ORIGINAL RESEARCH

Trophic ecology of Patagonian flounder *Paralichthys patagonicus* (Jordan, 1889) in the Argentine-Uruguayan Coastal Ecosystem

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ABSTRACT. Food habits and diet composition of Patagonian flounder *Paralichthys patagonicus* (Jordan, 1889) were studied on the basis of stomach content analyses from 828 specimens (512 females, 304 males, 12 unsexed) collected during 16 commercial cruises between February 2009 and April 2010 in the Argentine-Uruguayan Coastal Ecosystem (34° S-41° S). A total of 272 stomachs (32.9%) contained food (184 females and 84 males), among which 20 prey taxa were identified. The most important prey category was pelagic fish, primarily Argentine anchovy (*Engraulis anchoita*), followed by rough scad (*Trachurus lathami*). Evidence showed that females consumed a higher total wet weight of prey compared to males. Results also suggested a specialised diet over *E. anchoita*, across all sex and size groups. The estimated trophic level for the population of *P. patagonicus* was 4.16. This study suggests that *P. patagonicus* is a tertiary piscivorous consumer of the trophic food web in the region, and reveals changes in the prey consumption compared with previous studies.

Key words: Diet, feeding strategy, spatio-temporal variation, trophic level.

Ecología trófica del lenguado patagónico *Paralichthys patagonicus* (Jordan, 1889) en el Ecosistema Costero Argentino-Uruguayo

RESUMEN. Se estudiaron los hábitos alimentarios y la composición de la dieta del lenguado patagónico *Paralichthys patagonicus* (Jordan, 1889) sobre la base del análisis del contenido estomacal de 828 especímenes (512 hembras, 304 machos, 12 indeterminados) recolectados durante 16 cruceros comerciales entre febrero de 2009 y abril de 2010 en el Ecosistema Costero Argentino-Uruguayo (34° S-41° S). Un total de 272 estómagos (32,9%) contenían alimento (184 hembras y 84 machos), entre los que se identificaron 20 taxones de presas. La categoría de presa más importante fue los peces pelágicos, principalmente la anchoíta argentina (*Engraulis anchoita*), seguida por el surel (*Trachurus lathami*). La evidencia mostró que las hembras consumieron un mayor peso húmedo total de presa en comparación con los machos. Los resultados también sugirieron una dieta especializada sobre *E. anchoita* para todos los sexos y tamaños. El nivel trófico estimado para toda la población de *P. patagonicus* fue 4,16. Este estudio sugiere que *P. patagonicus* es un consumidor piscívoro terciario de la trama trófica en la región, y revela cambios importantes en el consumo de presas en comparación con estudios previos.

Palabras clave: Dieta, estrategia alimenticia, variación espacio-temporal, nivel trófico.

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INTRODUCTION

Predation in nature is a central ecological process as it contributes to understanding the interactions of predators with their prey within an ecosystem (Elton 1927). Today, it is known that relationships between two or more species are described as nodes of a food web which can interact with each other and, therefore, any alteration can affect its stability (Lawton and Pimm 1978; Sterner et al. 1997).

The main coastal fishery in Argentina is carried out along the Argentine-Uruguayan Coastal Ecosystem (AUCE, 34° S-41° S), namely the Bonaerense Coastal Fishery (Carozza et al. 2004). More than 40 species are caught including crustaceans, molluscs and fish. The latter are grouped into the 'varied coastal', which is composed of about 30 species, both bony and cartilaginous fish (Lasta et al. 1998; Massa et al. 2004). In 2009, declared landings of 30 species making up the coastal assemblage was 105,361 t, from which 86.7% was obtained within the AUCE (Fernández Aráoz et al. 2010).

In particular, the Patagonian flounder (*Paralichthys patagonicus*) is one of the main fishing resources in the AUCE, due to both its excellent meat quality and its high market price (Fabré 1992). As a result of its high commercial importance, overfishing is a major threat in the region, leading this species to a vulnerable conservation status (Riestra et al. 2020). Over the past decades, annual catches ranged from 6,000 to 7,000 t year^{-1}, but more recently they shifted to an average of ~ 3,200 t year^{-1} (MAGyP 2021). In 2008, for example, catches of *P. patagonicus* contributed to 7% (6,930 t) of total declared landings in the AUCE (Rico and Lagos 2010), whereas in 2009, this percentage slightly decreased to 6,4% (5,890 t) (Fernández Aráoz et al. 2010). During 2020, the capture of flounders in Argentina and Uruguay diminished significantly to 1,891 t, accounting for 2.2% of total harvest (CTMFM 2021). Nevertheless, *P. patagonicus* continues to be the one that predominates the catches among the four species of flounder landed in the AUCE (Rico and Perrotta 2009; Rico 2010).

Paralichthys patagonicus is a benthic species inhabiting soft bottoms (Menni 1983), characterized as an ichthyophagous as well as a generalist mesopredator (Carneiro 1995; Sánchez and Díaz de Astarloa 1999). Its diet is based on fish with demersal-benthic habits (40.4%), mainly banded cusk-eel *Raneya brasiliensis*, and followed by pelagic fish (31.0%), including rough scad *Trachurus lathami* and Argentine anchovy *Engraulis anchoita* (Sánchez and Díaz de Astarloa 1999). Previous studies were based on qualitative analysis and did not provide the feeding strategy of *P. patagonicus*, nor its trophic role or any changes in diet concerning sex and size. Therefore, this work aimed to quantitatively determine the diet composition of *P. patagonicus* and find possible differences in prey consumption between sex and size groups, as well as its feeding strategies and trophic position in the AUCE.

MATERIALS AND METHODS

Study area

The study area is located in the AUCE region at the northern part of the Argentine Continental Shelf, between 34° S and 41° S and from the coastline to the 50 m deep isobath (Figure 1). On a large scale, the AUCE is influenced by various sources of oceanographic variability. In the northern area, it receives the influence of the coastal branch of the Brazil Current and the freshwater discharge from the Río de la Plata (Guerrero et al. 1997). In the southern area, it is influenced by the discharge of the Negro and Colorado rivers and the salty waters of San Matías Gulf (Lucas et al. 2005). In the outer eastern waters, it receives the

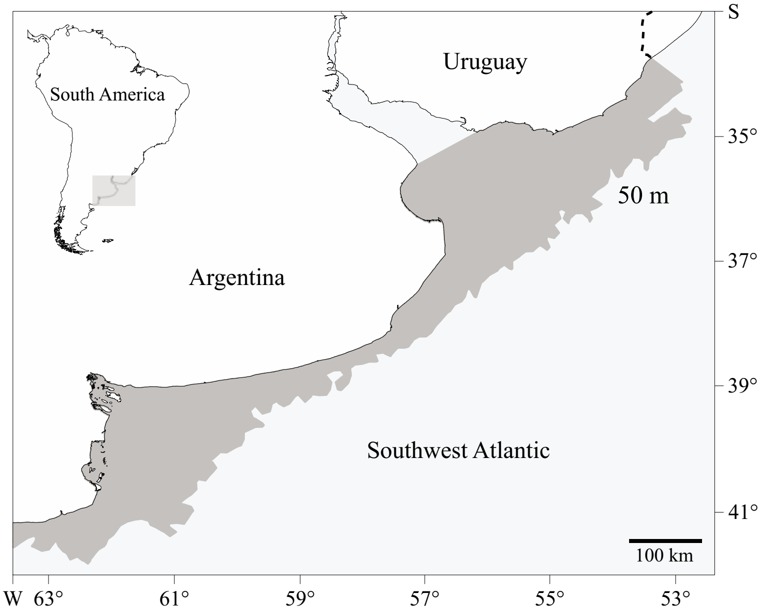

Figure 1. Study area (grey shade) from which samples were taken within the Argentine-Uruguayan Coastal Ecosystem (AUCE), delimited by the 50 m isobath.

influence of the Continental Shelf Current (Lucas et al. 2005).

Data sources

P. patagonicus were obtained from 16 fishery landings of the commercial coastal fleet, carried out between February 2009 and April 2010 in the AUCE. Total length (L_T, to the nearest cm), total wet weight (W_T, to the nearest g) and sex were recorded from each specimen, and stomachs were frozen to analyse prey composition.

Stomach content analysis

Prey items were identified to the lowest possible taxonomic level, counted and weighed. In the case of fish remains such as otoliths, L_T -W_T and otolith size-L_T regression curves to estimate the L_T and W_T of the prey were used (Koen Alonso et al. 1998; Waessle et al. 2003; Díaz de Astarloa 2005; Barquete et al. 2008). In order to quantify the importance of each prey item in the diet of *P. patagonicus*, the percentage in number (%N), percentage in W_T (%W), frequency of occurrence (%FO), Index of Relative Importance or IRI [IRIi = %FOi × (%Ni + %Wi) for each prey item i] (Pinkas et al. 1971), and the IRI expressed as a percentage (%IRI, Cortés 1997) were calculated.

Representativeness of stomach samples in the description of the diet of species was analysed by the minimum sample size and the intrinsic variability using randomization that considered 300,000 arrangements that produced curves for accumulated prey groups (i.e. pelagic fish, demersal fish, benthic fish, molluscs and crustaceans). For each randomization, the minimum, mean, maximum and coefficient of variation were obtained, which made possible to assess whether analysed sample met the minimum sample size.

Variations in the diet with sex and size

Possible quantitative differences in diet between females and males, and among size groups of *P. patagonicus*, were analysed by running a non-parametric Mann-Whitney and Kruskal-Wallis tests, respectively. Data were arranged into three different size groups according to the criteria provided by previous growth studies of the species (Riestra 2010): Group I (22-34 cm L_T; 2 to 4 years), Group II (35-47 cm L_T; 4 to 7 years) and Group III (> 47 cm L_T; > 8 years). In addition, prey type composition (main prey categories) was examined between sexes and among size groups.

Feeding strategy

In order to determine the feeding strategy (i.e. generalist or specialist) of *P. patagonicus* and the importance of the prey, the graphic method of Amundsen et al. (1996) was used. The specific abundance of prey *i* was plotted against %FO*i*.

Trophic level

The trophic level (TL) makes reference to the position of a species or population in the trophic web and its classification ranges from primary producers with a value of 1 to large top predators with values of 4 or 5 (Lindeman 1942). In the present work, the fractional form was used as suggested by Odum and Heald (1975), and then, TL was calculated for the population of *P. patagonicus* by applying the methodology suggested by Cortés (1999):

$$\mathrm{TL} = 1 + \left(\sum_{j=1}^{n} \mathrm{P}_j \times \mathrm{TL}_j \right)$$

where TL is the trophic level of *P. patagonicus* (predator), P_j is the proportion of the prey item *j* in the predator's stomach, TL_j is the trophic level of each prey item *j*, and *n* is the number of prey items recorded in the stomach of the predator. Trophic level of prey was obtained from online resources (Froese and Pauly 2019) and published literature (Jaureguizar and Milessi 2008; Milessi 2008).

RESULTS

Stomach contents

Out of 828 stomachs of *P. patagonicus* analysed, 272 (32.9%) presented prey contents, of which 184 were females and 84 males. Of the stomachs with contents, 36 (13.24%) corresponded to size group I, 176 (64.71%) to size group II, and 60 (22.05%) to size group III. In a very low percentage of specimens (1.45%), the sex could not be determined. The cumulative curves of the number of prey categories as a function of the number of stomachs sampled with prey content indicated that the number of samples was sufficient to describe and quantitatively analyse the diet of *P. patagonicus* and compare it between size groups and sexes (Figure 2).

Twenty prey items were identified, corresponding to three taxonomic groups: fish, molluscs and crustaceans. Fish were the most frequently encountered prey (%FO = 87.55), followed by crustaceans (%FO = 8.20) and cephalopod (%FO = 3.41) (Table 1). The most frequent prey item was *E. anchoita* (%FO = 37.60), followed by *T. lathami* (%FO = 18.12) and *R. brasiliensis* (%FO = 9.19). The most common prey item was *E. anchoita* (%N = 52.94), followed by *T. lathami* (%N = 18.21) (Table 1). Regarding the percentage by weight, fish were the most important group (%W = 96.53), followed by molluscs (%W = 2.31) and crustaceans (%W = 0.71) (Table 1). The best-represented species by weight were *E. anchoita* (%W = 36.62) and *T. lathami* (%W = 26.17). The Relative Importance Index (%IRI) indicated that the most important item in the diet was fish (98.73), followed by crustaceans (0.91) and cephalopods (0.35) (Table 1). Among fish prey, the species with the highest contribution was *E. anchoita* (%IRI = 74.25), followed by *T. lathami* (%IRI = 18.22) and *R. brasiliensis* (%IRI = 4.18). Among cephalopod prey, squid (*Loligo*

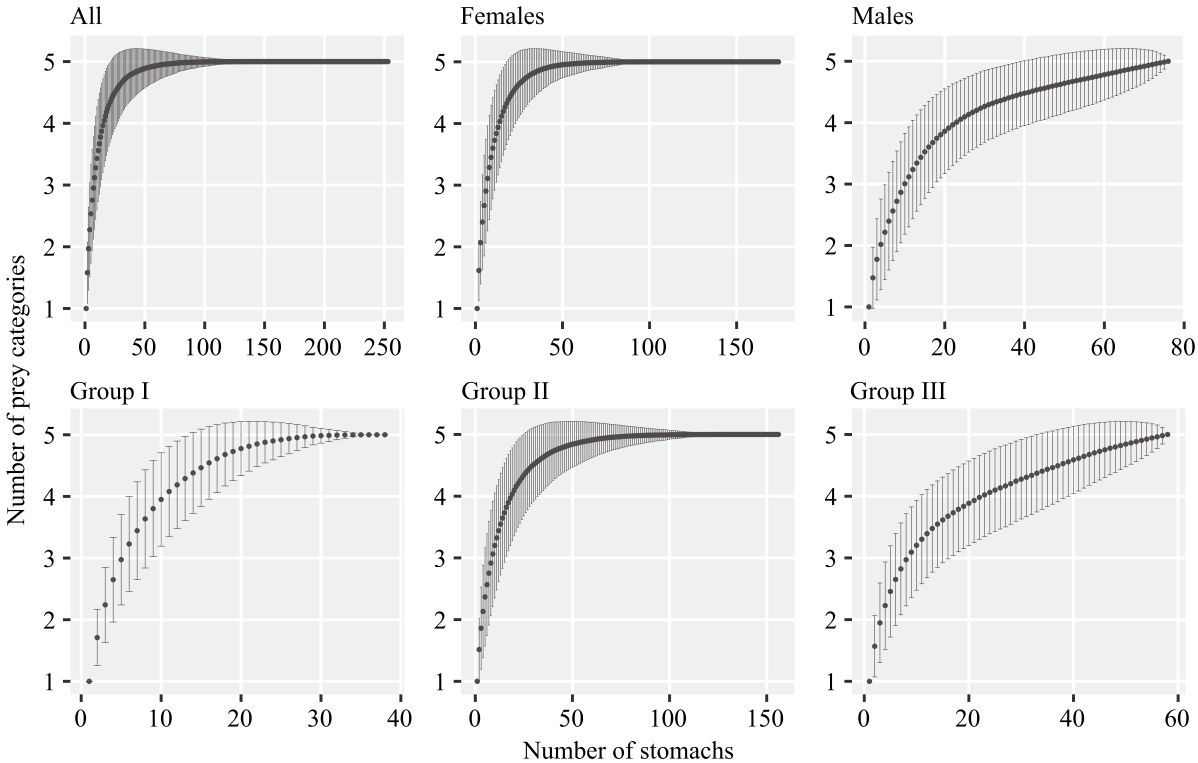

Figure 2. Cumulative number of prey categories of Patagonian flounder *Paralichthys patagonicus* as a function of stomachs sampled with prey content, arranged by sex or size group. Group I = 23-34 cm L_T, Group II = 35-47 cm L_T, and Group III = > 47 cm L_T. Mean values are denoted by points and standard deviation by error bars. Stomachs with only bony fish and/or unidentified rests were excluded from this analysis.

sanpaulensis) accounted for 0.35%, and the Argentine red shrimp (*Pleoticus muelleri*) represented 0.86% among crustaceans.

Variations in the diet according to sex and size

Results revealed that females consumed a greater amount of food than males, both in number and weight (Figure 3 A). Statistically significant differences between sexes were observed in both the number (Mann-Whitney, W = 8579; p = 0.006), and weight (Mann-Whitney, W = 9910; p < 0.001) of prey consumed. Size groups consumed the same amount of prey in number but not in weight, being size group III the category consuming the greatest weight of prey (Figure 3 B). Statistical analysis indicated no significant differences in number of prey consumed by size groups (Kruskal-Wallis, H = 4.74, p = 0.192) and significant differences in weight of prey (Kruskal-Wallis, H = 39.14, p < 0.001).

Pelagic fish were by far the predominant prey category both in number and weight in stomachs of all sex and size groups (Figure 4 A and B). The second most important prey category for group I was crustaceans, while benthic and demersal fish (number and weight) for groups II and III (Figure 4 B). Consumption of crustaceans was negligible across specimens larger than 47 cm L_T.

Feeding strategy

Based on Amundsen's graphical method, *P. patagonicus* presented a specialist type strategy

Table 1. Diet composition of Patagonian flounder (*Paralichthys patagonicus*) caught within the Argentine-Uruguayan Coastal Ecosystem (AUCE). Frequency of occurrence (%FO), number (%N), total wet weight (%W), and Index of Relative Importance (%IRI) were indicated and expressed in percentages. TL = trophic level.

Prey	TL	%N	%FO	%W	%IRI
Chordata					
Osteichthyes		**88.51**	**87.18**	**96.53**	**98.73**
Conger orbignyanus	3.40	1.68	2.21	1.68	0.16
Cynoscion guatucupa	3.74	3.36	4.41	6.41	0.97
Dules auriga	3.49	1.40	1.47	2.91	0.14
Engraulis anchoita	2.73	52.94	37.60	36.62	74.25
Menticirrhus americanus	3.73	0.28	0.37	0.04	0.00
Mullus argentinae	3.73	0.84	1.10	0.36	0.03
Prionotus nudigula	3.73	0.28	0.37	0.27	0.00
Raneya brasiliensis	3.73	7.28	9.19	13.89	4.18
Symphurus spp.	3.73	0.28	0.37	2.30	0.02
Trachurus lathami	3.51	18.21	18.12	26.17	18.22
Umbrina canosai	3.73	1.12	1.47	2.57	0.12
Urophycis brasiliensis	3.80	0.84	1.10	0.68	0.04
Remains	-	-	9.40	2.63	0.60
Chondrichthyes	-	**0.28**	**0.37**	**0.32**	**0.00**
Rajidae	3.59	0.28	0.37	0.32	0.00
Mollusca					
Cephalopoda	-	**3.08**	**3.41**	**2.31**	**0.35**
Loligo sanpaulensis	3.04	2.80	3.35	2.09	0.35
Octopus spp.	3.20	0.28	0.37	0.22	0.00
Arthropoda					
Crustacea	-	**8.13**	**8.20**	**0.71**	**0.91**
Grapsidae	2.00	1.68	1.10	0.03	0.04
Heterosquilla platensis	2.00	0.56	0.74	0.26	0.01
Leurocyclus tuberculosus	2.00	0.28	0.37	0.00	0.00
Pinixa patagonica	2.00	0.28	0.37	0.00	0.00
Pleoticus muelleri	2.20	5.33	5.62	0.42	0.86
Unidentified remains	-	-	**0.84**	**0.13**	**0.01**

due to the consumption of *E. anchoita* and *T. lathami* as main prey items (Figure 5). Argentine anchovy was the most selected prey among both female and male groups (Figure 5). Juvenile sizes of flounder specialized only on *E. anchoita*, whereas intermediate sizes on *E. anchoita* and *T. lathami*, and larger sizes on *E. anchoita*, *T. lathami* and *R. brasiliensis* (Figure 5).

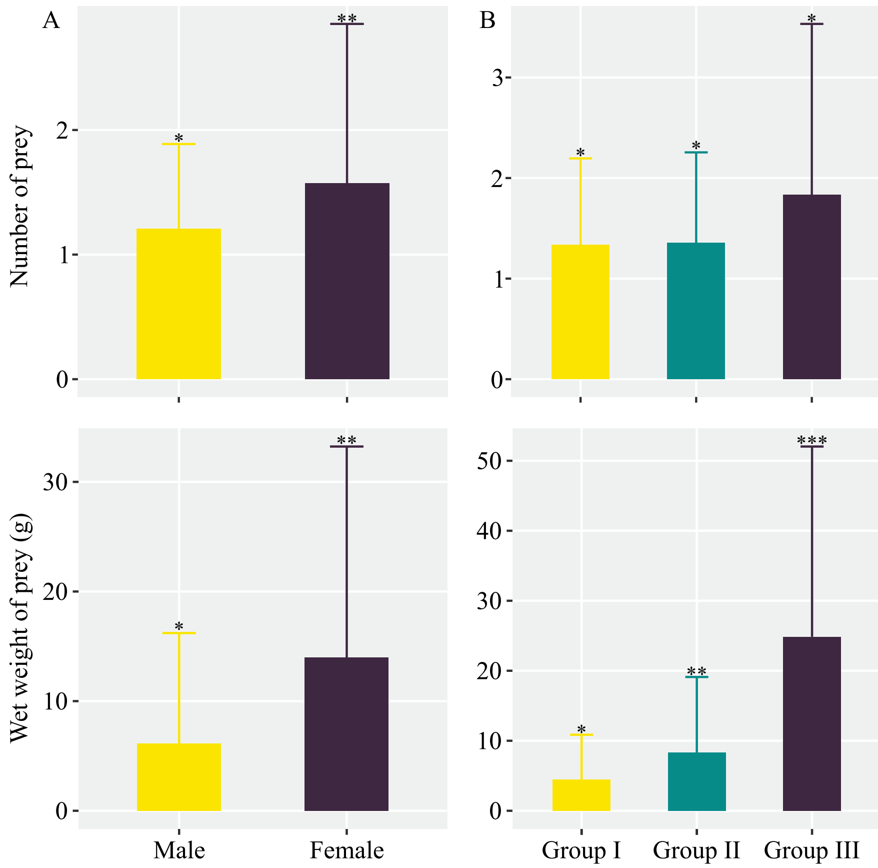

Figure 3. Diet composition (in number and wet weight of prey) of Patagonian flounder *Paralichthys patagonicus* arranged by sex (A) and size groups (B). Group I = 23-34 cm L_T, Group II = 35-47 cm L_T, and Group III = > 47 cm L_T. Asterisks indicate significant differences.

Trophic level

Estimated TL for the population of *P. patagonicus* between 2009 and 2010 was 4.16, with females presenting a value of 4.18 and males a value of 4.10.

DISCUSSION

Patagonian flounder diet presented 20 prey items and was specialized in pelagic fish. The main consumed species were *E. anchoita*, followed by *T. lathami* and *R. brasiliensis*. This study supports previous observations that *P. patagonicus* is an ichthyophagous predator, which bases its diet preferentially on *E. anchoita*, allowing it to be allocated as a tertiary consumer in the AUCE food web. The number of stomachs analysed was statistically adequate to describe the diet of *P. patagonicus*. Only 33% of the analysed specimens presented food in their stomachs, which is consistent with other studies on ichthyophagous bony fishes and flounder species (Carneiro 1995; Sánchez and Díaz de Astarloa 1999; Link et al. 2002). A high number of empty stomachs could be a consequence of fish suffering stress or water pressure differences during their extraction from the aquatic

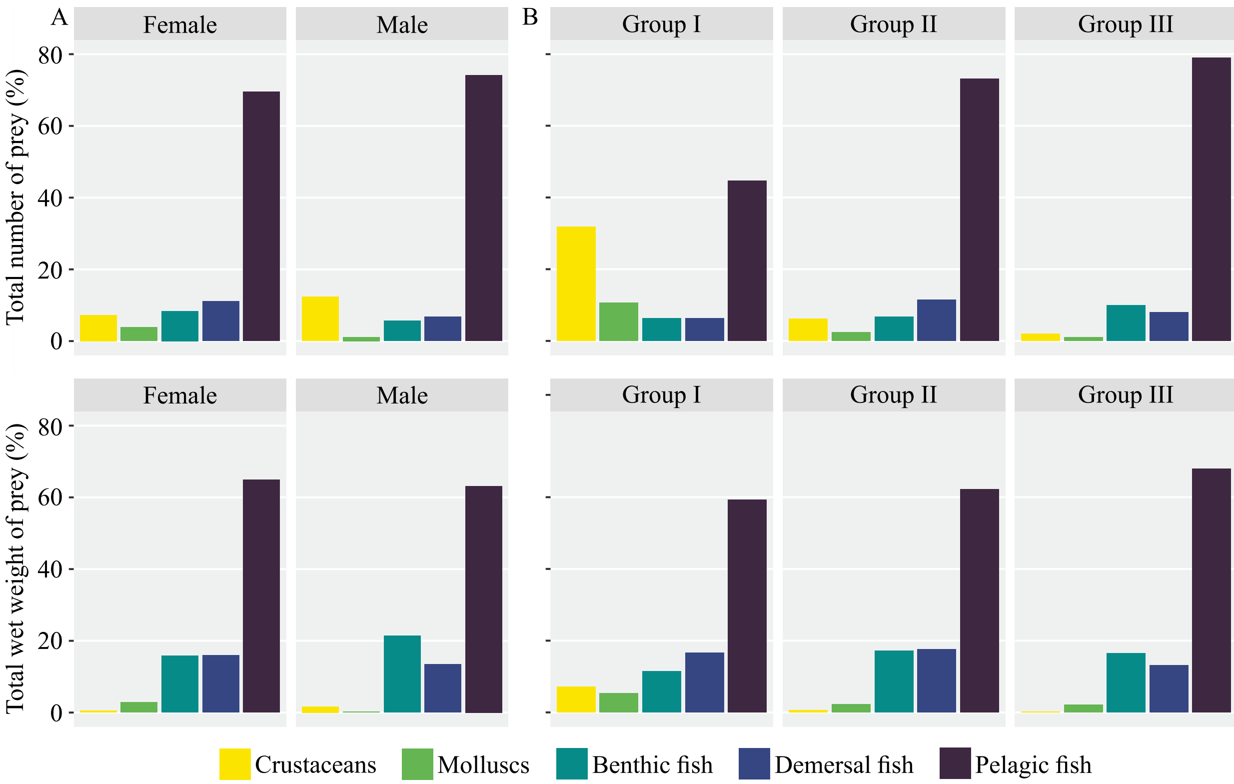

Figure 4. Prey type composition of Patagonian flounder *Paralichthys patagonicus* arraged by sex (A) and size groups (B). Values are expressed as percentage of total number and wet weight of main prey categories. Group I = 23-34 cm L_T, Group II = 35-47 cm L_T, and Group III = > 47 cm L_T.

environment, a process manifested with the stomach eversion or regurgitation of contents (Bowman 1986). In particular, regurgitations could be one factor explaining why the proportion of individuals with stomach content did not exceed 1/3 of the total, as it was repeatedly observed in *P. patagonicus* being caught on fishing gear (pers. obs. A Milessi). In addition, the samples used in this study came from bottom trawl fishing operations which are less likely to have associated bias regarding regurgitation rate, compared to other fishing gears (e.g. longlines).

Patagonian flounder bases its diet primarily on bony fish. Ichthyophagy seems to be a characteristic of intermediate and large-sized flounders like the species studied here, e.g., *P. dentatus* (Link et al. 2002), *P. orbignyanus* (Norbis and Galli 2004; López Cazorla and Forte 2005); *Syacium micrurum* (Marques et al. 2009), and *Cyclopsetta panamensis* (Amezcua and Portillo 2010), with a less important presence of crustaceans and molluscs in the diet. This characteristic is common in *P. patagonicus* from both southern Brazil (Carneiro 1995) and AUCE (Sánchez and Díaz de Astarloa 1999). However, *P. patagonicus* have changed past feeding patterns observed in the AUCE between years 1992-1993, when the diet was based predominantly on *R. brasiliensis*, followed by *T. lathami* and to a lesser extent by *E. anchoita* (Sánchez and Díaz de Astarloa 1999). This situation was also observed in other piscivorous fish like *Percophis brasiliensis* (Milessi and Marí 2012) and

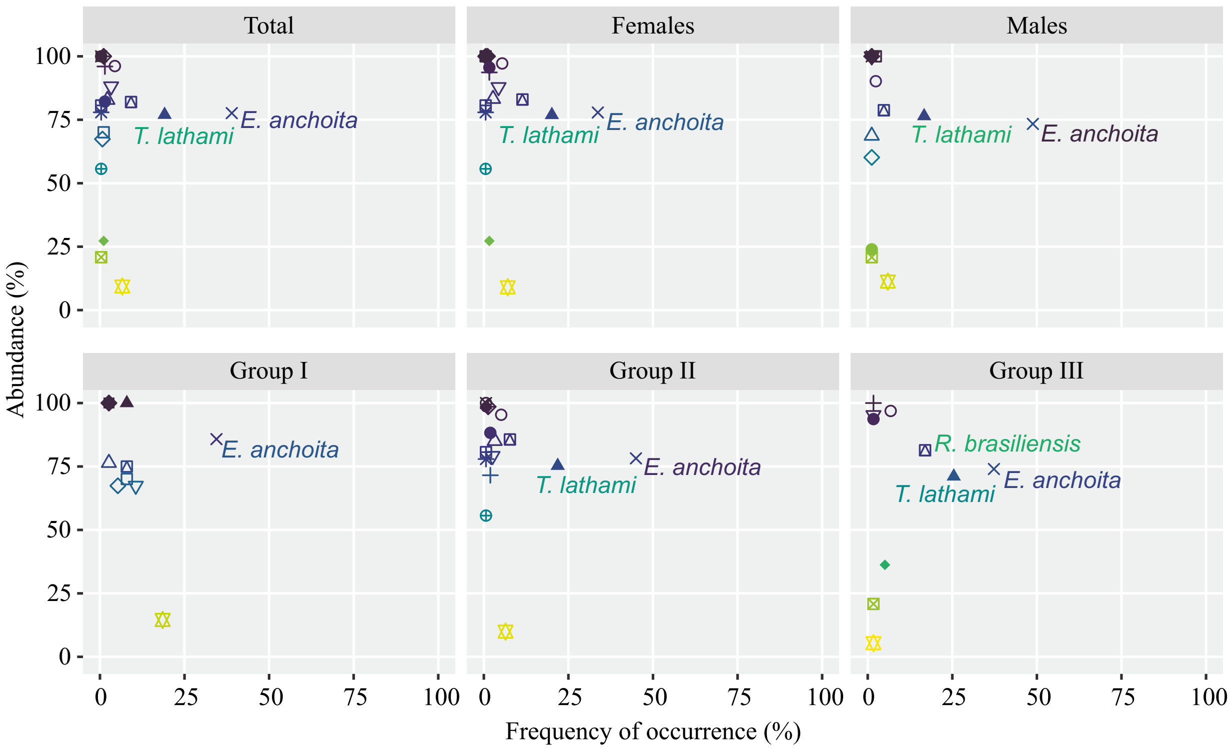

Figure 5. Abundance (% total wet weight) versus frequency of occurrence (% in number) of each prey found in stomachs of Patagonian flounder (*Paralichthys patagonicus*) arranged by sex and size. Group I = 23-34 cm L_T, Group II = 35-47 cm L_T, and Group III = > 47 cm L_T. The analysis is based on the method in Amundsen et al. (1996) to determine feeding strategies of fish. Each prey is represented by a unique symbol; only names from abundant and frequently occurring prey are shown to facilitate visualization. Darker colours in symbols and prey names indicate higher abundance and frequency of occurrence, respectively.

Squalus acanthias (Belleggia et al. 2012), which would reflect a change in the structure of the AUCE trophic web, mainly due to fishing exploitation (Jaureguizar and Milessi 2008). Another explanation for the observed shift between past and present diet may be due to a variation in the spatial operability of the coastal fishing fleet, which currently operates in areas that were not previously used, and consequently, prey captured by *P. patagonicus* in the present could be different from those found in stomachs from previous studies.

Statistical differences in diet between sexes found in *P. patagonicus* are likely a result of females consuming more prey both in number and weight because they attain larger sizes than males (Riestra 2010), and therefore have a higher consumption rate, greater stomach capacity and higher energy requirements (e.g. Scharf et al. 2000; Vögler et al. 2009). Although not possible to evaluate in this study, it has been proposed that there is a spatial overlap between sexes (Riestra 2010), suggesting that females and males would feed on the same prey but in different quantities. This last suggestion is in line with a study carried out on the Uruguayan coast, where no differences were observed in the prey type consumption between sexes of *P. patagonicus* (Correa 2011).

Furthermore, Amundsen graphical results indicated that *P. patagonicus* is specialized in consuming *E. anchoita* and *T. lathami*, and this preference increased with size. This was expected given that *E. anchoita* is the most abundant fish species in the AUCE with a biomass estimated between 1,000,000 and 5,000,000 t (Hansen and Madirolas 1996; Hansen et al. 2007; Pájaro et al. 2009), it represents the main food source not only for *P. patagonicus* but also for other teleosts (Bergonzi 1997; Sánchez 2002; Giberto 2008, Milessi and Marí 2012) and chondrichthyans (Vögler et al. 2003; Belleggia et al. 2011), as well as seabirds (Silva et al. 2000; Mauco et al. 2001; Mauco and Favero 2004; Barquete et al. 2008) and marine mammals (Rodríguez et al. 2002; Suárez et al. 2005). Dense shoals formed near the seafloor by *E. anchoita* as a result of daily vertical migrations (Hansen 2004), would allow predation by *P. patagonicus* in the AUCE. Therefore, *P. patagonicus* specialization on *E. anchoita* should be interpreted with caution because it is possible that the high consumption arises from the abundance of prey in the habitats used by the predator.

Molluscs and crustaceans were more consumed by *P. patagonicus* of smaller sizes than larger sizes. This behaviour was also observed in other congeners like *P. isosceles*, (García 1987) and *P. orbignyanus* (López Cazorla and Forte 2005), in which smaller sizes preyed more on crustaceans and molluscs. This pattern is probably explained by the ability of smaller fish sizes to capture small and less motile prey (e.g., molluscs and crustaceans), while bigger and more dynamic prey are captured as individuals reach greater size and experience in predation (Link et al. 2014).

The increase in the size of the consumed prey can be attributed to the increase in the size of the predator's mouth (Stoner and Livingston 1984; Mittelbach and Persson 1998), or to the elevated metabolic requirement for movement, growth and reproduction that is supported by the consumption of prey with higher energy value (Scharf et al. 2000). In this sense, pelagic fish have a higher lipid content and therefore a higher amount of calories (Massa et al. 2013); e.g. *E. anchoita* has a value of 129 kcal and *T. lathami* of 149 kcal, whereas the squid *L. sanpaulensis* of 80 kcal and Argentine red shrimp *P. muelleri* of 97 kcal (Mendez et al. 1996; Celik 2008). Thus, as flounders grow, they need to feed on prey that meets their basic energy requirements, which would be achieved with the increasing consumption of small pelagic fish.

Finally, the estimated TL (4.16) allowed the identification of the Patagonian flounder as a tertiary ichthyophagous consumer, a position similar to that outlined in the southern coasts of Brazil (TL = 4.18; Carneiro 1995). It represents an important predator of the Argentine anchovy (*E. anchoita*), which is the pelagic species with the highest abundance and widest geographic distribution in the Southwest Atlantic, ranging from 24° S to 48° S, with biomass estimates in the order of 5,000,000 t (Hansen et al. 2010). This characteristic highlights the role of *P. patagonicus* in regulating the abundance of its prey, among which the main prey not only represents the sustenance of a large number of marine fish, mammals and birds but it also contributes to be an important fishery resource in the AUCE (Hansen et al. 2010).

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