the dietary relations of a given predator because of the high uncertainty of this type of analysis without information on the stomach content (Vinson and Budy 2010). Therefore, combining both techniques to establish the dietary patterns of the deep-water toothfish will be useful in determining its feeding behavior because the stomach contents provide detailed information on prey composition but only represent a snapshot in time, while stable isotope signatures do not truly provide details on prey species but nevertheless integrate dietary evidence on the general trophic position and carbon sources over longer time periods. Accordingly, the general objective of this study was to describe the feeding habits and food consumption rates of *Dissostichus eleginoides* in waters of the austral Pacific Ocean using stomach contents and isotope stability.

Materials and methods

A total of 998 individuals of *D. eleginoides* were obtained from commercial deep-water longline fishing boats in the range of 500–700 m between 50° and 57°S and 67°–76°W during the year 2013 (Fig. 1). On board, the total length (TL) of each fish was measured, and a piece of muscle tissue (~1 g) and the stomach was extracted; these were immediately frozen at – 20 °C for later analysis in the laboratory.

Laboratory work

Each stomach was weighed, and its contents were carefully extracted and deposited on separate plates. The prey items were identified to the lowest taxonomic level possible, weighed and counted. The prey individuals that had undergone low levels of digestion (< 3 h) were stored at – 80 °C. The tissues of *D. eleginoides* individuals and their prey were washed with Milli-Q water and reduced to 1 mg. Due to the high quantity of lipids present in toothfish tissues, they were agitated continuously for 30 min in a 2:1 chloroform:methanol solution (Hussey et al. 2012). This lipid extraction procedure was repeated three times to obtain a whitish solution. Then, the tissue samples were washed with abundant Milli-Q water and dried at 40 °C for 12 h. Once dry, the samples were ground to a fine powder in an agate mortar; 0.5 mg samples were placed into tin capsules and stored in a vacuum until the isotope analysis was conducted. Isotope composition was analyzed at the Isotope Analysis Laboratory of the Universidad Andrés Bello using a Eurovector elemental analyzer coupled to a mass spectrometer (Nu instruments) in the continuous flow mode. Stable isotopes were reported in δ notation as standard deviations (Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N for $\delta^{15}\text{N}$). Thus, $\delta^{13}\text{C}$ and $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. The precision of the analyses was $> \pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$.

Data analysis

For the stomach content analysis, we used the indices of proportion (%N), frequency of occurrence (%F) and proportion of weight (%W), which were then applied to the equation of importance of a food item or the prey-specific index of relative importance (PSIRI) (Brown et al. 2012):

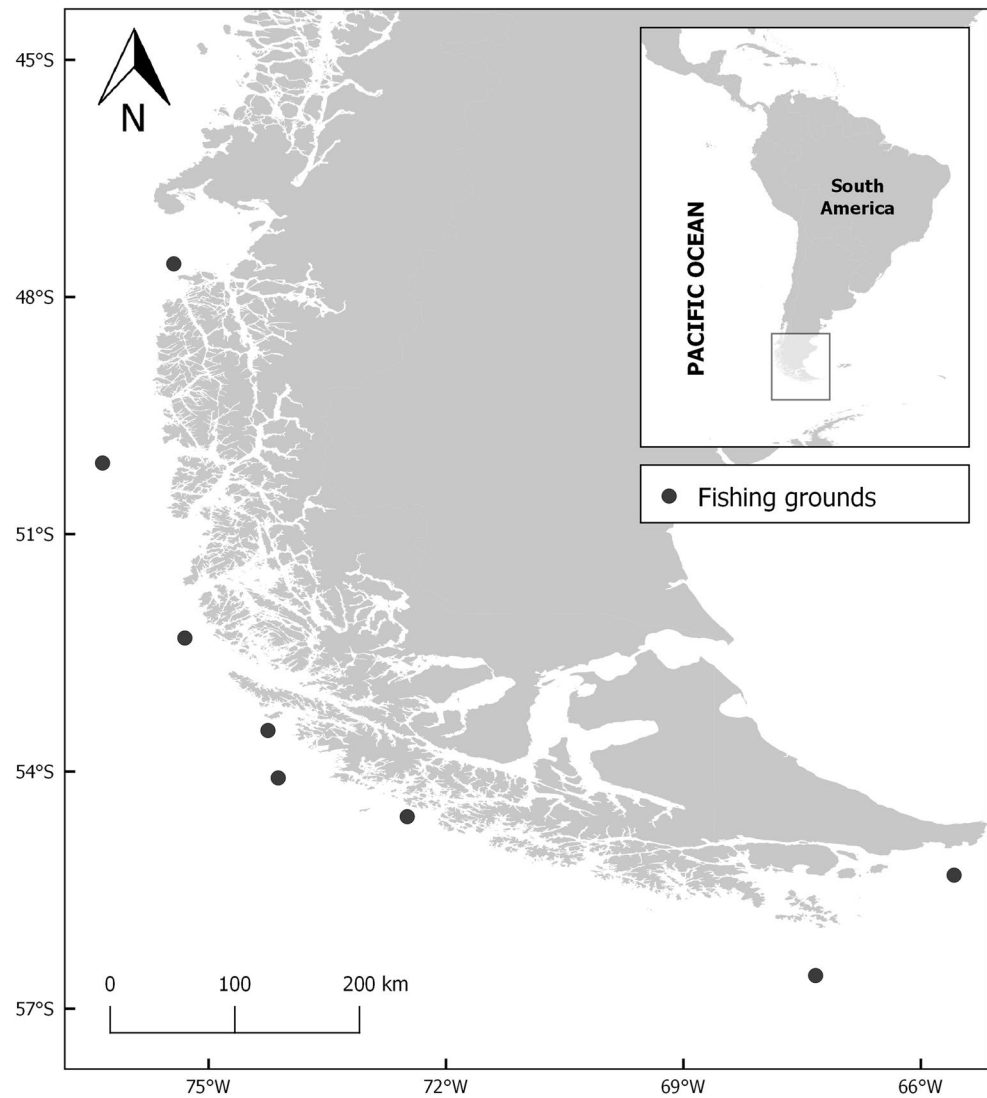
$$\text{PSIRI} = \%FO \times (\%PN + \%PW)/2$$

PSIRI is an index of the relative importance of a prey item; this was standardized to correct the IRI bias. The PSIRI includes two weight factors, PW and PN, which relate weight (PW) and number (PN) with respect to the weight and number of prey items found in stomachs. To obtain explanatory values, we calculated %PSIRI (Cortes 1997), where

$$\%PSIRI = \text{PSIRI}_i / \sum \text{PSIRI} \times 100$$

The isotope proportion data were modeled mathematically using the MixSIAR package in R (Stock and Semmens 2013), which uses mixing models based on Bayesian inference with Gaussian parsimony. The trophic enrichment factor (TEF) was calculated according to Caut et al. (2009) and Post (2002). According to Fry (2013), the prey species

Fig. 1 Fishing grounds of the Patagonian toothfish in Ocean Pacific during 2013



were grouped into greater categories; for example, the rat-tails were the species *Coelorinchus fasciatus* + *Macrourus carinatus* + *Macrourus holotrachys* (Table 1).

Food consumption

The rate of gastric evacuation (GER g h⁻¹), rate of food incorporation (RTI g h⁻¹) and daily food ration (DR g h⁻¹) were estimated using indirect stomach methods. Using a modification of the equations provided by Olson and Mullen (1986), GER, RTI and DR were calculated using the equations

$$\text{GER} = -\text{LN}(W_{\text{inf}}/W_{\text{sup}})/24 - T;$$

$$\text{RTI} = W_{\text{inf}} \times \text{GER} \times 1 - e^{-\text{GER} \times 24} / e^{-\text{GER} (24 \times T)} - e^{\text{GER} \times 24}; \text{ and}$$

$$\text{DR} = \text{GER} \times W_{\text{av}} \times 24$$

where W_{inf} is the lower weight limit of prey found in stomachs, W_{sup} is the upper limit, T is the temperature at the depth where the toothfish were captured, and W_{av} is the mean weight of the prey found in the stomachs. The body sizes of the toothfish were divided into two groups: G1 ≤ 100 cm TL and G2 > 100 cm TL. According to Quinn and Keough (2002), the data were previously tested using a Shapiro-Wilk normality test ($W=0.985$, $p=0.33$), and then the data were compared using one-way ANOVA. All statistical analyses were performed using the R statistical software (R Core Team 2017).

Results

Of the 998 stomachs analyzed, 420 (42.1%) had some type of content. The isotope values for all studied species are summarized in Table 1. The mean values of $\delta^{15}\text{N}$ and

Table 1 Stable isotope composition of Patagonian toothfish *Dissostichus eleginoides* and their prey group

Species	Group	$\delta^{15}\text{N} \text{ ‰}$	$\delta^{13}\text{C} \text{ ‰}$	n
<i>Dissostichus eleginoides</i>	Patagonian toothfish	18.30 ± 1.89	-16.88 ± 1.89	100
<i>Gonatus antarcticus</i>	Squids	10.41 ± 2.23	-18.09 ± 2.13	14
<i>Onykia ingens</i>				
<i>Todarodes filippovae</i>				
<i>Campylonotus semistriatus</i>	Shrimp	10.98 ± 2.90	-18.91 ± 2.68	6
<i>Acantheephyra carinata</i>				
<i>Macrourus carinatus</i>	Rattails	15.89 ± 1.76	-16.24 ± 1.71	8
<i>Coelorhynchus fasciatus</i>				
<i>Macrourus holotrachys</i>				
<i>Antimora rostrata</i>	Morids	13.85 ± 2.97	-16.66 ± 1.60	14
<i>Notophycis marginata</i>				
<i>Micromesistius australis</i>	Hakes	14.84 ± 2.13	-15.95 ± 1.31	9
<i>Macruronus magellanicus</i>				
<i>Merluccius australis</i>				
Total				151

$\delta^{13}\text{C}$ were similar between males and females [ANOVA, $F(1,98) = 3.26$, $p = 0.0743$ for $\delta^{15}\text{N}$ and $F(1,98) = 2.2$, $p = 0.1410$ for $\delta^{13}\text{C}$]. The two size groups of toothfish had similar $\delta^{13}\text{C}$ values [ANOVA, $F(1,98) = 3.24$, $p = 0.0752$] but were different in $\delta^{15}\text{N}$ [ANOVA, $F(1,98) = 114.5$, $p < 0.001$], thus indicating that fish of the G2 group had greater nitrogen enrichment than those of G1. Fifty-one prey species were found in the stomachs (Table 2) belonging to five food categories; rattails and toothfish had the largest mean $\delta^{15}\text{N}$ values, while squid and shrimp had $\delta^{15}\text{N}$ values

$< \sim 13\%$. The entire system showed benthic-demersal trophic dynamics for $\delta^{13}\text{C}$, which is characteristic of these deep-water environments (Fig. 2).

The integration of the results of the stomach content and isotope stability analyses indicates that the diet of the deep-water toothfish *D. eleginoides* is composed mostly of rattails ($54.1\% \pm 0.05$) (Fig. 3a). Hakes were the second most important prey ($33.3\% \pm 0.04$), followed by morids ($24.4\% \pm 0.03$), squids ($17.4\% \pm 0.03$) and shrimp ($8.7\% \pm 0.01$). The analysis by size groups (Fig. 3b) showed that rattails were the most important prey for G1 ($45.8\% \pm 0.2$) and G2 ($70.3\% \pm 0.4$). The second most important prey in the diet was morids, with 17.6 ± 0.2 for G1 and $27.8\% \pm 0.4$ for G2. The statistical analysis comparing G1 and G2 did not show a significant difference ($p = 0.5693$), indicating that the two size groups had similar diets.

The estimation of food consumption based on the 998 specimens showed a mean biomass of 15.45 kg of fish; the mean weight of the prey found in the stomachs was 70 g kg^{-1} . We estimated that the toothfish consumes 328.02 g kg^{-1} every 24 h; this represents 2.1% of their body weight, with a GER of 1.8 g h^{-1} (Table 2). We did not estimate a differential rate of consumption between sizes or sexes, since there was no significant difference between the weights of the prey found in the stomachs ($p = 0.147$).

Discussion

The results of the combination of the mixing models and %PSIRI provide a clear, integrated overview of the diet of the deep-water toothfish, since identifying the prey in the stomachs and integrating the isotope models achieved high precision in the diet inferences. Other authors have recommended integrated studies using stomach contents and isotopes to provide a better resolution of the diet (Wyatt et al. 2010; Vinson and Budy 2010). The results of this study provide new data on the diet of *D. eleginoides*, with rattails as the main prey, consistent with its demersal feeding

Table 2 Prey importance from stomachs; N number of individuals, W total prey weight, FO frequency of occurrence and PSIRI

Item	Gut contents					Stable isotopes			Food consumption
	N	W	FO	PSIRI	%PSIRI	General	G1	G2	
Morids	66	6440	50	97.7	16.6	24.4 ± 0.03	45.8 ± 0.2	70.3 ± 0.4	328.02 g kg^{-1} (2.12% Body wt)
Hakes	55	7879	53	143.4	24.3	33.3 ± 0.04	1.9 ± 0.04	0.5 ± 0.01	
Rattails	19	4981	19	262.2	44.4	54.1 ± 0.05	17.6 ± 0.2	27.8 ± 0.4	GER 1.8 g h
Shrimp	8	190	7	23.8	4	8.7 ± 0.01	17.1 ± 0.2	0.8 ± 0.02	
Squids	51	3199.8	48	62.9	10.7	10.6 ± 0.03	17.7 ± 0.2	0.6 ± 0.02	
Total	199	22,689.8	—	589.9	100	100	100	100	

Stable isotopes; G1 size group $< 100 \text{ cm TL}$, G2 size group $> 100 \text{ cm TL}$

GER gastric evacuation rate

Fig. 2 Biplot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD) for Patagonian toothfish and their trophic prey groups in the eastern South Pacific

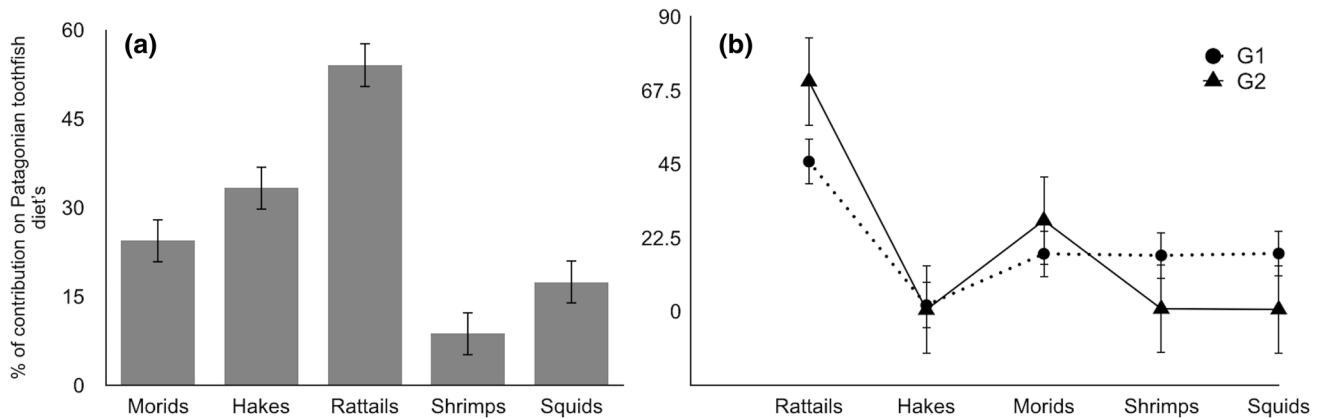
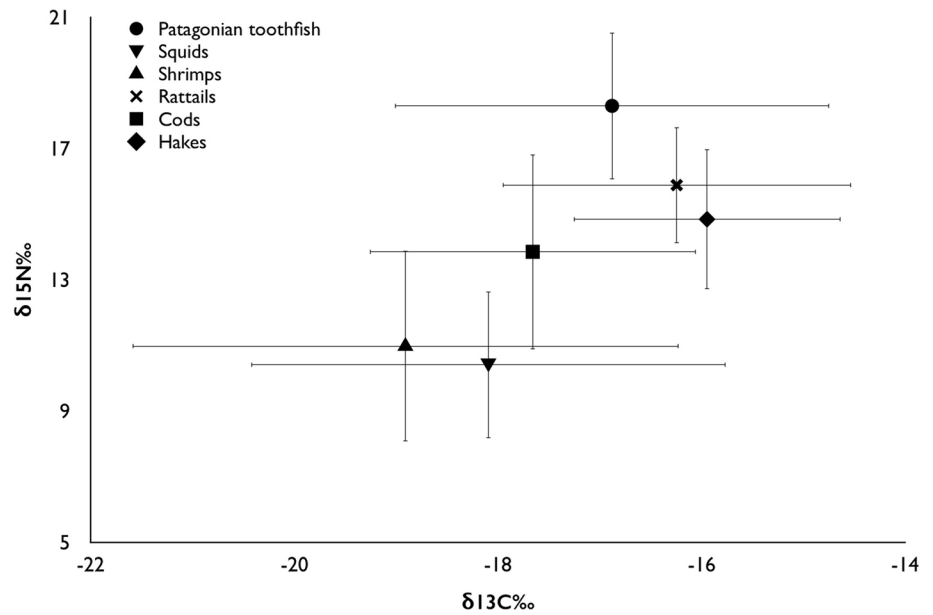


Fig. 3 Diet proportion inferred from mixing models for Patagonian toothfish in the eastern South Pacific waters. **a** General feeding. **b** Feeding by size

habit. Our results disagree with a report that indicated that the deep-water toothfish feeds mainly on ophiids, macrurids and cephalopods (Roberts et al. 2011). We did not find differences between sizes or sexes, which contrasts with the reports by Movillo and Bahamonde (1971) and Murillo et al. (2008). These differences may be an indication of a decrease in the abundance of prey; for example, in the last 10 years, catches of cephalopods have declined by 72%. A similar situation among macrurids and ophiids has been observed in South Pacific waters, with reductions of 38 and 24%, respectively (SERNAPESCA 2016). However, these dietary changes could also be attributed to the bias in studies based only on stomach content analysis; stomach contents represent a snapshot of the environmental offerings at a particular time, and this may vary among fishing areas and over time (Simenstad and Cailliet 2016). We did not find a difference

in the food consumed by the two size groups of toothfish; the study only analyzed adult individuals, and this result was thus expected. This finding appears to be usual in deep-water species, e.g., *Hoplostethus atlanticus* (Bulman and Koslow 1992); this lack of differences increases intraspecific competition in deep water, where prey is not abundant.

The available data on consumption rates for deep-water fish species indicate low rates (Drazen and Sutton 2017) compared with fishes of shallower waters (Bromley 1994; Collins et al. 2010) (2–5% of body weight). The results of this study indicate that the deep-water toothfish is an active predator with a low consumption rate in deep-water ecosystems of the austral Pacific Ocean. *D. eleginoides* showed a rate similar to that of some active deep-water predators, such as *Coelorinchus coelorhynchus*, *Etmopterus spinax* and *Galeus melastomus* (Madurell and Cartes 2005, 2006). It

seems clear that the fish that inhabit deep water have relatively low rates of feeding and digestion; however, we must be careful in evaluating the impact this predator has on its prey. Finally, this result reflects that *D. eleginoides* is a top predator with active feeding behavior and a heterogeneous diet in ecosystems of the austral Pacific Ocean, which is important for the evaluation and management of its fisheries.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All specimens used came from commercial deep-water longline fishing activities. The Chilean sea bass fisheries operate under all permissions approved by the Chilean Secretariat of Fisheries and Aquaculture (SUBPESCA).

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