ORIGINAL PAPER

The diet of the Patagonian toothfish *Dissostichus eleginoides*, a deep-sea top predator off Southwest Atlantic Ocean

Gonzalo Horacio Troccoli[1] · Eduardo Aguilar[1] · Patricia Alejandra Martínez[1] · Mauro Belleggia[1,2]

Abstract

The present study is a valuable contribution to the knowledge of feeding habits of Patagonian toothfish *Dissostichus eleginoides* in Southwestern Atlantic (53–55°S, 351 to 1073 m depth) near Burdwood Bank/Namuncurá marine-protected area, where diet has not been previously investigated. Based on stomach content analyses of 441 specimens ranging from 38 to 190 cm total length (TL), our study tested the hypotheses that diet was influenced by TL, sex, maturity stage, depth, and region, using generalized linear models and information theory selection criteria. The Patagonian toothfish fed primarily on fish (morid cod *Notophycis marginata*, myctophids, rattails *Macrourus holotrachys* and *Coelorinchus fasciatus*, notothenids *Patagonotothen ramsayi*, and hoki *Macruronus magellanicus*), followed by cephalopods (*Onykia ingens*, *Doryteuthis gahi*) and shrimps (*Acanthephyra pelagica*). One case of cannibalism was recorded. The trophic level was 4.57 (4.22 juveniles, 4.78 adults). The pelagic fish and bathypelagic shrimp were more consumed in the east region, whereas demersal fish and cephalopods were more consumed in the west one. Ontogenetic dietary changes associated with TL and maturity stage were reported: pelagic fish and shrimp *A. pelagica* had the main importance in the diet of intermediate-sized toothfish, reinforcing the hypothesis that juveniles exhibited a bento-pelagic behavior. Demersal fish were more heavily consumed by juvenile specimens, and the size of demersal fish predated by Patagonian toothfish increased according to the predator TL. Cephalopods were more consumed by adults. The preference of sexually mature specimens for cephalopods could have a positive effect on spawning and egg quality.

Keywords Feeding ecology · Trophic relationships · Nototheniidae · Burdwood bank · Trophic level · Top predator

Introduction

The family Nototheniidae is the most diverse of the Antarctic fish, consisting of 14 genera and 56 endemic species to the Southern Hemisphere (Nelson et al. 2016). The majority of notothenioids occur in Antarctica, but some species range northward to such regions such New Zealand, Macquarie

✉ Mauro Belleggia
belleggia@inidep.edu.ar

1   Instituto Nacional de Investigación Y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N°1, 7600, Mar del Plata, B7602HSA Buenos Aires, Argentina

2   Consejo Nacional de Investigaciones Científicas Y Técnicas (CONICET), Avenida Rivadavia 1917, C1033AAJ Buenos Aires, Argentina

Island, Chile, and Argentina (Nelson et al. 2016). This is the case of the genus *Dissostichus*, composed by two commercially important species: *D. eleginoides* and *D. mawsoni* (Collins et al. 2010). The Patagonian toothfish (or Chilean sea bass) *D. eleginoides* (Online Resource 1) inhabits the southern tip of South America (Argentina and Chile), sub-Antarctic Indian Ocean islands, and Pacific Macquarie Island (Cousseau and Perrota 2013). It was usually captured as a by-catch species in trawl fisheries off the South American continental shelf or by long-line fisheries targeting large adult Patagonian toothfish in deep water (Collins et al. 2010), but actually more than 95% of the catches are supported by directed trawl fisheries (Di Marco et al. 2019). In Argentina, the distribution is related with sub-Antarctic waters in the outer edge of the continental shelf, Malvinas/ Falklands Islands, and continental slope up to 35°S and 2500 m depth (Cousseau and Perrota 2013). Maturity is attained earlier by males, between 80 and 90 cm (Prenski and Almeida 2000; Laptikhovsky et al. 2006; Collins et al.

2010). The species appeared to be moderately fast growing and long-lived reaching at least 50 years (Horn 2002) and two meters in total length (Cousseau and Perrota 2013).

The diet of the Patagonian toothfish was studied in Kerguelen (Duhamel 1981) and Crozet Islands (Duhamel and Pletikosic 1983), South Georgia and Shag Rocks (Zhivov and Krivoruchko 1990; McKenna 1991; Garcia de la Rosa et al. 1997; Pilling et al. 2001; Xavier et al. 2002; Barrera-Oro et al. 2005; Collins et al. 2007), Macquarie Island (Goldsworthy et al. 2002), Malvinas/Falklands Islands (Arkhipkin et al. 2003), Argentinean continental shelf (Garcia de la Rosa et al. 1997), and central and south Chile (Murillo et al. 2008; Sallaberry-Pincheira et al. 2018). However, feeding habits of the Patagonian toothfish from the eastern end of the Argentinean continental shelf to the west surroundings of the Burdwood/Namuncurá Bank in the southern Atlantic Ocean (53–55°S) have not been investigated to date. In this context, the general objective of the present work was to examine the diet of the Patagonian toothfish by analyzing the stomach contents of specimens captured aboard the factory trawler *Centurión del Atlántico* during September and October 2017 and 2018. The specific objectives were as follows: (a) quantify the diet composition of the Patagonian toothfish in the Southwest Atlantic Ocean (53°S–55°S), (b) determine the trophic level, (c) evaluate the effect of total

length, sex, maturity, depth, and region on the diet, and (d) analyze prey–predator total length relationships.

Material and methods

Study area

The study is on the southernmost Patagonian shelf break in South America (53°–55°S, 351–1073 m depth) located in the western zone of Burdwood Bank/Namuncurá MPA (Fig. 1). The top of the Burdwood Bank/Namuncurá MPA is a large plateau of 80–150 m depth situated in the south of the Malvinas/Falklands Islands and to the east of Argentinean continental shelf break and Beagle Chanel, separated from them by deep water, 500–2000 m depth (Van Mieghem and Van Oye 1965). The Burdwood Bank/Namuncurá MPA includes a non-coastal marine-protected area created in 2013 considered an oceanic hot spot of benthic biodiversity (Schejter et al. 2016). Based on the distribution patterns of several groups of marine organisms, the study area is located within the Magellanic biogeographic province which occupies most of the southern Patagonian shelf (South of 43°S) (Perillo et al. 2006). Following the cold waters of the Malvinas Current, this assemblage of species extends its distribution

Fig. 1 Map of the study area showing the sample sites where specimens of Patagonian toothfish *Dissostichus eleginoides* were collected in each region (E: east region, W: west region) aboard the commercial fishing vessel *Centurión del Atlántico* to study the diet in the southwest Atlantic Ocean
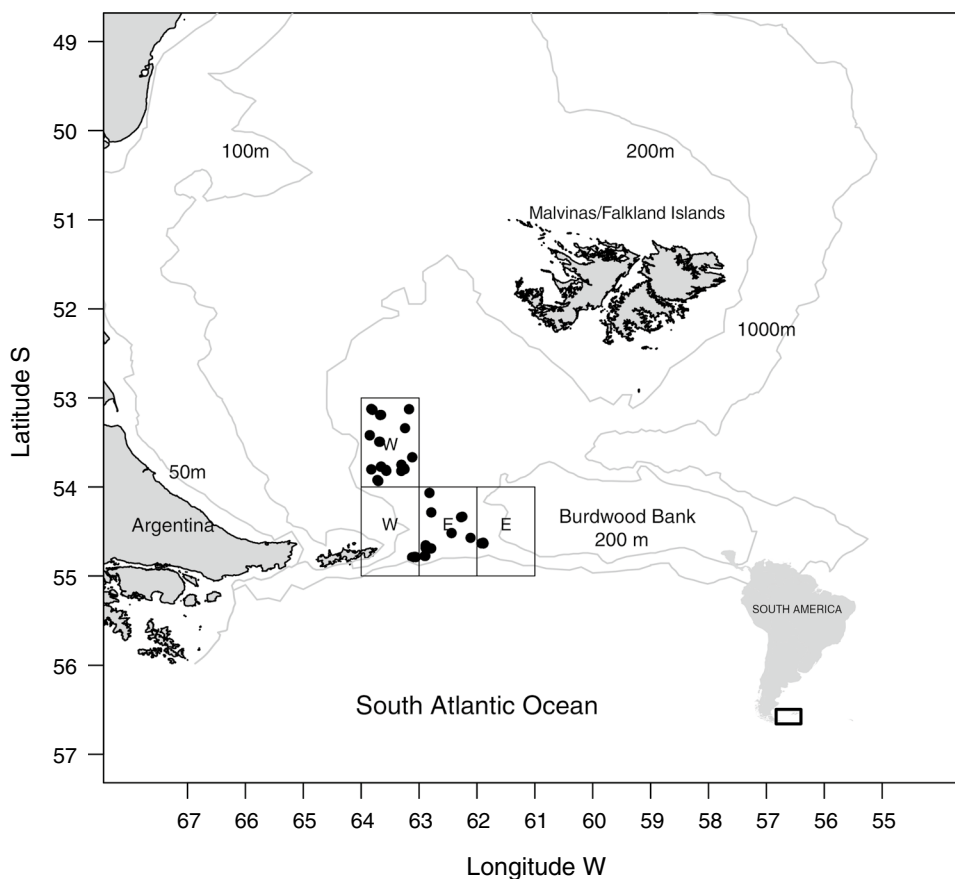
towards outer, northern, and deeper areas of the shelf and slope (Perillo et al. 2006).

Sample collection

The Patagonian toothfish *Dissostichus eleginoides* specimens were collected during September and October 2017 and 2018, between 53° and 55° S, and from 351 to 1073 m depth aboard the commercial fishing vessel *Centurión del Atlántico* (Fig. 1). Fishing was conducted in each sampling site (Fig. 1) using an Ergesund 716 bottom trawl net with rock hopper gear (200 to 150 mm mesh size in the body of the net, 120 mm mesh size in the cod end, 9 m vertical opening and 22 m horizontal aperture). The specimens captured from the Burdwood Bank/Namuncurá MPA surroundings were measured to the nearest cm (TL, total length), weighted (to the nearest 0.01 kg), and sexed. Sexual maturity (mature or immature) was determined for females according to the ovary condition and the presence of yolk eggs, whereas male maturity was determined by the size and color of testes (Macchi and Pájaro 2003). The stomachs were excised, opened, and the prey items found were identified to the lowest possible taxonomic level, counted, and weighed using an electronic scale Marel M1100 series, with an accuracy of 0.01 kg.

Statistical analysis

The parameters a and b of Weight–Length Relationship (WLR) were estimated by the least square method from logarithmically transformed data, and the degree of fit between weight and length variables was measured by the correlation coefficient (r^2) (Crawley 2005). This varied from 1, when the regression explains all of the variation, to 0, when the regression explains none of the variation (Crawley 2005). The exponent *b* provided information on fish growth: if $b = 3$ then growth is isometric, if > 3 is positive allometric growth, and < 3 is negative allometric growth (Froese et al. 2011).

The stomachs sampled were randomized 100 times, and the accumulation prey curve was plotted as a function of stomach number with their 95% confidence intervals in order to assess whether the number of stomachs analyzed was sufficient to accurately describe the diet of each group of specimens of Patagonian toothfish *D. eleginoides* considered in the dietary analysis (Ferry and Cailliet 1996; Cortés 1997).

The vacuity index (VI) was estimated as the percentage of empty stomachs in the sample (Moura et al. 2008) to evaluate the rate of feeding activity and to reveal whether the specimens ate on the site or not. The contribution of each prey to the diet of Patagonian toothfish *D. eleginoides* was evaluated by calculating the percentage frequency of occurrence (%F, the total number of stomachs in which a given prey was found expressed as percentage of the total number of stomachs with food), the percentage of number (%N, the total number of a given prey as percentage of the total number of prey found), the percentage of weight (%W, the weight of a given prey as percentage of the total weight of prey found). These three parameters were integrated into the Index of Relative Importance: $\text{IRI} = \%F \times (\%N + \%W)$ (Pinkas et al. 1971), expressed in percentage (%IRI; Cortés 1997). In addition to the traditional %IRI, the Prey-Specific Relative Importance Index (PSIRI) (Brown et al. 2012) was used to quantify the diet which is calculated according to the following formula:

$$\%\text{PSIRI} = \frac{\%F \times (\%PN + \%PW)}{2}$$

where $\%PN = \frac{\%N}{\%F}$ and $\%PW = \frac{\%W}{\%F}$ This index was recently introduced and recommended to replace %IRI for its demonstrated more balanced treatment of the relative measures of prey quantity. Moreover, the %PSIRI is additive with respect to taxonomic levels, such that the sum of %PSIRI for species will be equal to the %PSIRI of the family containing those species (Brown et al. 2012).

The trophic level (TR) was estimated for the Patagonian toothfish *D. eleginoides* following the method proposed by Cortés (1999) as follows:

$$\text{TR} = 1 + \left(\sum_{j=1}^{n} P_j \times Tr_j \right).$$

where Tr_j is the trophic level of each prey item *j* and P_j is the percentage of weight (%W) of each prey item *j* in the diet of Patagonian toothfish *D. eleginoides*, and *n* is the total number of prey items. The Tr_j were obtained from the literature (Ebert and Bizzarro 2007; Sea around us 2019). The TR was calculated for adults and juvenile specimens.

To test the hypotheses that the diet of the Patagonian toothfish *D. eleginoides* was influenced by TL, sex, maturity stage, depth, and region, we used Generalized Linear Models (GLM) and the information theory selection criteria (Venables and Ripley 2002). The number (counts) of the main prey items of the Patagonian toothfish (pelagic fish, demersal fish, cephalopods and shrimp *Acanthephyra pelagica*) were used as dependent variables. This kind of numerical data has many zeros, a variance much greater than the mean, and it exhibits a negative binomial distribution (Crawley 2005). All these issues allowed to build GLM with negative binomial error distribution and a log link (Crawley 2005). The independent variables selected to explain the consumption of the main prey were as follows: total length (TL, cm), sex, maturity stage (juvenile, adults), depth, and region (east, west). Models including a quadratic term of TL (TL^2) as independent were also fitted in order to test a curvilinear relationship between TL and the consumption of any prey. Models with

all possible combination of two independent variables were constructed. A theoretical model without an independent variable was also fitted to test the hypothesis that none of the independent variables selected in this work influenced the consumption of any prey (Lucifora et al. 2009). Akaike's information criterion (AIC) and Akaike's weight (w) were used to compare and rank a total of the 21 competing models and to estimate which of them best fit the data (Franklin et al. 2001; Johnson and Omland 2004). The model with the lowest AIC was selected and plotted (Franklin et al. 2001; Johnson and Omland 2004). All analyses were performed using R program 3.3.1, 64 bits (https://www.R-project.org).

The relationships between the total length of predator and prey were evaluated by analyzing the presence of more than a single slope across the whole distribution of the response variable by fitting quantile regression models (Koenker and Bassett 1978; Cade and Noon 2003). The total length of pelagic and demersal fish consumed was used to test the

hypothesis that prey size increased in accordance with the size of the Patagonian toothfish *D. eleginoides*. Regressions of 10, 50, and 90% quantiles were fitted to test the minimum, medium, and maximum increase of prey size consumed with increasing TL of the predator, respectively (Cade and Noon 2003). The analyses were performed with quantreg R package (Koenker 2007).

Results

From a total of 441 specimens sampled, 318 (VI: 27.89%) ranging from 38 to 190 cm TL (Fig. 2a) contained food in their stomachs. The VI was 27.69% and 28.26% in the west and east region, respectively. The WLR indicated that the Patagonian toothfish had isometric growth ($b = 3$) (Fig. 2b). The sample sizes were sufficient to describe diets in all groups considered and to make statistical analyses as

Fig. 2 **a** Total length frequency distribution of the Patagonian toothfish *Dissostichus eleginoides* with food in the stomachs, collected to study the diet in the southwest Atlantic Ocean, **b** Relationship of weight with total length (TL) of the Patagonian toothfish *D. eleginoides* showing exponential and isometric growth
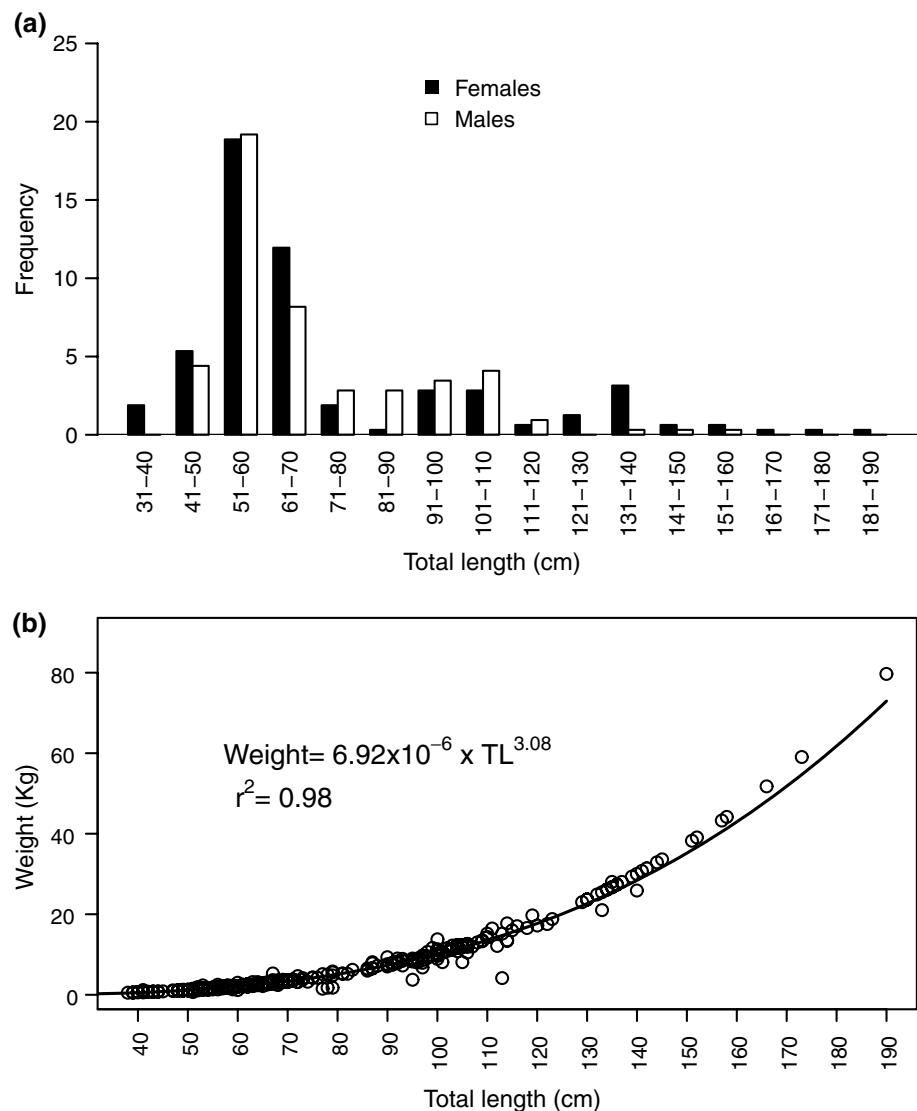
the cumulative prey curves reached an asymptote (Online Resource 2). The Patagonian toothfish *D. eleginoides* fed mainly on fish, followed by cephalopods and other invertebrates (Table 1). Among fish, the most important were the morid cod *Notophycis marginata*, myctophids, large rattail *Macrourus holotrachys*, notothenids *Patagonotothen ramsayi*, hoki *Macruronus magellanicus*, and small rattail *Coelorinchus fasciatus* (Table 1). One case of cannibalism was registered in one Patagonian toothfish of 190 cm and 79.66 kg that consumed another specimen of 107 cm and 11.16 kg. The cephalopods were mainly represented by the squid *Onykia ingens* and the small-sized squid *Doryteuthis gahi* (Table 1). The most important within the other invertebrate group was the bathypelagic shrimp *Acanthephyra pelagica* (Table 1). The trophic level (TR) of the Patagonian toothfish *D. eleginoides* was 4.57. Juveniles specimens showed a TR of 4.22, whereas adults TR was 4.78.

The pelagic fish were the main prey of intermediate size predators in the east region (Fig. 3a, Table 2), whereas demersal fish were more heavily consumed in the west region and by juvenile specimens (Fig. 3b, Table 2). The cephalopods were more consumed by adult specimens in the west region (Fig. 3c, Table 2). The bathypelagic shrimp *Acanthephyra pelagica* was more important in the diet of intermediate size Patagonian toothfish, and it was more important in the east region (Fig. 3d, Table 2).

The minimum, medium, and maximum values of the total length of the pelagic fish consumed by the Patagonian toothfish *D. eleginoides* were independent of the TL of the predator (slope of the quantil 10% = 0.00; $p = 1$; slope of the quantil 50% = 0.02; $p = 0.58$; slope of the quantil 90% = −0.03; $p = 0.38$; Fig. 4a). On the other hand, minimum, medium, and maximum values of the total length of the demersal fish consumed by the Patagonian toothfish *D. eleginoides* were positively correlated with the TL of the predator (slope of the quantil 10% = 0.16; $p < 0,001$; slope of the quantil 50% = 0.37; $p < 0,001$; slope of the quantil 90% = 0.60; $p < 0,001$; Fig. 4b).

Discussion

The Patagonian toothfish *Dissostichus eleginoides* in the austral shelf break off the Southern Atlantic Ocean (Burdwood Bank/Namuncurá MPA surroundings, 53–55°S) foraged predominantly on pelagic and demersal fish. The diet also included cephalopods and other invertebrates such as shrimps. These results are in accordance with those reported for Patagonian toothfish in Kerguelen (Duhamel, 1981), central and southern Chile (Murillo et al. 2008; Sallaberry-Pincheira et al. 2018), Malvinas/Falkland Islands (Arkhipkin et al. 2003), Argentine continental shelf (Garcia de la Rosa et al. 1997), and in South Georgia and Shag Rocks (McKenna 1991; Barrera-Oro et al. 2005; Collins et al. 2007). However, other studies differed and showed higher consumption of crustaceans in Crozet Islands (Duhamel and

Table 1 Diet composition of the Patagonian toothfish *Dissostichus eleginoides* off Southwest Atlantic Ocean expressed by the percentage frequency of occurrence (%F), the percentage of number (%N), percentage of weight (%W), the percentage of Index of Relative Importance (%IRI), and the percentage of the Prey-Specific Relative Importance Index (%PSIRI)

Prey	%F	%N	%W	%IRI	%PSIRI
Fish	91.19	82.97	93.02	98.48	87.99
Notophycis marginata	30.82	27.51	8.32	47.90	17.91
Myctophidae	19.49	21.40	7.45	24.40	14.42
Macrourus holotrachys	5.97	5.68	29.39	9.09	17.53
Fish not identified	14.15	10.26	3.10	8.20	6.68
Patagonotothen ramsayi	6.92	5.24	4.26	2.85	4.75
Macruronus magellanicus	5.69	4.15	7.00	2.75	5.58
Coelorinchus fasciatus	3.77	2.62	1.73	0.71	2.18
Salilota australis	2.52	1.96	3.02	0.54	2.49
Dissostichus eleginoides	0.31	0.22	26.14	0.36	13.18
Genypterus blacodes	2.52	1.75	1.17	0.32	1.46
Micromesistius australis	1.57	1.53	1.03	0.17	1.28
Sprattus fueguensis	0.63	0.44	0.09	0.01	0.26
Idiacanthus atlanticus	0.31	0.22	0.30	0.01	0.26
Cephalopods	11.95	12.01	6.35	1.35	9.18
Onykia ingens	5.66	6.99	4.38	2.79	5.68
Doryteuthis gahi	5.97	4.58	1.83	1.66	3.21
Octopus spp.	0.63	0.44	0.14	0.02	0.29
Other invertebrates	5.03	5.02	0.63	0.17	2.83
Shrimp—*Acanthephyra pelagica*	4.40	4.585	0.61	0.99	2.60
Polychaet—*Idanthyrsus macropaleus*	0.31	0.437	0.02	0.01	0.23

Fig. 3 Generalized linear models (GLMs) fitted for the number of the main prey of the Patagonian toothfish *Dissostichus eleginoides* off Southwest Atlantic Ocean, selected using Akaike's information criterion, which explain changes in the consumption of **a** pelagic fish, **b** demersal fish, **c** cephalopods, and **d** shrimp *Acanthephyra pelagica*. The GLMs have negative binomial error distribution and a log link
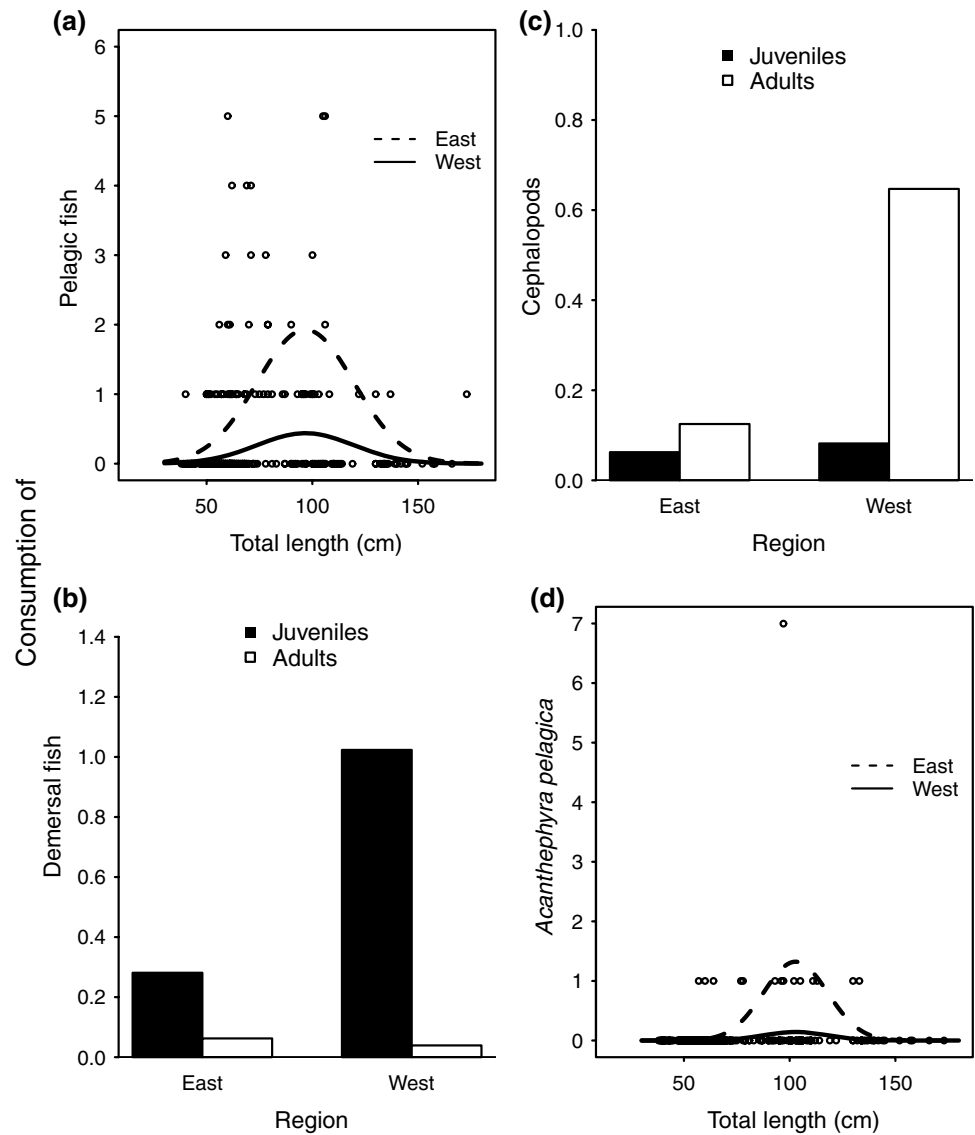
Table 2 Best generalized linear models that explain the consumption of the most important prey of the Patagonian toothfish *Dissostichus eleginoides* off Southwest Atlantic Ocean

Prey	Intercept	Parameters	w	AIC
Pelagic fish	− 8.25(1.54)	$0.18(0.04)$ TL $- 9.5 \times 10^{-4}(1.9 \times 10^{-4})$ TL^2—$1.48(0.26)$ West	0.98	402.77
Demersal fish	− 1.19(0.22)	$- 2.73(0.50)$ Adults $+ 1.21(0.24)$ West	0.99	535.92
Cephalopods	− 3.42(0.45)	$1.81(0.34)$ Adults $+ 1.05(0.43)$ West	0.59	276.92
Acanthephyra pelagica	− 22.61(5.61)	$0.44 (0.12)$ TL $- 2.2 \times 10^{-3}(6 \times 10^{-4})$ TL^2 $- 2.22(0.66)$ West	0.32	117.08

The intercept and coefficients with the standard errors in parentheses (s.e) for the variables, the Akaike's weights (*w*), and the Akaike information criterion (AIC) are presented for each model. TL, total length (cm); west, west region

Pletikosic 1983) and in South Georgia and Shag Rocks (Zhivov and Krivoruchko 1990; Garcia de la Rosa et al. 1997; Pilling et al. 2001; Xavier et al. 2002) and higher proportion of cephalopods in Macquarie Islands (Goldsworthy et al. 2002). These comparisons suggested an opportunistic

or adaptive foraging behavior for the Patagonian toothfish *D. eleginoides* with diets influenced by the distinct prey availability in each region. Only one case of cannibalism was previously reported, where the remnants of a juvenile Patagonian toothfish were found in the stomach of one

Fig. 4 Quantile regressions of the total length of **a** pelagic fish and **b** demersal fish, with the total length of the Patagonian toothfish *Dissostichus eleginoides* off Southwest Atlantic Ocean. The dotted, solid, and dashed lines represent 10%, 50%, and 90% quantile regressions, respectively
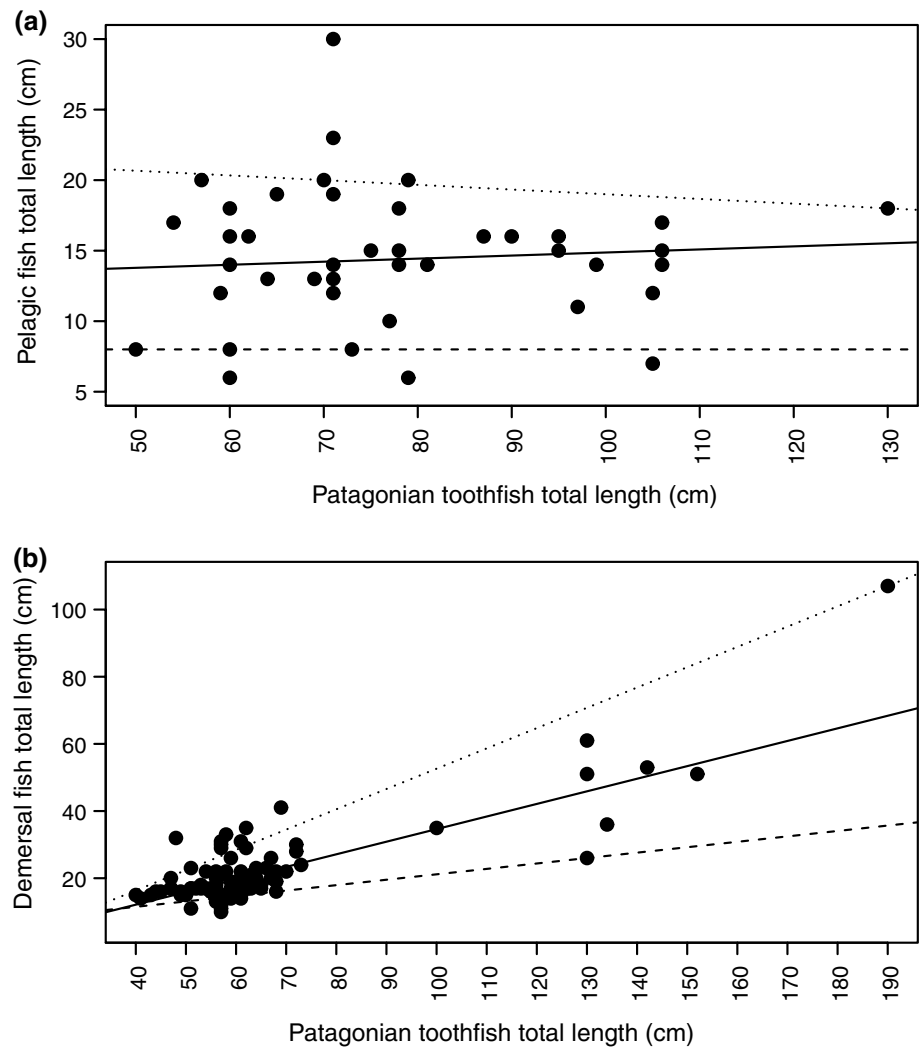
animal (Arkhipkin et al. 2003). Here, cannibalism accounted 26.14% in weight, as one Patagonian toothfish of 190 cm and 79.66 kg consumed another of 107 cm and 11.16 kg.

The trophic level of Patagonian toothfish indicated that it was tertiary consumer, or top predator (TR > 4), throughout the analyzed ontogeny. In addition, the trophic level of Patagonian toothfish increased with ontogeny from 4.22 in juveniles to 4.78 in adults. This was in accordance with previous studies which indicated that for most marine species, TR increased with length of the predator (Stergiou and Karpouzi 2002; Ebert and Bizzarro 2007). Given the different functional trophic groups identified in the Mediterranean Sea, the Patagonian toothfish could be classified as carnivorous with preference for fish and cephalopods (Stergiou and Karpouzi 2002). Since exploited marine ecosystems are characterized by a decline of the mean TR in landings (Pauly et al. 1998), the monitoring of the TR, the food web structure, and fisheries landings will be the most appropriate future management. It was already demonstrated the fishing down the food webs phenomenon by fisheries operating on

the other species of the genus, the Antarctic toothfish *D. mawsoni*, along the Antarctic continental margin (Ainley and Pauly 2014).

The present work reported regional variations in the diet of the Patagonian toothfish: the pelagic fish and bathypelagic shrimp *Acanthephyra pelagica* were more consumed in the east region, whereas demersal fish and cephalopods were more consumed in the west one. These regional differences could be related to distinct differences in the prey availability between the two regions. The myctophids and bathypelagic shrimp *A. pelagic* exhibited a meso and bathypelagic distribution, reaching depths of about 2000 and 3500 m, respectively (Boschi et al. 1992; Catul et al. 2011); thus, they were more abundant in the eastern region and more consumed by the Patagonian toothfish there. Conversely, demersal fish and cephalopods are abundant species at the continental shelf end and shelf break (Brunetti and Ivanovic 1992; Brunetti et al. 1998; Cousseau and Perrota 2013) and more heavily consumed by Patagonian toothfish in the west region. Differences in the specific composition of the

toothfish diet between Shag Rocks and South Georgia have been previously reported (Barrera-Oro et al. 2005; Collins et al. 2007). This pattern suggested a flexible and adaptive feeding behavior of the Patagonian toothfish that fed upon pelagic fish and crustaceans in a region, changing to feed on cephalopods and demersal fish where this type of prey increases its availability.

Ontogenetic dietary changes associated with total length and maturity stage of the Patagonian toothfish were confirmed. Pelagic fish and the bathypelagic shrimp *Acanthephyra pelagica* had the greatest importance in the diet of intermediate-sized Patagonian toothfish. Demersal fish were more heavily consumed by juveniles, and cephalopods were more consumed by adult specimens. In South Georgia Collins et al. (2007) reported that diet changed with size, with an increase in myctophid fish and krill as toothfish grow and disperse. The ontogenetic diet shifts appeared to be a universal phenomenon in fish as a consequence of the morphological changes that accompany growth (increasing mouth dimensions and stomach capacity, improvement in their locomotion ability, etc.) and allow to capture a broader range of prey size and types (Wootton 1990). Moreover, the preference of sexually mature specimens for cephalopods could have a positive effect on spawning and egg quality, since high concentration of polyunsaturated fatty acids were detected in this mollusk, mainly docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) (Watanabe et al. 1984; de Moreno et al. 1998; Salman et al. 2007). This hypothesis has been previously proposed for the common hake *Merluccius hubbsi*, and suggested that the most marine bony fish diet switch to cephalopods registered is driven by these essential lipids for spawn and for the survival and growth of eggs and larvae, rather than functional limitations e.g., gape size (Macchi et al. 2013).

There was a positive relationship between the total length of the demersal fish consumed by the Patagonian toothfish *D. eleginoides* and the predator TL. The size of prey also increased with fish size in South Georgia and Shag Rocks, with a greater range of prey sizes consumed by larger fish (Collins et al. 2007). However, the total length of the pelagic fish consumed in the present work was independent of the TL of the predator. The lack of a positive relationship between predator and prey may be due to the morphological trait (size range) of each ecological prey type or to the biased range of Patagonian toothfish that fed on pelagic fish. For example, pelagic fish herein consumed represented narrow TL range (6–30 cm) in comparison with demersal fish (10–107 cm). In addition, the demersal fish were predated throughout ontogeny. On the other hand, the pelagic fish were heavily consumed by intermediate-sized Patagonian toothfish. These results reinforce the hypothesis that juveniles exhibited a bento-pelagic behavior, utilizing lipid deposits and reducing skeletal mineralization to attain near-neutral buoyancy in the absence of a swim bladder (Collins et al. 2010; Nelson et al. 2016). The Patagonian toothfish migrate into deeper water as they grow, and adults live in deep water (1000-2000 m) where they feed, moving only slightly shallower during the spawning season in July–August (Collins et al. 2010).

Compliance with ethical standards

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, in accordance with the ethical standards of the institution at which the study was conducted. This study was carried out with permission from the INIDEP (National Institute for Fisheries Research and Development) and the fishing companies, following the Argentinean regulations regarding health, environment, and safety.

References

Ainley DG, Pauly D (2014) Fishing down the food web of the Antarctic continental shelf and slope. Polar Rec 50:92–107. https://doi.org/10.1017/S0032247412000757

Arkhipkin A, Brickle P, Laptikhovsky V (2003) Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. J Fish Biol 63:428–441. https://doi.org/10.1046/j.1095-8649.2003.00164.x

Barrera-Oro ER, Casaux RJ, Marschoff ER (2005) Dietary composition of juvenile *Dissostichus eleginoides* (Pisces, Nototheniidae) around Shag Rocks and South Georgia, Antarctica. Polar Biol 28:637–641. https://doi.org/10.1007/s00300-005-0723-8

Boschi EE, Fischbach CE, Iorio MI (1992) Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. Frente Marít A 10:7–94

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 95:3–20. https://doi.org/10.1007/s10641-011-9959-z

Brunetti NE, Ivanovic ML (1992) Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. ICES J Mar Sci 49:175–183. https://doi.org/10.1093/icesjms/49.2.175

Brunetti NE, Ivanovic M, Rossi G, Elena B, Pineda S (1998) Fishery biology and life history of Illex argentinus. In: Okutani T (ed) Contributed paper to International Symposium on Large Pelagic Squid. Marine Fishery Resources Research Center, Tokyo, Japan, pp 217–232

Cade B, Noon B (2003) A Gentle Introduction to Quantile Regression for Ecologists. Front Ecol Env 1:412–420. https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2

Catul V, Gauns M, Karuppasamy PK (2011) A review on mesopelagic fishes belonging to family Myctophidae. Rev Fish Biol Fish 21:339–354. https://doi.org/10.1007/s11160-010-9176-4

Collins MA, Brickle P, Brown J, Belchier M (2010) The Patagonian toothfish: biology, ecology and fishery. Adv Mar Biol 58:227–300. https://doi.org/10.1016/B978-0-12-381015-1.00004-6

Collins MA, Ross KA, Belchier M, Reid K (2007) Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). Mar Biol 152:135–147. https://doi.org/10.1007/s00227-007-0667-3

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54:726–738. https://doi.org/10.1139/f96-316

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717. https://doi.org/10.1006/jmsc.1999.0489

Cousseau MB, Perrota RG (2013) Peces Marinos de Argentina: Biología, Distribución y Pesca, 4th edn. INIDEP, Mar del Plata

Crawley MJ (2005) Statistics: an introduction using R. Wiley, Chichester

de Moreno JEA, Moreno VJ, Ricci L, Roldan M, Gerpe M (1998) Variations in the biochemical composition of the squid *Illex argentinus* from the South Atlantic Ocean. Comp Biochem Physiol B 119:631–637. https://doi.org/10.1016/S0305-0491(98)00038-8

Di Marco E, Martinez P, Wöhler O, Troccoli GH (2019) Evaluación de abundancia y estado de explotación de la Merluza negra (*Dissostichus eleginoides*) del Atlántico Sudoccidental durante el período 1980–2018. Captura biológicamente aceptable para el año 2020. Informe Técnico Oficial 43:1–33

Duhamel G (1981) Characteristiques biologiques des principals especes de poissons du plateau continental des Iles Kerguelen. Cybium 5:19–32

Duhamel G, Pletikosic M (1983) Donnes biologiques sur les Notothenidae des Iles Crozet. Cybium 7:43–57

Ebert DA, Bizzarro JJ (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). Environ Biol Fish 80:221–237. https://doi.org/10.1007/s10641-007-9227-4

Ferry LA, Cailliet GM (1996) Sample size and data analysis: are we characterizing and comparing diet properly? In: MacKinlay D, Shearer K (eds) Feeding Ecology and Nutrition in Fish: Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish, International Congress on the Biology of Fishes, American Fisheries Society, San Francisco, pp 71–80

Franklin AB, Shenk TM, Anderson DR, Burnham KP (2001) Statistical model selection: the alternative to null hypothesis testing. In: Shenk TM, Franklin AB (eds) Modeling In Natural Resource Management: Development, Interpretation, and Application. Island Press Washington DC, pp 75–90

Froese R, Tsikliras AC, Stergiou KI (2011) Editorial note on weight–length relations of fishes. Acta Ichthyol Piscat 41:261–263. https://doi.org/10.3750/aip2011.41.4.01

Garcia de la Rosa SB, Sanchez F, Figueroa D (1997) Comparative feeding ecology of Patagonian toothfish (*Dissostichus eleginoides*) in the South-western Atlantic. CCAMLR Sci 4:105–124

Goldsworthy SD, Lewis M, Williams R, He X, Young JW, Van Den Hoff J (2002) Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific Ocean. Mar Freshwater Res 53:49–57. https://doi.org/10.1071/MF00075

Horn PL (2002) Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea. Antarctica Fish Res 56:275–287. https://doi.org/10.1016/S0165-7836(01)00325-3

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108. https://doi.org/10.1016/j.tree.2003.10.013

Koenker R, Bassett G (1978) Regression quantiles. Econometrica 46:33–50. https://doi.org/10.2307/1913643

Koenker R (2007) Package 'quantreg', Quantile Regression, R package version 5.38. https://cran.r-project.org/web/packages/quantreg/quantreg.pdf/. Accessed 31 January 2018

Laptikhovsky V, Arkhipkin A, Brickle P (2006) Distribution and reproduction of the Patagonian toothfish *Dissostichus eleginoides* Smitt around the Falkland Islands. J Fish Biol 68:849–861. https://doi.org/10.1111/j.0022-1112.2006.00973.x

Lucifora LO, Garcia VB, Escalante AH (2009) How can the feeding habits of the sand tiger shark influence the success of conservation programs? Anim Conserv 12:291–301. https://doi.org/10.1111/j.1469-1795.2009.00247.x

Macchi GJ, Leonarduzzi E, Diaz MV, Renzi M, Rodrigues KA (2013) Maternal effects on the fecundity and egg quality of the Patagonian stock of the Argentine Hake (*Merluccius hubbsi*). Fish Bull 111:325–336. https://doi.org/10.7755/FB.111.4.3

Macchi GJ, Pájaro M (2003) Comparative reproductive biology of some commercial marine fishes from Argentina. Fisken og Havet 12:69–77

McKenna JE (1991) Trophic relationships within the Antarctic demersal fish community of South Georgia Island. Fish Bull 89:643–654

Moura T, Figueiredo I, Farias I, Serra-Pereira B, Neves A, Gordo L, Borges MF (2008) Ontogenetic dietary shift and feeding strategy of *Raja undulata* Lacepède, 1802 (Chondrichthyes: Rajidae) in the Portuguese continental shelf. Sci Mar 72:311–318 https://doi.org/10.3989/scimar.2008.72n2311

Murillo C, Oyarzun C, Fernandez J (2008) Latitudinal and temporal variation in the diet of *Dissostichus eleginoides* Smitt, 1898 (Perciformes: Notothenidaein) deep environments of the south and center coast of Chile. Gayana 72:94–101. https://doi.org/10.4067/S0717-65382008000100011

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world. John Wiley & Sons, Hoboken, NJ

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. Science 279:860–863. https://doi.org/10.1126/science.279.5352.860

Perillo G, Piccolo M, Marcovecchio J (2006) Coastal Oceanography of the Western South Atlantic continental shelf (33°S to 55°S). In: Robinson AA, Brink K (eds) The Sea. Harvard University Press Cambridge, Massachusetts, The Global Coastal Ocean. Regional studies and Syntheses, pp 295–327

Pilling GM, Purves MG, Daw TM, Agnew DA, Xavier JC (2001) The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). J Fish Biol 59:1370–1384. https://doi.org/10.1111/j.1095-8649.2001.tb00198.x

Pinkas L, Oliphant MS, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. Fish Bull 152:1–150 https://content.cdlib.org/view?docId=kt8290062w&brand=oac4

Prenski LB, Almeida S (2000) Some biological aspect relevant to Patagonian toothfish (*Dissostichus eleginoides*) exploitation in the Argentine exclusive economic zone and adjacent ocean sector. Frente Marítimo 18:103–124

Sallaberry-Pincheira P, Galvez P, Molina-Burgos BE, Fernandoy F, Melendez R, Klarian SA (2018) Diet and food consumption of the Patagonian toothfish (*Dissostichus eleginoides*) in South Pacific Antarctic waters. Polar Biol 41:2379–2385. https://doi.org/10.1007/s00300-018-2360-z

Salman Y, Salman A, Ozkizilcik S (2007) The Fatty Acid Profile of the Marine Cephalopod *Loligo vulgaris*. Isr J Aquac-Bamid 59:133–136 https://hdl.handle.net/10524/19226

Schejter L, Rimondino C, Chiesa I, Diaz de Astarloa JM, Doti B, Elias R, Escolar M, Genzano G, López-Gappa J, Tatián M, Zelaya D, Cristobo J, Perez C, Cordeiro R, Bremec C (2016) Namuncurá Marine Protected Area: an oceanic hot spot of benthic biodiversity at Burdwood Bank, Argentina. Polar Biol 39:2373–2386. https://doi.org/10.1007/s00300-016-1913-2

Sea Around Us (2019) A global database on marine fisheries and ecosystems. https://www.seaaroundus.org. Accessed 1 February 2019

Stergiou KI, Karpouzi VS (2002) Feeding habits and trophic levels of Mediterranean fish. Rev Fish Biol Fish 11:217–254. https://doi.org/10.1023/A:1020556722822

Van Mieghem J, Van Oye P (1965) Biogeography and Ecology in Antarctica. W Junk Publishers, The Hague, Dr

Venables WN, Ripley BD (2002) Modern applied statistics with S-Plus. Springer, New York

Watanabe T, Arakawa T, Kitajima C, Fujita S (1984) Effect of nutritional quality of broodstock diets on reproduction of Red Sea bream. Bull Jap Soc Sci Fish 50:495–501. https://doi.org/10.2331/suisan.50.495

Wootton RJ (1990) Ecology of teleost fishes. Chapman & Hall, London

Xavier JC, Rodhouse PG, Purves MG, Daw TM, Arata J, Pilling GM (2002) Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. Polar Biol 25:323–330. https://doi.org/10.1007/s00300-001-0343-x

Zhivov VV, Krivoruchko VM (1990) On the biology of the Patagonian toothfish, *Dissostichus eleginoides*, of the Antarctic part of the Atlantic. J Ichthyol 30:142–146