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ARTICLE

Diet Composition and Feeding Strategy of the New World Silverside *Odontesthes argentinensis* in a Temperate Coastal Area (South America)

Gustavo A. Thompson* and Alejandra V. Volpedo
Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad de Buenos Aires, Instituto de Investigaciones en Produccion Animal, Codigo Postal 1427, Buenos Aires, Argentina

Abstract

The diet composition and feeding strategy of the New World silverside *Odontesthes argentinensis* were evaluated in a temperate coastal area during austral summer. This species is an economically significant resource for the fishing industry in South America. The food preference of *O. argentinensis* varied with its size-class: the smallest size-classes preferred diatoms and annelids, larger size-classes seemed to prefer barnacle cypris larvae, and the largest size-classes showed a preference for decapod megalopa larvae. Plankton samples were dominated by calanoid and cyclopoid copepods; however, contrary to what was expected, *O. argentinensis* showed negative selectivity for both groups. A selectivity index indicated that *O. argentinensis* selects the food it eats with regard to prey availability in the environment. The information obtained in this study demonstrates the importance of knowing the food preference of *O. argentinensis* to obtain a better condition factor, which will be key to its potential farming in closed systems.

The genus *Odontesthes* belongs to the family Atherinopsidae (New World silversides; order Atheriniformes; Nelson et al. 2016), which is widespread in inland and marine waters of the Americas. Silversides in general (i.e., Atherinopsidae and Atherinidae) are a group of fish that adapt easily to new and changing environments. Bamber and Henderson (1988) suggested that silversides readily colonize inland from the coast. Indeed, most fish that inhabit brackish lagoonal systems and the great majority of estuarine fish are derived from marine stocks. In particular, the genus *Odontesthes* includes at least five freshwater species and two marine species (Dyer 2006). One of the marine species, *O. argentinensis*, is a large silverside that is considered to have a wide distribution along the southwestern Atlantic Ocean coast between Rio de Janeiro, Brazil (22°S), and Rawson, Argentina (43°S; Dyer 2000; Di Dario et al. 2014). This species inhabits both estuaries and coastal waters (Cousseau 1986) and is an economically significant resource for local fishermen in the southern region of South America (De Buen 1953; Chao et al. 1985; Sampaio 2006). *Odontesthes argentinensis* is captured by both artisanal fishermen and by recreational coastal fishing. However, despite the importance of *O. argentinensis* to the regional fishing industry, the main difficulty of the capture fishery and potential aquaculture production of this species is the limited knowledge about key biological aspects regarding its growth, reproduction, and feeding (Bemvenuti 1987, 2002; Moresco and

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*Corresponding author: gustavo@ege.fcen.uba.ar
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Bemvenuti 2006; Llompart et al. 2013; Gurdek and Acuña-Plavan 2014). Thus, further studies involving analysis of the food consumed by this species are required to better understand its biology.

Based on studies of several species belonging to the genus *Odontesthes*, the growth performance in environments where these fish have evolved seems to be regulated by the availability of appropriate food (Hualde et al. 2011; Garcia de Souza et al. 2015, 2017; Solimano et al. 2015). For a planktivorous species, *O. bonariensis*, fish biomass production in aquaculture was regulated by the available zooplankton resources in quality and quantity (Garcia de Souza et al. 2015). Knowledge of the feeding behavior of *O. argentinensis* and its role in the trophic chain will be important for future management of this resource, since the growth rates attained under intensive culture conditions without a proper formulation of an artificial food cannot be as high as the growth achieved in natural environments (Solimano et al. 2015). Moreover, one of the main constraints in *Odontesthes* aquaculture production is the acquisition of large juveniles for stocking or fattening (Garcia de Souza et al. 2015).

The aim of this study was to contribute to the understanding of the diet composition and feeding strategy of *O. argentinensis*. Considering that silverside species adapt easily to changing environments, it could be hypothesized that the feeding strategy and consequently the diet composition of *O. argentinensis* depend on the abundance and availability of food items in the environment.

METHODS

Study site and field methods.— In total, 595 samples of *O. argentinensis* were collected during three sampling occasions (January 2013: $n = 104$ specimens; February 2013: $n = 109$; January 2014: $n = 382$) in the Partido de la Costa, Buenos Aires Province, Argentina (36°39′S, 56°40′W). Fish were collected overnight by using a lift net (10-mm mesh size) and fishing rods 100–200 m out from the coast. Specimens collected with fishing rods constituted less than 3% of the total, so they were not considered separately in this study. Total length (L_T), standard length (L_S), and mouth width (M_b) of collected specimens were measured in millimeters, and total weight (W_T) was measured in grams. We measured L_T and L_S with a standard icthyometer of 50-cm length and 0.5-mm precision; M_b was measured with a 0–70-mm/0.05-mm mini Vernier caliper; and W_T was measured with a digital field scale to the nearest 0.01 g. In addition, during each fish sampling event, qualitative zooplankton samples were taken using a conical-type net (diameter = 0.4 m; mesh size = 60 μm) and were preserved in an 80% solution of alcohol.

Size-classes.— On each sampling occasion, *O. argentinensis* were divided according to L_T (mm) into size-classes of 10-mm intervals (40–50, 50–60, … , 110–120 mm L_T) except that the last interval ranged from 120 to 350 mm L_T. The nine size-classes were used for most analyses of the diet; approximately 15–20 specimens from each size-class of *O. argentinensis* collected on each sampling occasion were examined.

Stomach content preservation and identification.— In the analysis of food preferences, the stomach from each selected specimen was removed and preserved in 80% alcohol. Stomach contents and zooplankton samples were analyzed using Bogorov-type zooplankton counting chambers. Prey items were identified by using published keys (Boschi et al. 1992; Boltovskoy 1999; Boschi and Cousseau 2004) and were weighed to the nearest 0.1 mg by using an analytical laboratory scale (Sartorius ED224S).

Data analysis.— The length–weight relationship for *O. argentinensis* was calculated using specimens ranging in size from 60 to 350 mm L_T (January 2013), from 50 to 140 mm L_T (February 2013), and from 40 to 330 mm L_T (January 2014); corresponding wet weights were 1.5–240, 0.7–110, and 0.5–382 g, respectively (Figure 1). For each sampling occasion, L_T and W_T were log transformed, and the resulting linear relationship was fitted by least-squares regression using W_T as the dependent variable. The significance of the regression was assessed with ANOVA testing the null hypothesis, H_0: $\beta = 0$, against the alternative hypothesis, H_A: $\beta \neq 0$ (Zar 1999). The regression slopes were compared among sampling occasions with a parallelism test (Zar 1999). Additionally, the 95% confidence limits of the parameters a and b were estimated. The linear regression equation was calculated to describe the relationship between log-transformed M_b and L_T. Le Cren's relative condition factor (Murphy et al. 1991) was determined as an indicator of the physiological state of the organisms. Relative condition factors were compared among sampling occasions and fish L_T using a two-way ANOVA to determine whether changes in general fish condition could be expected.

The contribution of each prey type to the diets consumed by the different size-classes of *O. argentinensis* was evaluated using three of the methods reviewed by Hyslop (1980): (1) frequency of occurrence (%O), defined as the number of stomach samples in which a prey occurs expressed as a percentage of all stomachs; (2) numeric percentage (%N), defined as the number of individuals in each prey category recorded for all stomachs, with the total expressed as a percentage of the total individuals in all prey categories; and (3) wet weight percentage (%W), defined as the wet weight of each prey category recorded for all stomachs, with the total expressed as a percentage of the total wet weight of all prey categories.

To evaluate the contribution of each prey category, we calculated the index of relative importance (IRI; Pinkas et al. 1971) for each *O. argentinensis* size-class. The IRI of

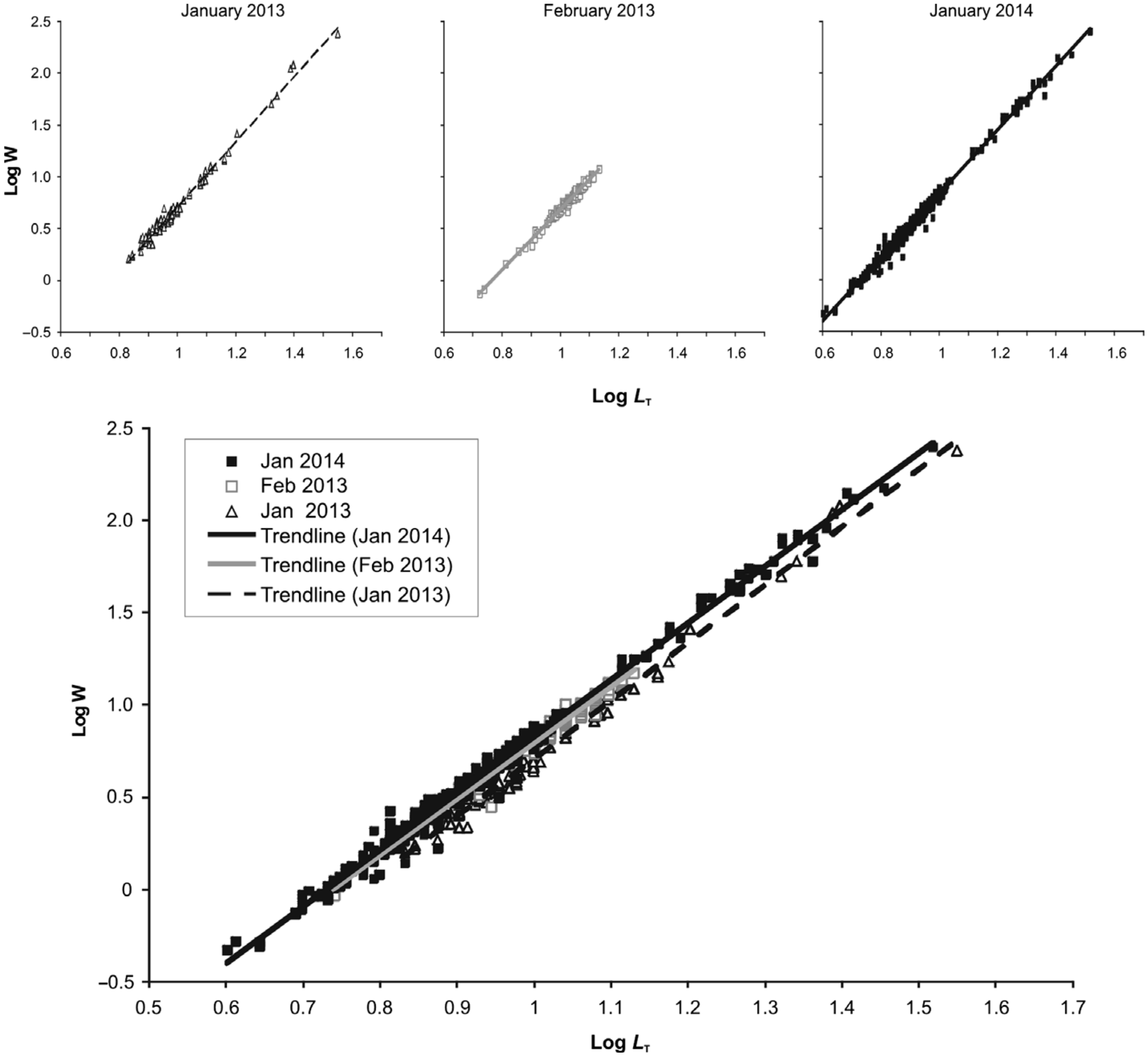

FIGURE 1. Relationship between $\log_{10}$(total length [L_T, mm]) and $\log_{10}$(total wet weight [W_T, g]) of *Odontesthes argentinensis* for each sampling occasion in waters of Buenos Aires Province, Argentina. Trendlines are included.

prey categories was calculated as $\%O(\%N + \%W)$. The relative contribution of each prey (i.e., %IRI) was also calculated. The IRI was calculated for each size-class (total of eight size-classes used) collected on each sampling occasion, and size-classes were then compared across sampling occasions. The importance of each prey type and the feeding strategy of *O. argentinensis* were also evaluated by the three-dimensional graphical method of Cortés (1997) and the graphical method of Amunsen et al. (1996). In the latter, the prey-specific abundance, defined as the contribution of a given prey category *i*, was plotted against the frequency of occurrence for that category ($\%O_i$).

Prey selection was determined using a selectivity index, which was a relative measure of preference based on calculation of the log odds ratio (LOR; Gabriel 1978). The LOR is useful because it allows for calculation of the SE and testing whether there is a significant difference. In addition, the LOR is symmetrical around zero, varying from $+\infty$ (when the prey is eaten but not present in samples from the environment) to $-\infty$ (when the prey is not eaten but is present in samples from the environment). The LOR was calculated as $\log_e(p_1q_2/p_2q_1)$, where p_1 is the percentage of prey of a given taxon in the diet, q_1 is the percentage of all other prey in the diet, p_2 is the percentage of prey of a given taxon in the seawater, and q_2 is the percentage of all other prey in the seawater. The SE of LOR was calculated as $\sqrt{\{[1/(n_1p_1q_1)]+[1/(n_2p_2q_2)]\}}$, where n_1 is the total number of prey in a diet sample; n_2 is the total number of prey in situ; and p_1, q_1, p_2, and q_2 are as defined above. The significance test can be applied by using the standard normal deviate (Z distribution): $Z = (\text{LOR observed} - \text{LOR expected})/\text{SE(LOR)}$. The percentage of prey in situ was determined from analysis of the mesozooplankton collected in the same place and time as fish sampling.

RESULTS

Odontesthes argentinensis presented slightly positive allometric growth, with $W_T = 0.006 \times (L_T)^{3.01}$ ($n = 595$), and the parallelism test showed no significant differences in the values of the slope between samples ($F_{0.05[1],\ 2,589} = 2.04$, $P = 0.13$; Figure 1). The 95% confidence limits of the parameters a and b were 0.0055–0.0065 and 2.991–3.027, respectively.

The relative condition factor ranged between 0.60 and 1.49, with average values between 0.95 and 1.05 depending on the size-class. The condition factor showed no significant variation over the sizes or sampling occasions studied (Table 1; Figure 2). A significant positive correlation between L_T (mm) and M_b (mm) was recorded: $\log_{10}(M_b) = -2.1765 + 1.3723 \cdot \log_{10}(L_T)$ ($n = 264$; $r^2 = 0.86$; $P < 0.0001$).

The results obtained from stomach content analysis of 293 specimens ($L_T = 45$–350 mm) indicated a high incidence of empty stomachs (with values between 30% and 50% for all sizes) during both sampling occasions in 2013 and a low incidence (with values of 5–20%, only sizes >120 mm) during 2014. All of the specimens registered with empty stomachs were collected using a lift net.

Stomach contents were variable between samplings; however, certain similarities were observed. Barnacle cypris larvae had a high occurrence in the stomachs of all fish size-classes up to 120 mm (2013) and 110 mm (2014), being predominant in terms of %O, %N, and %W. Although 13 specimens with more than 1,000 cypris larvae in their stomachs were recorded (one with up to 4,800 cypris larvae), the predominant trend was a decrease in the frequency of occurrence as the size of the fish increased. Calanoid copepods, pteropods (family Limacinidae), and annelid larvae followed the same pattern in which the frequency of occurrence decreased with increasing fish size: these prey types were recorded in fish up to 130 mm L_T during 2013 and in fish up to 80 mm L_T during 2014.

TABLE 1. Results of two-way ANOVAs examining the effects of sampling occasion (January 2013, February 2013, and January 2014) and range of total length (L_T; 10-mm size-classes) on the relative condition factor of *Odontesthes argentinensis.*

Factor	df	*F*-ratio	*P*
Sampling period	2	0.823	0.44
L_T range	6	0.713	0.64
Sampling occasion × L_T range	12	1.474	0.13
Error	574		

On the other hand, the presence of parasites of the genus *Aponorus* was recorded in 5–8% of total stomachs and only in individuals between 60 and 100 mm L_T. In addition, during 2013, remains of Argentine stiletto shrimp *Artemesia longinaris* and occasionally insects and decapod megalopa larvae were identified. It was difficult to identify megalopa larvae to the species level. During 2014, megalopa larvae showed an increase in their contribution in terms of occurrence and number in the diet composition as fish size-class increased, being the dominant dietary component for larger size-classes of *O. argentinensis*.

Plankton samples were dominated by calanoid copepods (specimens of *Labidocera* sp., *Paracalanus* sp., and *Acartia tonsa* were found) and secondarily by cyclopoid copepods, which altogether represented more than 60% of the components of all samplings. Cypris larvae of the barnacle *Balanus glandula* represented less than 10% in 2013 and around 16% in 2014. Pteropod mollusks, annelids (>1 mm), juvenile Argentine stiletto shrimp (2–3 mm), and chaetognaths had highly variable contributions and represented less than 10% of the components of all samplings. The latter two groups were 10 times more abundant in 2013 than in 2014. The only organisms that were not recorded in any plankton sample were gastropod mollusks, megalopa larvae of *Cyrtograpsus* sp. (Decapoda: Brachyura; only in 2014), and ichthyoplankton (fish larvae, only in 2013; Table 2).

The IRI value for each identified prey type varied with *O. argentinensis* size and with sampling occasion (Figure 3A). In *O. argentinensis* specimens of up to 50 mm L_T, diatoms, annelids, and barnacle cypris larvae had similar values of IRI (between 25% and 31%). In specimens between 50 and 80 mm L_T, cypris larvae predominated, with IRI values between 61% and 77%. *Odontesthes argentinensis* specimens larger than 80 mm L_T showed the most important differences between samples. During 2013, cypris larvae predominated, with IRI values between 40% and 90%, and calanoid copepods (>1,000 μm) were present in specimens larger than 100 mm L_T, with IRI values higher than 30%. On the other hand, in 2014, copepods and annelids disappeared from the diet, and megalopa and cypris

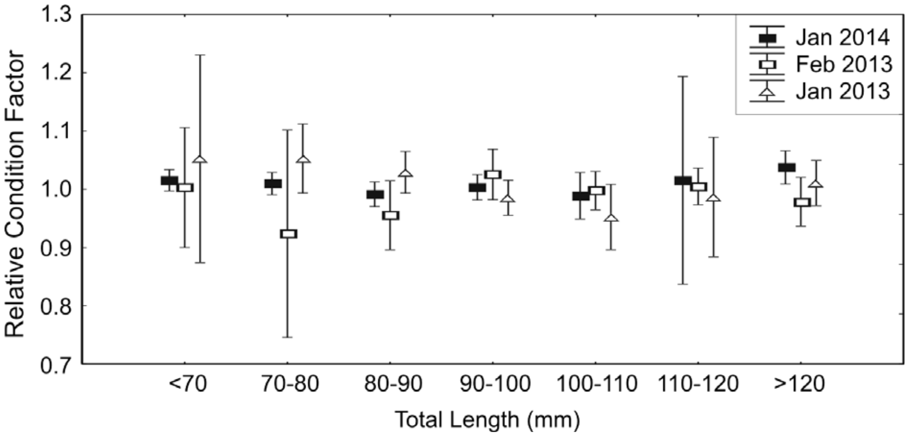

FIGURE 2. Condition factor (average, maximum, and minimum) for each total length class (seven size-classes used) of *Odontesthes argentinensis* captured on each sampling occasion.

TABLE 2. Percent occurrence of zooplankton taxa in plankton samples collected from Buenos Aires Province, Argentina, during January 2013, February 2013, and January 2014 (L_T = total length).

Taxon	Jan 2013	Feb 2013	Jan 2014
Copepoda			
Calanoida ($L_T > 1{,}000$ μm)	53.21	72.27	32.49
Calanoida ($L_T < 1{,}000$ μm)	12.56	2.85	19.64
Harpaticoida		0.95	
Cyclopoida ($L_T > 1{,}000$ μm)			0.67
Cyclopoida ($L_T < 1{,}000$ μm)		0.48	11.32
Nauplii		0.95	0.98
Indeterminate Copepoda			0.36
Mollusca			
Gastropoda			0.78
Pteropoda	12.82	2.85	0.60
Crustacea			
Cirripedia (barnacle) cypris larvae	2.15	9.98	16.23
Decapoda larvae (megalopae)			1.05
Argentine stiletto shrimp *Artemesia longinaris*	10.86	4.60	0.38
Other			
Annelid larvae ($L_T > 1{,}000$ μm)	0.38	1.43	14.90
Chaetognatha	6.56	3.33	0.18
Ichthyoplankton ($L_T < 2{,}500$ μm)		0.32	
Indeterminate	1.45		0.42

larvae predominated in specimens between 80 and 90 mm L_T (similar values of IRI: 45% and 55%), whereas megalopa larvae predominated in specimens greater than 90 mm L_T (IRI > 80%) and in those larger than 110 mm L_T (IRI = 100%).

The graphical methods of Cortés (1997) and Amunsen et al. (1996) corroborated the trend of food preferences for each sampling occasion; because the trend varied in 2014, two size-groups (>90 and <90 mm L_T) were considered. Graphical methods demonstrated that *O. argentinensis* preyed mainly upon barnacle cypris larvae during both sampling occasions in 2013, so those values were averaged and plotted (Figure 4A); cypris larvae were a permanent component of the diet for smaller size-classes or were consumed rarely and in small amounts by larger size-classes during 2014 (Figure 4B, C). *Odontesthes argentinensis* preyed mainly upon megalopa larvae during 2014. As they grew, *O. argentinensis* restricted the number of food items ingested, and the number of megalopa larvae consumed increased (Figure 4B, C). The remaining prey components identified were consumed rarely and in small amounts during 2014, mainly by the smaller size-classes of *O. argentinensis* (Figure 4B).

The LOR index (Figure 3B) indicated positive selectivity for cypris larvae by *O. argentinensis* specimens of up to 90 mm L_T in 2014 and by all sizes analyzed in 2013, demonstrating a decreasing trend with increasing L_T. In the case of megalopa larvae, an exponentially growing selectivity was observed (with increasing size; $\text{LOR} = 0.36 \times e^{0.28 L_T}$; $R^2 = 0.98$) starting at a size of 50 mm L_T in 2014, and positive values close to zero were observed for specimens larger than 90 mm L_T in 2013. During 2014, the LOR was negative for diatoms and copepod nauplii, whereas it decreased with L_T for pteropods and annelids, being $-\infty$ for fish larger than 80 mm L_T. For all food items, the LOR value was significant ($P < 0.05$), indicating selectivity in the food consumed with regard to that available in the environment. During all sampling events and for all sizes of *O. argentinensis*, LOR was negative for calanoid copepods (>1,000 μm).

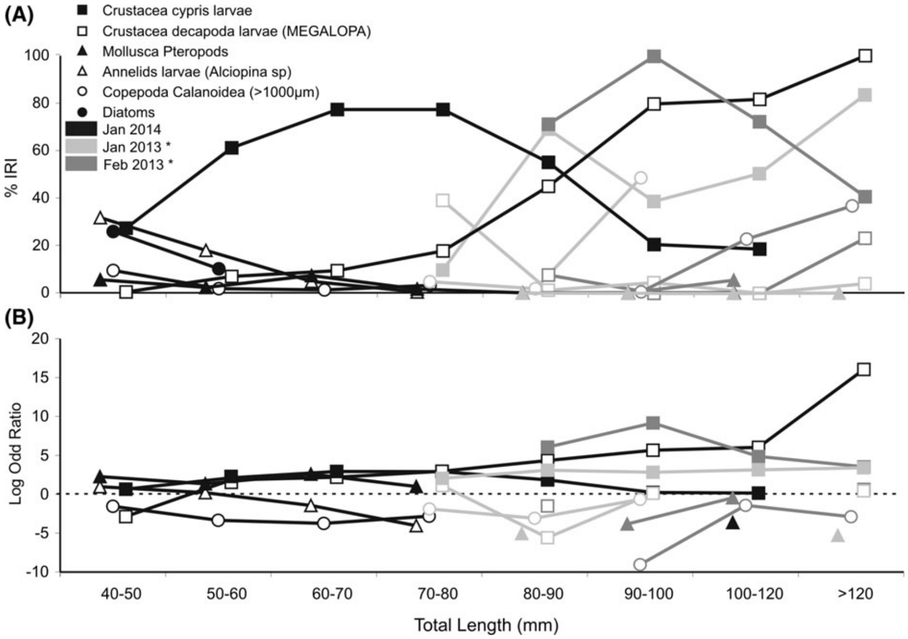

FIGURE 3. **(A)** Index of relative importance (IRI) and **(B)** log odds ratio (LOR) selectivity index of each prey type consumed by *Odontesthes argentinensis* for each available total length (L_T) class and each sampling occasion. Size-classes less than 70 mm L_T were considered a single class for the January and February 2013 sampling occasions (asterisks).

DISCUSSION

The parameters (*a* and *b*) of the length–weight relationship determined in this study are similar to those reported for *O. argentinensis* caught along the Uruguayan coast with a similar range of sizes (32–420 mm L_T; Gurdek and Acuña-Plavan 2014). The parameters are also similar to those reported for this species at the southern limit of its distributional range (Bahía Anegada), with a somewhat higher range of sizes (Molina 2012). In relation to the diet, existing studies of *O. argentinensis* are scarce and inconclusive. In our study, throughout the size range tested (40–350 mm L_T), *O. argentinensis* showed a preference for planktonic organisms. This differs from the dietary preferences reported for *O. argentinensis* captured along the Uruguayan coast, where there was a greater abundance of insects or Polychaeta (Cristobo 2014), and from that observed in the estuarine region of southern Brazil, where juvenile *O. argentinensis* showed a preference for zooplankton while adults demonstrated a preference for benthic prey (Bemvenuti 1990).

Bemvenuti (1990) reported a prey composition of copepods (63.8%) and Diptera insects (35.5%) for juvenile *O. argentinensis* and of Tanaidacea (35.6%), polychaetes (25.7%), and amphipods (22%) for adults. Although we did not make this differentiation, the food components recorded in the stomach contents during the present study (Figure 4) were similar to those recorded by Bemvenuti (1990) for juveniles: cyclopoid copepods, calanoids, harpacticoids, nauplii, and barnacle cypris larvae.

The abundance and availability of food items in the environment varied between years, influencing the diversity of the diet throughout the range of fish sizes recorded. However, the predominant items in the diets were not those that were most abundant in the environment (values of LOR significantly different from zero). Therefore, along the Buenos Aires coast, *O. argentinensis* would be selecting its food, which differs from the observations made by Bemvenuti (1990). Regarding our results, it is important to highlight the negative selection of calanoid copepods, which represented more than 50% of the food items available in plankton and were the predominant food items recorded in previous studies (e.g., see references in Bemvenuti 1990).

In extensive cage culture of *O. bonariensis*, Garcia de Souza et al. (2015) determined that for the early stage, mouth size appeared to influence the food particle sizes that the fish were able to ingest. However, most of the specimens of *O. argentinensis* recorded in our study were smaller than 100 mm L_T, which corresponds to a mouth opening of less than 3.5 mm—ideal for capturing most calanoid copepods. This situation is very striking because the availability of "large" copepods is thought to determine the food intake and growth conditions of fish (i.e., Beaugrand and Reid 2003; Richardson and Schoeman 2004; Ware and Thomson 2005; Van Deurs et al. 2013). The access to larger zooplankton appeared to be a critical factor in promoting better growth performance; for example, in the Garcia de Souza et al. (2015) study, the stomach

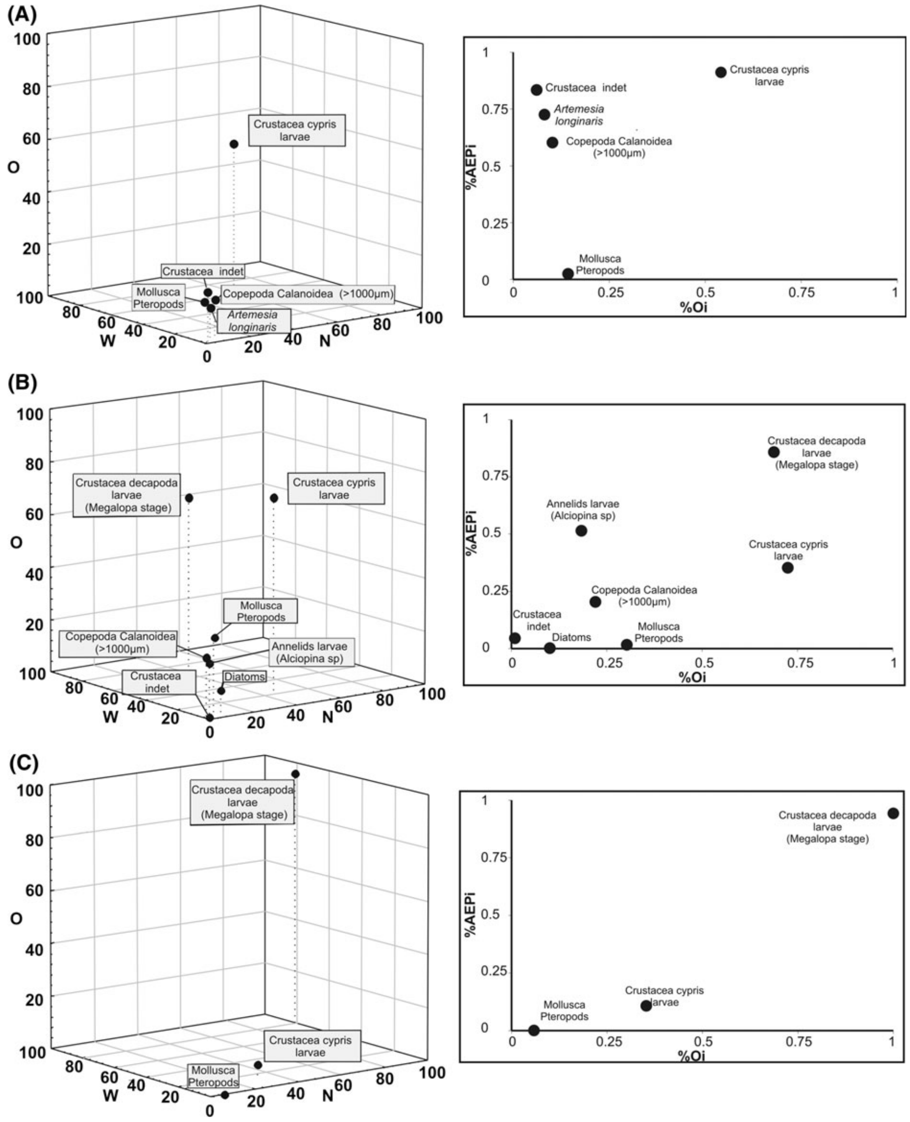

FIGURE 4. Three-dimensional graphical method of Cortés (1997; left panels) and the graphical method of Amunsen et al. (1996; right panels) depicting the food preferences of *Odontesthes argentinensis* for **(A)** both sampling occasions (January and February) in 2013; **(B)** fish smaller than 90 mm total length (L_T) collected during the January 2014 sampling occasion; and **(C)** fish larger than 90 mm L_T collected during January 2014 (O = percent frequency of occurrence; W = percent wet weight; N = percent numerical abundance; %AEP$_i$ = percent prey-specific abundance [prey type *i*]; %O_i = percentage frequency of occurrence for prey type *i*).

content composition for *O. bonariensis* was clearly different from the zooplankton composition in the cages and showed a trend toward inclusion of larger individuals. Moreover, Garcia de Souza et al. (2015) determined that the increment in the percentage of smaller-sized zooplankton in the stomach contents implied an exponential reduction in *O. bonariensis* growth rate.

In our study, the dominant calanoid copepod was *Acartia tonsa*, which has a superior ability (compared with the genus *Paracalanus* and other calanoid copepods) to avoid predation by planktivorous fish (Paffenhofer and Stearns 1988). This suggests the possibility that *Acartia tonsa* is responsible for the negative selectivity. In her work, Bemvenuti (1990) indicated the presence of calanoid copepods at the study site but did not detail the species found. In examining the diets of Brazilian Silversides *Atherinella brasiliensis* (Atherinopsidae), Contente et al. (2011) found that calanoid copepods were the main and more speciose dietary category consumed. However, calanoid copepods of the genus *Acartia* represented a low (7%) proportion of the diet, with a low frequency of occurrence (<22%)—values similar to those registered here for calanoid copepods according to the graphical method of Amunsen et al. (1996; Figure 4).

This difference (no selection of dominant available large copepods) in the diet of *O. argentinensis* during summer could also potentially be explained by the presence of barnacle cypris larvae. Most of the available literature reports that barnacles of the genus *Balanus* (*B. glandula* in our work; *B. improvisus* in Bemvenuti's [1990] work) have one peak of recruitment per year, in approximately winter. However, *B. glandula* along the Argentine coast shows two peaks in recruitment, with the second occurring in summer (Savoya and Schwindt 2010). Mills et al. (1984) explained that due to their gastric inefficiency, larval and juvenile fish prefer smaller prey, which may be an adaptation to assimilate energy from small prey due to the higher surface-to-volume ratio (*Acartia tonsa* adults are 900–1,500 μm in length, while *B. glandula* cypris larvae are about 700 μm). Moreover, cypris larvae are lecithotrophic larvae whose nutrition depends entirely on naupliar food, and they are specialized in habitat and settlement selection (Spivak and Schwindt 2014); therefore, cypris larvae have an important energy reserve and a low ability to avoid predation. Based on this information, it might be suggested that cypris larvae could be positively selected by *O. argentinensis* instead of calanoid copepods. Mouth size and eye size in these fish indicate that they are particulate feeders, mainly using their sense of sight to find and capture their prey (Gerking 1994).

The choice of organisms with a low ability to avoid predation might be corroborated by the change in the diet from cypris larvae to megalopa larvae as the fish grow (higher L_T). The megalopa larvae of decapod crustaceans (20–25 mm) are characterized by slow forward-swimming movement (Pohle et al. 1999), and they constitute a transitional stage (i.e., away from plankton) between the zoeal stages characterized by vigorous swimming and the first stage of juvenile crabs, which is completely benthic (Pohle et al. 1999).

Due to the economic importance of the genus *Odontesthes*, efforts are being made to farm these fish in captivity (Sampaio 2006; Rodrigues et al. 2009; Hualde et al. 2011; Garcia de Souza et al. 2015, 2017). In Japan, there are several farms and intensive farming systems for this genus, whereas farming systems in South America are currently restricted to the artisanal farming of *O. bonariensis* (Tavares et al. 2014; Garcia de Souza et al. 2015, 2017). In recent years, it has been possible to successfully complete the production cycle of the species under intensive culture in tanks, but its culture has not yet reached a productive scale (Berasain et al. 2006; Velasco et al. 2008). *Odontesthes bonariensis* is used in aquaculture due to its high-quality meat, which is appreciated by local and foreign consumers (Carriquiriborde and Ronco 2006). Tavares et al. (2014) indicated that silverside production techniques are improving gradually and that the farming cycle can be completed in closed systems for several other species of the genus *Odontesthes*. Tavares et al. (2014) determined that the condition factor tended to decrease with increasing days of rearing for these species. The information obtained in the present study demonstrates the importance of knowing the food preferences of *O. argentinensis* to obtain a better condition factor during rearing. This information will be key to the potential farming of *O. argentinensis* in closed systems, as has been developed for other marine *Odontesthes* species.

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