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Trophic ecology of the whitemouth croaker, *Micropogonias furnieri* (Pisces: Sciaenidae), in south-western Atlantic waters

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Ontogenetic and seasonal diet changes of the juveniles of the marine fish *Micropogonias furnieri*, a species inhabiting Bahía Blanca estuary (Argentina), were investigated. Two size-related dietary shifts, at 4.00 cm and 7.00 cm total length (L_T), respectively, were found. Small juveniles (1.00–3.99 cm L_T) ate mostly chaetognaths (*Sagitta friderici*); medium-sized juveniles (4.00–6.99 cm L_T) fed intensively on mysid shrimps (mainly *Neomysis americana*) and polychaetes, whereas large juveniles (7.00–15.99 cm L_T) fed almost exclusively on epibenthic crustaceans (primarily *Peisos petrunkevitchi*). Increased mouth gape was related to increased size spectrum and mean size of the most important prey items consumed by *M. furnieri*. Juveniles <10 cm L_T ate prey items almost as large as their mouth opening, whereas juveniles >10 cm L_T were capable of consuming larger prey items than those found in their stomachs, indicating that the maximum size of prey eaten was not constrained by mouth gape. Seasonal and selectivity dietary analyses showed that *M. furnieri* can be a highly opportunistic selective feeder. Juveniles relied on *S. friderici* and *P. petrunkevitchi* throughout the year, except in summer, when mysids abundance increased in the estuary. Electivity values also showed that prey size and prey relative abundance are important factors in prey selection mechanisms.

INTRODUCTION

The whitemouth croaker, *Micropogonias furnieri* Desmarest 1823, is a demersal species which lives in the coastal waters of the south-western Atlantic. It is widely distributed within an area extending from the Gulf of Mexico (20°N) to the Gulf of San Matías, Argentina (41°S) (Vazzoler, 1991; Cousseau, 2000), and it constitutes the support to an important fishery activity in Brazil, Uruguay and Argentina. In Bahía Blanca estuary (Figure 1) *M. furnieri* is the second most important fishing resource. It reached 16% of the commercial landings between 1972 and 1992 although in the last ten years landings strongly decreased and values as low as 2% were reported between 1994 and 1996 (Lopez Cazorla, 1997).

Studies on the food habits of young *M. furnieri* have been conducted in Brazil (Tanji, 1974; Vazzoler, 1991; Mandali de Figueiredo & Viera, 1998; Gonçalves et al., 1999; Mendoza-Carranza, 2002), Uruguay (Puig, 1986), and Argentina (Lopez Carzorla, 1987; Sanchez et al., 1991; Hozbor & Garcia de la Rosa, 2000). In Bahía Blanca estuary, a study carried out by Lopez Cazorla (1987) reported polychaetes to be the predominant food in the stomachs of juveniles during the cold season, yet, this study was based on juveniles captured during a limited period of time. The present research aims at providing a detailed analysis of the diet changes during the ontogeny of *M. furnieri* as well as interpreting these changes in terms of morphology and habitat utilization. The present study also aims at contrasting stomach contents with simultaneously available prey offer in order to elucidate the feeding selectivity mechanisms of juvenile *M. furnieri*.

MATERIALS AND METHODS

Study area

Bahía Blanca estuary, the second largest estuary in Argentina, is located between 38°30′–39°25′S and 61°15′–63°00′W (Figure 1). It covers an area ranging from 750 (low tide) to 1900 (high tide) km^2. The estuary is very shallow, with a mean depth of ~10 metres, and it is highly turbid due to the predominance of fine sediment and the turbulent mixing of waters. Temporal changes are complex, depending mainly on the generally low and variable freshwater input. Water temperature varies seasonally, with highest values in summer (approximately 21°C from December to February) and lowest values in winter (approximately 8°C from June to August). Normally, salinity varies ~30–35 ppt although in summer values as high as >40 ppt may occur.

Field samples and laboratory procedures

Samples of juvenile *Micropogonias furnieri* were collected on a monthly basis in diurnal net tows in Bahía Blanca estuary between March 2000 and February 2001. Samples were taken from the Canal del Embudo zone (Figure 1) using shrimp nets of 1-cm-tail bag mesh (knot-to-knot). Zooplankton samples were collected simultaneously with fish samples using a conical 200-μm mesh plankton net (1.0 m long and 0.3 m in diameter). Three horizontal 5 min tows at 2 kn were made prior to each fish collection, and samples were preserved in formaldehyde (5%). Water temperature was recorded using a HORIBA U10 water analyser.

Figure 1. Bahía Blanca estuary, Argentina. The arrow indicates the sampling station (Canal del Embudo).

In the laboratory, all fish were measured to the nearest mm L_T and subsequently grouped into 1-cm size-classes. A subsample composed of ten randomly selected specimens of each size-class was used for diet analysis. Mouth height (i.e. mouth fully open) and width (i.e. the distance between the angles of the jaw with the mouth opened) were measured in 484 randomly selected fish from a pooled yearly collection covering at least ten animals per size-class. Stomach contents were sorted, counted, and identified to the lowest possible taxon. Maximum widths of intact dietary items were measured. The copepod species *Acartia tonsa* and *Paracalanus parvus* were labelled together as *A. tonsa*/*P. parvus* due to the difficulty in identifying them separately within the digested content.

Stomach contents were compared to the zooplankton prey present at the time of collection. Zooplankters were identified to the lowest possible taxon and counted. Counts were standardized to individuals/m^3.

Data analysis

Diet assessment

Diet was evaluated in terms of frequency of occurrence (FO), numerical composition (N) and biomass composition (W) of the prey items found in the stomach contents.

Multidimensional scaling (MDS) analysis was used to pinpoint dietary size-related and seasonal shifts. Seasons were defined as follows: autumn (March, April, and May), winter (June, July, August, and September), and summer (December, January, and February). The data used were standardized prey numerical abundances per 1 cm predator size-class (Bray & Curtis (1957) dissimilarity index). The adequacy of the representation obtained was measured using the 'stress coefficient' (Clarke & Warwick, 1994).

One-way analyses of variance (ANOVA) were used to test the significance of variation of mean prey number/stomach (MPN) and mean prey biomass/stomach (MPB) among fish size-classes and among seasons. Data were transformed (log, squareroot) to homogenize variances. The normality of the data was verified using Lilliefors' test ($P>0.05$). Also, non-parametric Kruskal–Wallis test was used to evaluate for significant differences in the mean vacuity (%VM) among fish size-classes and among seasons.

Fish and prey morphometric relations

The mouth gape of the fish was estimated as follows: $\mathit{Mouth\ gape}=\mathit{mouth\ height}\times\mathit{mouth\ width}\times\pi$. This equation, which is the area of an ellipse ($\mathit{Area}=\mathit{diameter\ 1}\times\mathit{diameter\ 2}\times\pi$), was used for two reasons. Firstly, we consider it the best way to estimate the mouth opening of the species. Secondly, it involves both the mouth height and width. Regression equations were calculated to evaluate the relationship between fish L_T and fish mouth gape vs maximum prey size.

Table 1. *Water temperature (T°C), total juveniles collected (N), mean total length ±standard deviations (L_T±SD), size range (r), and total number of stomach analysed (n) of juvenile* Micropogonias furnieri *captured in Bahía Blanca estuary between March 2000 and February 2001.*

	T°C	N	L_T ±SD	r (cm)	n
March	22.1	315	5.51 ±1.94	1.5–10	147
April	17.9	825	6.12 ±2.33	1.5–14	186
May	13.4	575	5.43 ±2.68	1.0–16	196
June	12.0	259	4.45 ±2.24	1.5–03	141
July	6.9	391	9.89 ±2.81	2.5–18	199
August	7.4	994	10.67 ±2.83	3.5–18	224
September	11.3	1	14.5 ±0.00	—	—
October	—	0	—	—	—
November	—	0	—	—	—
December	20.3	0	—	—	—
January	22.5	0	—	—	—
February	21.7	24	3.33 ±0.64	2–07	22
Total		**3384**	**7.57 ±3.54**	**1–18**	**1115**

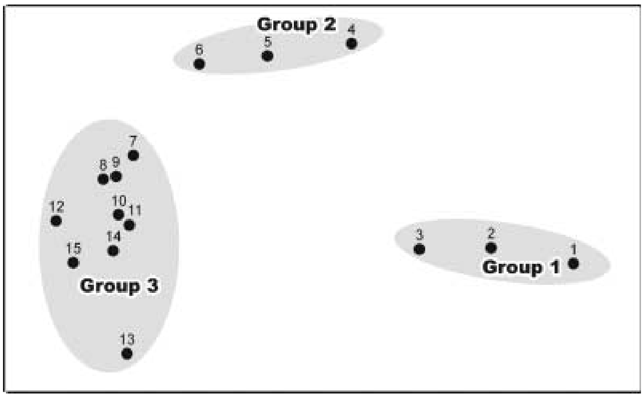

Figure 2. Two-dimensional multidimensional scaling configuration (MDS, stress=0.06) based on the standardized numerical abundances of prey found in the stomach contents of juvenile *Micropogonias furnieri* (N=1115), showing the classification into three trophic groups according to size: Group 1, Group 2, and Group 3. Numbers indicate 1 cm total length (1=1.00–1.99 cm total length (L_T), 2=2.00–2.99 cm L_T, and so on).

Prey selection

Feeding selectivity was evaluated using Vanderploeg & Scavia's (1979) relativized electivity index (E^*): $E^*=[W_i-(1/n)]/[W_i+(1/n)]$, where n=number of prey types and W_i=Chesson's (1983) alpha (α_i) index. Values of E^* range from $E^*=1$, indicating strong selection for a particular prey type, to $E^*=-1$, indicating strong avoidance. E^* values ~ 0 indicate random use of a resource.

RESULTS

Water temperature ranged from 6.9 to 22.5°C, the lowest values occurring in winter (June–September) and the highest ones, in summer (December–February) (Table 1).

Micropogonias furnieri was captured from March to September 2000, and during February 2001, respectively (Table 1). A total of 3384 juveniles ranging from 1 to 18 cm L_T was collected, of which, 1115 between 1.00 and 15.99 cm L_T were used for the diet analyses.

Ontogenetic feeding changes

Stomach contents allowed the identification of three trophic groups in *M. furnieri* (Figure 2, stress=0.06). *Sagitta friderici* was the main food item in terms of frequency, number, and biomass in the diet of members of Group 1 (small juveniles from 1.00–3.99 cm L_T) (Table 2). It was also the most frequent and abundant prey in the stomach contents of members of Group 2 (medium-sized animals from 4.00–6.99 cm L_T), while polychaetes were

Table 2. *Diet composition of the total sample and of three trophic groups (Small, Medium and Large, for grouping see Figure 2) of* Micropogonias furnieri.

		Total			**Small**			**Medium**			**Large**	
cm L_T		1.00–15.99			1.00–3.99			4.00–6.99			7.00–15.99	
Total stomachs		1115			178			320			617	
Empty stomachs		330			44			69			217	
	%FO	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**
Prey items												
Polychaetes	18.09	5.13	16.36	4.48	0.94	7.22	19.12	6.11	40.68	22.00	6.29	14.05
Sagitta friderici	27.77	29.99	1.40	74.63	69.65	53.26	34.26	45.91	6.91	8.00	4.94	0.24
Acartia tonsa	8.41	3.46	0.01	23.88	9.59	0.38	10.76	4.27	0.03	1.75	0.51	0.00
Labidocera fluviatilis	10.45	4.57	0.10	10.45	4.25	1.82	18.73	9.69	0.65	5.25	1.86	0.02
Calanoides carinatus	1.02	0.33	0.01	0.00	0.00	0.00	2.39	0.92	0.10	0.50	0.13	0.00
Copepods*	5.48	2.32	0.00	13.43	4.40	0.13	6.37	3.23	0.02	2.25	0.96	0.00
Total		10.68	0.12		18.24	2.33		18.11	0.80		3.47	0.03
Arthromysis magellanica	5.48	1.67	0.79	2.24	0.47	0.97	5.18	2.19	2.83	6.75	1.86	0.59
Neomysis americana	8.92	2.74	0.42	10.45	2.67	2.50	11.16	3.81	1.30	7.00	2.18	0.31
Mysids*	9.17	2.45	0.56	11.19	2.52	8.15	12.75	3.69	2.74	6.25	1.73	0.26
Total		6.86	1.77		5.66	11.62		9.69	6.87		5.78	1.15
Penaeids	10.32	3.63	11.30	0.75	0.31	2.41	8.37	3.00	8.22	14.75	5.33	11.71
Peisos petrunkevitchi	28.54	22.02	51.28	1.49	0.31	4.81	10.76	4.38	18.55	48.75	40.69	55.08
Crabs	2.93	0.75	1.39	1.49	0.31	0.02	1.20	0.35	8.20	4.50	1.16	0.73
Amphipods	10.19	9.60	0.42	4.48	0.94	0.07	6.37	3.11	0.55	14.50	16.75	0.41
Crustacea*	14.90	4.67	2.92	4.48	0.94	6.61	13.55	3.92	4.68	19.25	6.61	2.70
Sciaenidae	3.95	1.44	3.31	3.73	0.79	4.12	3.19	1.27	1.23	4.50	1.80	3.50
Engraulidae	2.55	0.95	4.05	–	–	–	0.80	0.23	0.98	4.50	1.73	4.40
Fish*	7.13	1.99	5.67	4.48	1.26	7.49	6.77	1.96	2.30	8.25	2.31	5.99
Total		4.38	13.03		2.04	11.62		3.46	4.52		5.84	13.89
Other taxa	7.01	2.29	0.02	2.99	0.63	0.03	5.98	1.96	0.03	9.00	3.15	0.02

%FO, per cent frequency of occurrence; %N, per cent number; %W, per cent wet weight. *, unidentified species.

Table 3. *Mean vacuity (%VM), mean prey number/stomach (MPN) and mean prey biomass/stomach (MPB) in the diets of three trophic groups of* Micropogonias furnieri *(Small=1.00–3.99 cm total length (L_T) (N=15), Medium=4.00–6.99 cm L_T (N=19), and Large=7.00–15.99 cm L_T (N=44)) and three seasons: (A) %VM, MPN and MPB in autumn (N=37) and winter (N=38) taking into consideration the three trophic groups; (B) %VM, MPN and MPB in autumn (N=8), winter (N=4) and summer (N=5) taking into consideration only the 'small' trophic group.*

	% VM	MPN	MPB
Size			
Small	32.78 ±32.81	3.65 ±2.38	0.005 ±0.003
Medium	26.19 ±20.66	2.93 ±1.87	0.02 ±0.03
Large	27.58 ±29.09	3.61 ±3.08	0.21 ±0.26
Season			
(A)			
Autumn	8.46 ±11.87	5.15 ±2.87	0.21 ±0.28
Winter	48.66 ±24.8	1.85 ±1.13	0.06 ±0.11
(B)			
Autumn	15.10 ±18.80	4.99 ±2.25	0.006 ±0.003
Winter	74.00 ±17.82	1.55 ±0.58	0.003 ±0.005
Summer	12.50 ±14.43	1.90 ±0.90	0.007 ±0.006

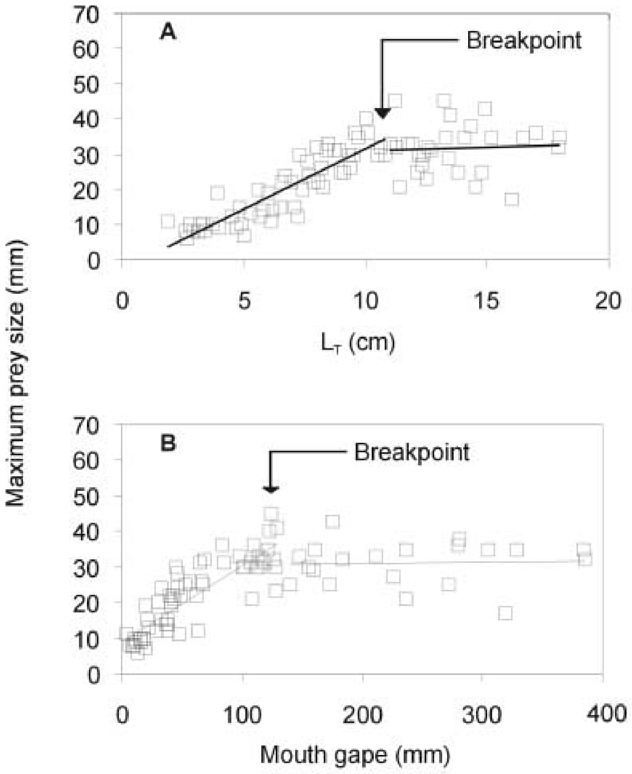

Figure 3. Maximum prey size as a function of (A) fish total length (L_T) and (B) fish mouth gape of the juveniles of *Micropogonias furnieri* from Bahía Blanca estuary (N=85). Both regressions yielded a breakpoint. In (A) regression was significant for individuals <10 cm L_T (maximum prey size=3.6 L_T−3.55, r^2=0.77, $P<0.01$) but was not significant for those >10 cm L_T (P=0.77). In (B) regression was significant for mouth gape <120 mm^2 (maximum prey size=0.23, mouth gape+8.37, r^2=0.76, $P<0.01$). Upon 120 mm^2, regression was not significant (P=0.69).

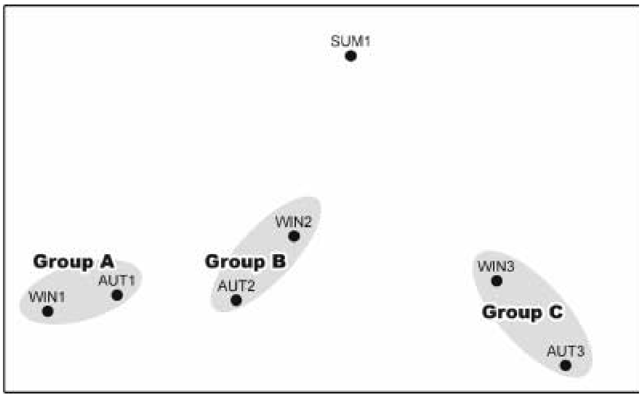

Figure 4. Two-dimensional multidimensional scaling configuration (MDS, stress=0.02) based on the standardized numerical abundances of prey found in the stomach contents of three trophic groups: 1, small *Micropogonias furnieri* (1.00–3.99 cm total length (L_T)); 2, medium *M. furnieri* (4.00–6.99 cm L_T); 3, large *M. furnieri* (7.00–15.99 cm L_T) (N=1115), showing the classification by season into three groups: Group A, Group B, and Group C.

dominant in terms of biomass. As to the members of Group 3 (large individuals ranging from 7.00 to 15.99 cm L_T), *Peisos petrunkevitchi* was the dominant prey in terms of frequency, number, and biomass (Table 2).

Mean vacuity (%VM) and mean prey number (MPN) and biomass (MPB) per stomach were calculated and compared for each trophic group identified by MDS analysis. The %VM decreased from small to large *M. furnieri* (Table 3), however, no statistical differences were found among trophic groups (P=0.77). Also, no statistical differences were found in the MPN among trophic groups (P=0.74). On the other hand, MPB increased significantly across the three-trophic groups (Table 3).

Fish and prey morphometric relations

A linear regression model was fitted to the data of fish L_T vs maximum prey size, which yielded a breakpoint in the regression model at 10 cm L_T (Figure 3A). The regression was significant in individuals <10 cm L_T ($P<0.01$) although it was not significant in larger fish (P=0.77). A linear regression was also fitted to the data of fish mouth gape vs maximum prey size, which also yielded a breakpoint at 120 mm^2 of mouth gape. Upon 120 mm^2, regression was not significant (P=0.69, Figure 3B).

Seasonal feeding changes

The MDS was carried out taking into consideration the trophic groups identified by the ontongenetic MDS analysis (see above). Medium juveniles from summer were not included in the seasonal and selectivity (see below) analyses because only four individuals of this trophic group were captured in summer. Three seasonal groups and one ungrouped season (small juveniles from summer) were identified (Figure 4, stress=0.02). Group A included small juveniles from autumn and winter and was characterized by the dominance of chaetognaths in their diets

Table 4. *Seasonal diet composition of three trophic groups (1, 1.00–3.99 cm total length (L_T); 2, 4.00–6.99 cm L_T; and 3, 7.00–15.99 cm L_T) of* Micropogonias furnieri.

	AUTUMN									WINTER									SUMMER		
Trophic groups	1			2			3			1			2			3			1		
Total stomachs	112			176			241			48			140			376			18		
Empty stomachs	3			13			12			29			56			203			2		
	%FO	%N	%P	%FO	%N	%P	%FO	%N	%P	%FO	%N	%P	%FO	%N	%P	%FO	%N	%P	%FO	%N	%P
Prey items																					
Polychaetes	5.5	1.0	8.6	27.0	7.0	46.8	29.3	6.2	14.3	–	–	–	3.6	1.8	23.2	12.1	6.4	12.8	–	–	–
S. friderici	76.1	72.5	60.6	38.7	49.4	7.6	10.0	3.5	0.2	83.3	76.7	90.1	27.4	31.3	6.6	5.2	10.3	0.7	18.8	9.7	2.4
A. tonsa/P. parvus	23.9	8.5	0.4	12.3	4.1	0.0	3.1	0.6	0.0	5.6	3.3	0.2	8.3	4.9	0.0	–	–	–	31.3	35.5	0.4
L. fluviatilis	11.0	4.3	2.0	20.9	8.3	0.6	6.6	1.6	0.0	11.1	6.7	6.4	14.3	15.3	1.7	4.0	2.7	0.0	–	–	–
C. carinatus	–	–	–	–	–	–	–	–	–	–	–	–	7.1	4.9	0.9	1.2	0.6	0.0	–	–	–
Copepods*	15.6	4.7	0.2	8.6	3.7	0.0	3.9	1.3	0.0	–	–	–	2.4	1.2	0.0	–	–	–	6.3	3.2	0.1
Total		17.6	2.5		16.1	0.6		3.6	0.0		10.0	6.6		26.4	2.7		3.3	0.1		38.7	0.5
A. magellanica	1.8	0.3	1.1	6.1	1.4	3.8	4.8	1.1	0.4	–	–	–	4.8	3.1	9.1	9.2	5.2	1.7	6.3	3.2	0.5
N. americana	8.3	1.7	1.8	13.5	4.0	10.0	7.4	1.9	0.1	–	–	–	4.8	2.5	2.3	6.4	3.3	1.2	31.3	22.6	7.6
Mysids*	11.0	2.1	2.2	6.1	1.4	1.1	6.6	1.4	0.2	–	–	–	9.5	4.9	14.7	5.8	3.3	0.6	18.8	12.9	50.5
Total		4.2	5.1		6.8	14.9		4.3	0.7		–	–		10.4	26.1		11.8	3.5		38.7	58.6
Peaneids	0.9	0.3	2.9	8.0	3.3	6.5	21.8	5.9	13.3	–	–	–	9.5	4.9	14.9	5.2	3.0	3.6	0.0	0.0	0.0
P. petrunkevitchi	0.9	0.2	4.3	15.3	5.0	13.5	67.7	45.7	57.1	–	–	–	3.6	1.8	3.0	23.1	21.2	44.9	6.3	3.2	9.6
Crabs	1.8	0.3	0.0	6.1	1.4	0.9	6.1	1.1	0.9	–	–	–	4.8	2.5	0.9	2.3	1.2	0.1	–	–	–
Amphipods	5.5	1.0	0.1	7.4	3.3	0.6	12.2	16.5	0.3	–	–	–	7.1	3.7	2.6	17.9	17.9	0.9	–	–	–
Crustacea*	2.8	0.5	3.6	9.2	2.1	3.4	15.7	4.9	1.5	5.6	3.3	0.0	21.4	11.0	16.1	23.7	12.7	8.8	12.5	6.5	19.3
Sciaenidae	4.6	0.9	4.9	4.9	1.6	1.5	7.9	2.2	4.1	–	–	–	–	–	–	0.6	0.3	0.6	–	–	–
Engraulidae	–	–	–	1.2	0.3	1.2	7.9	2.2	5.3	–	–	–	–	–	–	–	–	–	–	–	–
Fish*	4.6	1.2	7.5	9.2	2.1	2.3	6.6	1.5	2.3	–	–	–	6.0	3.1	3.9	11.6	6.1	24.1	6.3	3.2	9.6
Total		2.1	12.4		4.0	5.0		5.8	11.7		–	–		3.1	3.9		6.4	24.7		3.2	9.6

%FO, per cent frequency of occurrence; %N, per cent number; %W, per cent wet weight. *, unidentified species.

Table 5. *Seasonal zooplankton densities (mean ind/m*^{3} *±SD) and selectivity values (E*) for zooplankton taxa that were found in the diet of three trophic groups (1, 1.00–3.99 cm total length (*L_T*); 2, 4.00–6.99 cm* L_T*; 3, 7.00–15.99 cm* L_T*) of juvenile* Micropogonias furnieri *from Bahía Blanca estuary.*

	AUTUMN				WINTER				SUMMER	
		E*				**E***				E*
Zooplankton taxa	Ind/m^3	**1**	**2**	**3**	Ind/m^3	**1**	**2**	**3**	Ind/m^3	**1**
Acartia tonsa + *Paracalanus parvus*	719.24 ±631.09	−0.99	−1	−1	37.68 ±35.35	−1	−1	−1	763.87 ±345.15	−1
Euritemora americana	–	–	–	–	0.42 ±0.52	–	–	–	–	–
Labidocera fluviatilis	0.62 ±0.75	–	–	–	0.04 ±0.05	0.59	0.67	0.54	4.07 ±1.23	−1
Calanoides carinatus	0.52 ±0.90	−1	−1	−1	0.45 ±0.73	−1	−0.7	−0.8	0.20 ±0.34	−1
Ctenocalanus vanus	7.48 ±10.54	–	–	–	0.69 ±0.57	–	–	–	12.64 ±5.31	–
Euterpina acutifrons	104.34 ±89.39	–	–	–	71.52 ±84.36	–	–	–	77.30 ±57.97	–
Oithona sp.	–	–	–	–	0.53 ±0.90	–	–	–	7.49 ±2.21	–
Monstrillida sp.	–	–	–	–	0.19 ±0.25	–	–	–	1.09 ±1.42	–
Cyclopoids	–	–	–	–	0.16 ±0.31	–	–	–	0.60 ±0.54	–
Copepod nauplii	0.89 ±0.61	–	–	–	0.55 ±0.52	–	–	–	4.72 ±2.87	–
Cirripedia nauplii	–	–	–	–	2.23 ±2.40	–	–	–	0.23 ±0.41	–
Crab zoeae and megalopae	1.93 ±1.08	−0.98	−1	−0.9	–	–	–	–	23.86 ±8.83	−1
Gamamarids	–	–	–	–	–	–	–	–	0.43 ±0.38	–
Mysids	0.05 ±0.09	0.61	0.67	0.55	1.78 ±1.75	−1	−0.7	−0.3	16.28 ±6.86	−0.5
Peisos petrunkevitchi	0.22 ±0.38	−0.99	−0.8	0.03	–	–	–	–	0.01 ±0.01	0.72
Crustacea eggs	13.30 ±8.70	–	–	–	0.11 ±0.22	–	–	–	9.25 ±4.92	–
Sagitta friderici	5.70 ±5.93	0.28	−0.2	−0.9	0.64 ±0.30	0.37	−0.3	−0.2	2.59 ±0.11	−0.2
Veliger larvae	11.21 ±7.17	–	–	–	0.15 ±0.15	–	–	–	56.70 ±51.63	–
Tintinids	–	–	–	–	71.24 ±82.55	–	–	–	0.61 ±0.61	–
Conopeum sp.	1.65 ±1.12	–	–	–	0.53 ±0.44	–	–	–	4.97 ±2.59	–
Bivalve larvae	1.18 ±1.07	–	–	–	0.05 ±0.1	–	–	–	1.90 ±0.85	–
Polychaete larvae	1.15 ±1.10	–	–	–	2.56 ±2.35	–	–	–	4.30 ±2.96	–
Hydromedusae	0.14 ±0.24	–	–	–	0.13 ±0.27	–	–	–	1.18 ±0.52	–
Fish	0.01 ±0.02	0.02	0.08	0.41	0.02 ±0.03	−1	−0.7	0.17	0.68 ±0.54	−0.2
Other taxa	0.15 ±0.002	–	–	–	0.36 ±0.35	–	–	–	3.98 ±3.00	–
Total	**869.78 ±82.30**				**192.05 ±88.70**				**1000.00 ±295.06**	

(Table 4). Group B was represented by medium *M. furnieri* from autumn and winter, with their diets dominated by chaetognaths in terms of frequency and number, and by polychaetes and mysids in terms of biomass. Group C included large juveniles from autumn and winter, with their diets dominated by *P. petrunkevitchi* in terms of frequency, number, and biomass. In small *M. furnieri* from summer, the calanoid copepods *Acartia tonsa/Paracalanus parvus* and mysids were the most important prey items in terms of frequency and number, whereas mysids were the most important prey item in terms of biomass (Table 4).

To test for significant differences in %VM, MPN and MPB among seasons, two sets of statistic tests (Kruskal–Wallis and ANOVA analyses) were carried out. In the first one, autumn and winter were compared taking into consideration the three trophic groups identified by the ontogenetic MDS analysis (see Table 3A). In the second one, autumn, winter, and summer were compared taking into consideration only the 'small' trophic group (see Table 3B). The %VM was always higher in winter than in the other two seasons (Table 3). The MPN was lower in winter than in autumn and summer, although statistical differences were only found between winter and autumn ($P<0.01$). Similarly, MPB was always lower in winter than in autumn and summer. However, significant differences were only found between autumn and winter ($P<0.01$).

Prey selection

Total zooplankton density ranged from 464 ind/m^3 (mean ±SD=116 ±79 ind/m^3) in winter to 3067 ind/m^3 (1022 ±319 ind/m^3) in summer (Table 5). There was a clear dominance of copepods throughout the year (65–95% of the total abundance). *Acartia tonsa*, *P. parvus*, and the harpapticoid *Euterpina acutifrons* were the dominant species. As to the zooplankton taxa that contributed to the juveniles' diets, mysids increased in summer whereas *Peisos petrunkevitchi* was more abundant in autumn. *Sagitta friderici* was present throughout the year and was more abundant in autumn and summer. Similarly, fish larvae were found during the three seasons considered in the present study although the highest numbers were registered in summer (Table 5).

Sagitta friderici was always positively selected by small *M. furnieri* (except in summer, when it was negatively selected) and was always avoided by medium and large *M. furnieri* (Table 5). On the other hand, fish were only selected by large *M. furnieri*, and were always randomly or negatively selected by small and medium *M. furnieri*. Mysids were positively selected by all juveniles from autumn. In contrast, they were always avoided in winter and summer. Similarly, the calanoid *Labidocera fluviatilis* was positively selected by all size-classes in winter, and was negatively selected in summer (this copepod was not captured in the zooplankton nets in autumn). The sergestid *P. petrunkevitchi* was avoided in autumn by small and medium juveniles, and randomly eaten by large ones. In contrast, it was positively selected by small juveniles from summer. The copepods *A. tonsa/Paracalanus parvus* and *Calanoides carinatus*, and crabs were negatively selected in all the seasons considered in the present study (Table 5).

DISCUSSION

Micropogonias furnieri has been identified as a generalist feeder (Sánchez et al., 1991; Gonçalves et al., 1999; Hozbor & García de la Rosa, 2000; Mendoza-Carranza, 2002), meaning it has a broad dietary niche width. In the present study, a different feeding strategy for the juvenile population inhabiting Bahía Blanca estuary was observed. All trophic groups evidenced a narrow diet spectrum, with one or two prey species dominating their diet. In small *M. furnieri*, the chaetognath *Sagitta friderici* represented 70% of the total diet in terms of frequency and number, and more than 50% in terms of biomass. The diet of medium juveniles was more diversified with respect to that of small juveniles although it consisted mainly of two prey items, namely, *S. friderici* and polychaetes. Large *M. furnieri* consumed almost exclusively *Peisos petrunkevitchi*. In these juveniles, the sergestid was eaten by more than half of the collected fish and represented 50% of the total diet biomass. The differences in the trophic spectrum and feeding strategy found among populations from different geographic areas in Argentina could be explained in terms of the idea that populations with a wide trophic niche may include individuals with narrow or wide niches, or a combination of both (Amundsen et al., 1996). Under this condition, the feeding strategy of the species is dependent on the population under analysis. In this study, we analysed the juvenile population ranging from 1 to 15 cm L_T. Sánchez et al. (1991) reported on the diets of the entire population, including juveniles and adults ranging from 1 to 50 cm L_T, from Samborombón Bay in the province of Buenos Aires, Argentina, whereas Hozbor & García de la Rosa (2000) described the diets of juveniles ranging from 1 to 28 cm L_T from a coastal lagoon in the province of Buenos Aires. On account of the fact that the feeding strategy is related to population, these differences in the size-structure of the populations may account for the differences in their feeding strategy.

Micropogonias furnieri has also been identified as an opportunistic feeder (Sánchez et al., 1991; Gonçalves et al., 1999; Hozbor & García de la Rosa, 2000). Thus, stomach contents largely reflect seasonal changes in prey availability. This was corroborated in the juvenile population from Bahía Blanca estuary. In fact, seasonal dietary analysis indicated that *M. furnieri* fed on *S. friderici* and *P. petrunkevitchi* in autumn and winter, and on mysids in summer, when the abundance of this prey item increased in the estuary. Juveniles from summer apparently preferred mysids to other prey available, namely, *S. friderici* and *Labidocera fluviatilis*. However, and although mysids were the principal component in the diet of *M. furnieri* in summer, electivity values showed that juveniles from summer ate fewer mysids than expected from their availability in the water column. A similar pattern was observed for *P. petrunkevitchi*. Although *P. petrunkevitchi* was the principal food item for juveniles in autumn, it was avoided by small and medium *M. furnieri* and randomly eaten by large *M. furnieri*. Negative or random selection over abundance prey resources could be related to several factors, such as differences in the vertical distributions of the predator and prey, prey morphology, prey relative abundance, availability of other prey taxa, and the predator's innate preferences. In this respect, the negative electivity values for mysids and *P. petrunkevitchi* in seasons when they were the principal dietary components, are likely to be related to their high availability during such seasons. Abundance values for *P. petrunkevitchi* are probably underestimated because of this sergestid net avoidance during sampling. Our observations in the field as well as previous published data (Mallo & Cervellini, 1988) indicate that *P. petrunkevitchi* is very abundant in Bahía Blanca estuary during autumn.

On the other hand, prey selection was also found to be related to prey size and to fish energy requirements. Electivity values show that *S. friderici* was only positively selected by small *M. furnieri*. In addition, selection values were more strongly negative in larger juveniles than in smaller ones (see Table 5). In contrast, fish were only selected by large *M. furnieri* and selection values increased with fish size. These findings are in agreement with previous studies carried out in the area of study regarding a closely related species, the striped weakfish (*Cynoscion guatucupa*), which was also found to prefer larger prey items with increasing fish size (Sardiña & Lopez Cazorla, 2005).

Published data on the diet of juvenile *M. furnieri* are scarce in Argentina. Hozbor & García de la Rosa (2000) reported that polychaetes and crustaceans, mostly gammaridea amphipods and isopoda, are the dominant prey items of *M. furnieri* from Mar Chiquita lagoon. In contrast to the observations in the present study, *P. petrunkevitchi* was considered to be a secondary food item. Also, the above-mentioned authors found ontogenetic dietary shifts, in which copepods were the main food item for fish from 2 to 4 cm L_T, and polychaetes and amphipods were the most important food item in those from 5 to 15 cm L_T. Sánchez et al. (1991) reported mysids to be the main prey item in the diets of juveniles and adults (4–42 cm L_T) from Samborombón Bay. These authors also found size-related dietary shifts wherein copepods, eggs, and larvae of fish and crustaceans dominated the diets of *M. furnieri* smaller than 14 cm L_T, and wherein fish and benthic crustaceans dominated in those larger than 14 cm L_T. In agreement with our study, *P. petrunkevitchi* was considered to be an important prey item for larger juveniles.

Vazzoler (1991) reported that polychaetes are the dominant food item in the Brazilian coast. On the other hand, Mandali de Figueiredo & Vieira (1998) claimed that the tanaidacean *Kalliapseudes schubartii* dominated the diet of juveniles and subadults from the Los Patos lagoon, whereas Gonçalves et al. (1999) described 13 dietary groups for juveniles (2–31 mm L_T) from the same lagoon, including copepods, mysids, and cumaceans. Mendoza-Carranza (2002) reported polychaetes, tanaidaceans and bivalves to be the main components in the diet of juveniles (3–20 cm L_T) captured in five estuaries from Rio Grande do Sul, Brazil.

The ontogenetic shifts registered in *M. furnieri* coincide with those registered in *Micropogonias undulatus* from the US Atlantic coast (Govoni et al., 1983; Soto et al., 1998). In both species small individuals feed mainly on copepods, whereas larger ones feed mainly on polychaetes. Conversely, our data show that although copepods and polychaetes are important prey groups, the diet is dominated by *S. friderici* (a chaetognath, in small juveniles) and *P. petrunkevitchi* (a crustacean, in large juveniles). While the dominance of the crustacean in the diet of *M. furnieri* is most probably due to its abundance in many coastal areas of Argentina, including Bahía Blanca estuary (Mallo & Cervellini, 1988), the dominance of the chaetognath involves active positive selection. Interestingly, and although *S. friderici* is common in the area, it is significantly less abundant and widespread than *Acartia tonsa*, *Paracalanus parvus* and other copepod species found in the estuary. The biomass contribution of *S. friderici* in the diets of *M. furnieri* was always much larger than that of copepods. The preference for this chaetognath is therefore most probably related to the energetic requirements of the fish as well as to the need to optimize energy intake.

The dietary shifts registered in the present study are related to changes in habitat utilization and morphology. During development, juveniles switch from pelagic to an epibenthic predation. These changes involve an increase in the quality of the diet wherein more profitable food, such as polychaetes and crustaceans are incorporated in the diet. In fact, as *M. furnieri* grew, net prey biomass (and therefore the nutritional value of the diet) also increased (see Tables 2 & 3). Changes in habitat utilization were also reported by Vazzoler (1991), who indicated that *M. furnieri* switches from a planktonic to a more diversified demersal and benthic diet.

Growth in length and weight is generally accompanied by increased mouth dimensions, allowing larger prey items to be ingested (Boubée & Ward, 1997). Our data support this relationship in small *M. furnieri* although it is less obvious in larger juveniles. In fish >10 cm L_T, the maximum size of prey consumed was not constrained by the mouth gape. This indicates that mouth opening is not a limiting factor for the ingestion of larger prey types among the larger juveniles. In fact, the preference for prey items that are substantially smaller than those presumably permitted depending on mouth-size is common among fish (Boubée & Ward, 1997) most probably because factors other than mouth gape are involved, such as sight, swimming, and handling abilities, etc.

Feeding activity was also found to be directly dependent on water temperature. In summer and autumn, feeding was more intense while it decreased during winter. It was also observed that MPN and MPB decreased during winter. This could be indicative of the fact that juveniles reduce their feeding activity as temperature decreases (7°C in July and August). Also, the total zooplankton density decreased to 464 ind/m^3 in winter (compared to 1500 and 3000 ind/m^3 registered in autumn and summer, respectively), suggesting that the decreased availability of prey, particularly high-energy food such as *Peisos petrunkevitchi*, also affected feeding. Our data suggest that the limited food supply and the low water temperatures are limiting factors for winter juveniles in Bahía Blanca estuary. These factors may also directly influence the seaward migration of large numbers of *M. furnieri* that is registered at the end of every autumn. Little is known about the migration patterns of this species in Bahía Blanca estuary. Lopez Cazorla (1987) suggested that juveniles with a mean size of 10 cm L_T leave the estuary at the end of autumn (June–July) following on the decrease in water temperature. These individuals develop and grow in the open sea, and return to the estuarine zone as adults to reproduce and spawn. Our results, together with those of Lopez Cazorla (1987), suggest that migration patterns are likely to be regulated by environmental as well as biological factors, among which, temperature and availability of food resources are the most important ones.

The emigration of juvenile *M. furnieri* from Bahía Blanca estuary undoubtedly represents a crucial transfer of energy to the relatively low production areas outside the estuary. As a result, and in view of the data collected from our research, it can be concluded that juvenile *M. furnieri* plays an important trophic role not only as an important consumer of zooplankton during estuarine residency but also as an exporter of estuarine production to the ocean during winter seaward migrations.

CONCLUSION

In contrast to what was observed in *Micropogonias furnieri* from other geographic areas in Argentina, our results indicate that juvenile population of *M. furnieri* from Bahía Blanca estuary has a more specialized diet, with a narrow dietary breadth, dominated by a few prey items (i.e. *Sagitta friderici*, *Peisos petrunkevitchi*, polychaetes and mysids). Our results also demonstrate important size-related shifts in the diet of the juveniles of this species. These shifts are related to changes in habitat use (from pelagic to epibenthic and benthic predation), foraging behaviour (wherein smaller fish ate at higher feeding rates over smaller prey items and in lower quantities, in terms of biomass, than larger fish) and morphological features (related to size changes in the feeding apparatus) and entail an increase in the quality of the diet, replacing chaetognaths with more energetically profitable food items, such as polychaetes, mysids and *P. petrunkevitchi*. Seasonal dietary changes were also found and evidenced the changes in the availability of organisms in the environment.

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