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Feeding ecology of *Brevoortia aurea* larvae (Clupeidae, Alosinae) from Río de la Plata estuary off Uruguay

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ABSTRACT

This study analyses the feeding ecology of *Brevortia aurea* (Brazilian menhaden) larvae during a reproductive season in the Río de la Plata estuary (RPE), and explores its changes along larval development. Data were obtained from stomach content analyses of 205 individuals collected with a Bongo net during spring 2001. Larvae were discriminated into preflexion (PF), flexion (F) and post-flexion (PsF) stages. Feeding was described using complementary metrics like Feeding incidence (FI), the Relative Importance of different prey types consumed (IRI), the Degree of prey digestion (E) and Diet overlap (D), which were estimated and compared between stages. Also, larval morphometric relationships (body length, BL vs mouth width, MW) and between MW and maximum prey width (Wmax) were established for the range of observed larval sizes. The overall FI was 46.3% and increased with the development stage: 40.4% PF, 63.3% F, 78.6% PsF. Feeding occurred mainly during sunlit hours but no clear daily cycle could be established. Copepods and in particular *Acartia tonsa* were well represented among ingested preys, followed by invertebrate eggs and nauplii. Prey diversity and overlap between stages tended to decrease as development progressed. *B. aurea* exhibited isometric growth of MW in relation to BL. Average Wmax was 222.5 µm ± 100.9 SD, and increased non-linearly with both BL and MW. Gape size alone did not seem to be the limiting factor for prey choice (size), and we hypothesize that factors involved in the feeding mechanism other than mouth gape and linked with capture performance substantially influence the feeding ecology of this species in the RPE.

Descriptors: Fish larval feeding, Larval morphometry, Brazilian menhaden, Lacha, *Acartia tonsa*.

INTRODUCTION

Brevoortia aurea (Spix and Agassiz, 1829) -locally named as Lacha (Uruguay)- is an estuarine-dependent, pelagic coastal species present in South West Atlantic coastal waters between 13°S (Brazil) and 40°S (Argentina). This is the only *Brevoortia* species that inhabits South American Atlantic waters (Cousseau and Díaz de Astarloa, 1993; García et al., 2008). It is an important and often dominant component of the fish community of the Río de la Plata Estuary (RPE) (Cousseau, 1985; Boschi, 1988), and other microtidal estuaries along the Uruguayan coast (Santana and Fabiano, 1999; Gurdek and Acuña-Plavan, 2016; Gurdek et al., 2016; Rodríguez, 2016). As other clupeids, *B. aurea* plays an important role in the cycling of

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matter in pelagic marine ecosystems linking primary producers and higher consumers. Adults are filter feeders which feed mainly on plankton (Sánchez, 1989; Giangiobbe and Sánchez, 1993), and are in turn important components in the diet of several larger fishes (Rivera Prisco et al., 2001; Norbis and Galli, 2004; López Cazorla and Forte, 2005; De Wysiecki et al., 2018), and birds (Mauco and Favero, 2004). The species also supports coastal artisanal and industrial-scale fisheries in Brazil, Argentina and Uruguay (Lorenzo et al., 2015; Biolé et al., 2020).

Based on previous investigations, there is well established knowledge on the biogeography, phylogeny (Cousseau and Díaz de Astarloa, 1993; García et al., 2008; Bonetti Pozzobon et al., 2021) and life history of juvenile-adult stages of *B. aurea* (e.g. Acha and Macchi 2000; Valiñas et al., 2012; Bruno et al., 2015; Lajud et al., 2016; Rodríguez, 2016). Knowledge on larval stages has lagged behind, but few studies have addressed larval development (de Ciechomski 1968; Cassia and García de la Rosa, 1993), the distribution of eggs and larvae, and their occurrence in relation to hydrography (Berasategui et al., 2004; Hoffmayer et al., 2009; Machado et al., 2011, 2021). However, knowledge on the trophic ecology of *B. aurea* during larval stages is fragmentary. Larvae of *B. aurea* were described as zooplanktivores, with the bulk of their diet made up of developmental stages of calanoids copepods (Giangiobbe and Sánchez, 1993; Machado et al., 2017), and with indirect significant carbon contributions of macrodetritus and resuspended debris in shallow coastal lagoons (Bruno, 2014).

Studies based on larval feeding contribute relevant information to understand recruitment processes, their mechanisms and the fluctuations of fish populations (Fuiman and Werner, 2000). Traits such as size and biochemical composition of preys (Machado et al., 2017) appear to be key determinant of successful feeding in fish larvae. In turn, endogenous factors as body length and mouth gape size correlate with the size of prey consumed (e.g. Pepin and Penney, 1997), and it has been hypothesized that fish larvae are gape-limited predators. However, the average size of prey consumed is in many cases well below that predicted by mouth-size *vs* prey-size relationships (Arthur, 1976; Krebs and Turingan, 2003).

The RPE and inner shelf waters are important spawning and nursery areas for several fish species including *B. aurea,* where the salinity front and wind patterns favour larval retention within the estuary (Acha and Macchi, 2000; Simionato et al., 2008; Braverman et al., 2009). That area offers shelter and higher temperatures which benefit larval survival (Berasategui et al., 2004). Despite the relevance for fish recruitment, current knowledge on the trophic ecology of fish larvae from of RPE is very scarce (Rodríguez-Graña et al., 2018), and particularly for *B. aurea*.

In this context, the feeding ecology of larval *B. aurea* was analysed in terms of type and size of ingested prey, feeding preferences, and feeding variability along the daily cycle. The analysis considered different development stages during one reproductive season at RPE (austral spring). The larvae of *B. aurea* were expected to differ in feeding strategies between developmental stages, which were further explored based on the analysis of intraspecific morphometric relationships and their links to ecological descriptors such as prey size.

METHODS

Study area and sampling collection

Plankton samples were collected on board the R/V Aldebarán during November 2001 (From November 17 to 19). A total of 25 stations arranged in three transects (T1, T2, T3) were surveyed within the RPE (Fig. 1). Environmental data (vertical profiles of salinity and water temperature) were recorded with a CTD profiler SBE-19. Salinity derived from conductivity measurements corresponds to the practical scale and is reported without units.

Fish larvae were collected from oblique tows from near the bottom to the surface (bottom depth ranged from 6 to 36 m) with a 50 cm mouth diameter Bongo net fitted with a 300 µm mesh net and a General Oceanic® flowmeter to estimate the volume of water sampled. Tows were performed between 8:30 to 23:30 local time but mostly occurred during daylight hours. All samples were preserved in 4% marine formaldehyde buffered with borax.

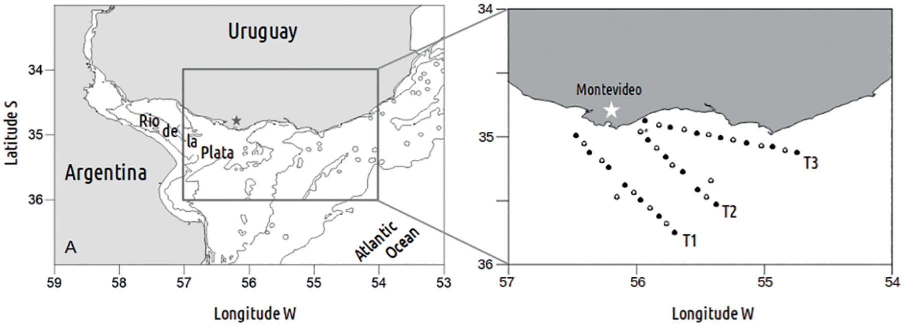

Figure 1. Study area. Left panel: Location of the study site at Rio de la Plata estuary off Uruguay. Right panel: sampling stations. Larvae of *B. aurea* and other plankton were sampled at stations marked as full circles. Open circles indicate hydrographic-only stations. The right inset expands the box in the bigger map. T = transect.

Brevoortia aurea larvae were sorted from plankton samples under stereomicroscope and identified based on taxonomical keys (Weiss, 1981; Cassia and García de la Rosa, 1993). Specimens were classified in three developmental stages: preflexion (PF), flexion (F) and posflexion (PsF). Larvae were dissected and their gut contents analysed. Prior to dissection, the following metrics were taken from each specimen to the nearest 0.1 mm: i) body length (BL) as notochord length (LN mm) in PF and F larvae, and standard length (SL mm) in PsF larvae, and ii) mouth width (MW mm; as the width between the posterior edges of the maxillae in ventral view).

Diet was determined by gut content analyses; the digestive tract from each larva was dissected under high-magnification microscope and prey items identified, counted, and measured to the nearest 0.01 mm using an inverted microscope. Prey size was expressed as its maximum width (Wmax; µm) according to Busch (1996).

Feeding incidence (% FI) was assessed as the percentage of larvae with prey in the guts (Pepin et al., 2015). Feeding rhythm was described based on FI according to the time of the day when the corresponding sample was collected. The degree of digestion (E) of food items was determined according to a qualitative scale into three categories: (E1) not digested or only slightly digested prey (entire and recognizable items), (E2) half digested (items not complete but still recognizable), (E3) digested (disintegrated, unrecognizable items) (Rodríguez-Graña et al., 2005).

The composition of the diet was summarized as frequency of occurrence (% FO) and percent in number (% N) of prey items in PF, F and PsF larval stages (Hyslop, 1980). The product of these two factors yields an index of relative dietary importance referred to as IRI (%) (Pinkas et al., 1971).

Diet overlap between stages was compared using the similarity index D (Schoener, 1968):

$$D = 1 - 0.5 \times \Sigma \left| (pi - pi) \right|,$$

where pi is the proportion of item i in the diet of stage p, and qi is the proportion of item i in the diet of stage q. D ranges between 0 (diets do not overlap) and 1 (diets completely overlap) where values above 0.6 are considered as indicative of ecologically significant overlap (Wallace, 1981). Index D was estimated for prey items classified according to two alternative criteria: i) prey type (taxonomic affiliation), and ii) prey size. Prey sizes were classified in six categories that approximately match functional groups: ≤ 50 µm (e.g. phytoplankton, small protozoan microplankton: tintinnids, dinoflagellates), 51-100 µm (e.g eggs of copepods and of other invertebrates, large microzooplankton), 101-150 µm (nauplii and other invertebrate larvae), > 151-200 µm (larger nauplii, and other invertebrate larvae), 201-300 µm (copepodites and small adult stages of small copepod species) and > 300 µm (copepodites and adult copepods).

All the calculations and statistical analyses were performed under the R platform (R Core development team 2020). Body morphometric relationships (mouth width *vs* body length) and morphometrics relationships with prey size (mouth width and body length *vs* prey width) were explored using nonlinear squares fitting. For body morphometric relationships alternative model formulations were explored and selected based on Akaike information criterion (Burnham and Anderson, 2002). The relationship between prey sizes *vs* larval length, and prey size *vs* larval mouth width were explored using non-linear quantile regression as implemented in *{quantreg}* library for R. That allowed to evaluate the change in upper and lower size limits of ingested prey along larval development wichwere represented by quantiles 90 and 10 (upper and lower prey size limits, respectively).

RESULTS

ENVIRONMENTAL CONDITIONS AT RPE

Hydrographic conditions over the surveyed area were characterised by ample ranges in temperature (14.84 – 22.07 °C) and salinity (< 1 – 31.57) (Fig. 2).

Brevoortia aurea larvae were found in stations representing the whole range of environmental conditions, i.e., in nearly the full spectrum between freshwater and full marine conditions (Fig. 2).

FEEDING INCIDENCE AND FEEDING RHYTHM

A total of 242 *B. aurea* larvae were collected and feeding analyses were performed on 205 individuals (total numbers per stage, PF n = 161, 78.5 %; F n = 30, 14.6 %; PsF n = 14, 6.8 %). Larvae in yolk sac stage were excluded from all analyses (37 individuals).

Overall feeding incidence FI was 46.3 %, discriminated in: 40.4 % for PF, 63.3 % for F, and 78.6 % for PsF larvae. Gut contents were mostly found in larvae collected in daylight hours, when PF and F larvae tended to exhibit higher FI values during the morning, while PsF larvae did so during the afternoon (Fig. 3A). Prey exhibited different degrees of digestion along the day but with no clear pattern; undigested prey (E1) represented 51.2 % of the total ingested prey, half-digested (E2) represented 37.6% and highly digested (E3) represented 11.2 % (Fig. 3B).

DIET COMPOSITION, PREY DIVERSITY AND DIETARY OVERLAP

The diet of *B. aurea* was composed by eleven types of prey: copepods and their developmental stages (copepodites and nauplii), invertebrate eggs, cladocerans, phytoplankton (diatoms and other non identified species), dinoflagellates, gastropods and bivalve larvae, ostracods and tintinnids (Fig. 4). *Acartia tonsa* represented 60.4 % of copepods ingested followed by *Oncaea* sp. (4.4 %).

The index of relative importance (IRI) showed slight differences between stages, mainly in the proportion of similar items: PF larvae fed on a wide variety of preys (11 items) dominated by juvenile and adult copepods (IRI = 81.4 %), invertebrate eggs (IRI = 10.32 %) and copepod nauplii (IRI = 3.83%); F larvae fed on 5 types of prey where copepods showed an IRI = 87.3 %, invertebrate eggs IRI = 8.3 % and phytoplankton 2.1%; PsF larvae fed on 3 types of prey, but with an overwhelming dominance of copepods (IRI = 99.9 %, Table 1).

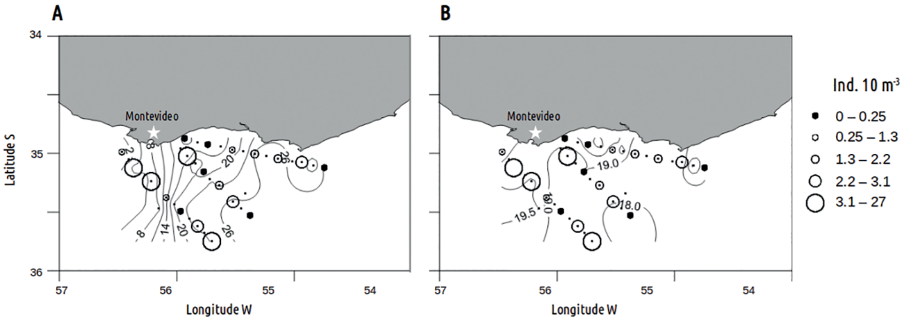

Figure 2. Horizontal fields of (A) surface salinity and (B) surface temperature (°C) at Río de la Plata Estuary during spring 2001. Circles correspond to *Brevoortia aurea* larvae abundances (ind. 10 m^{-3}).

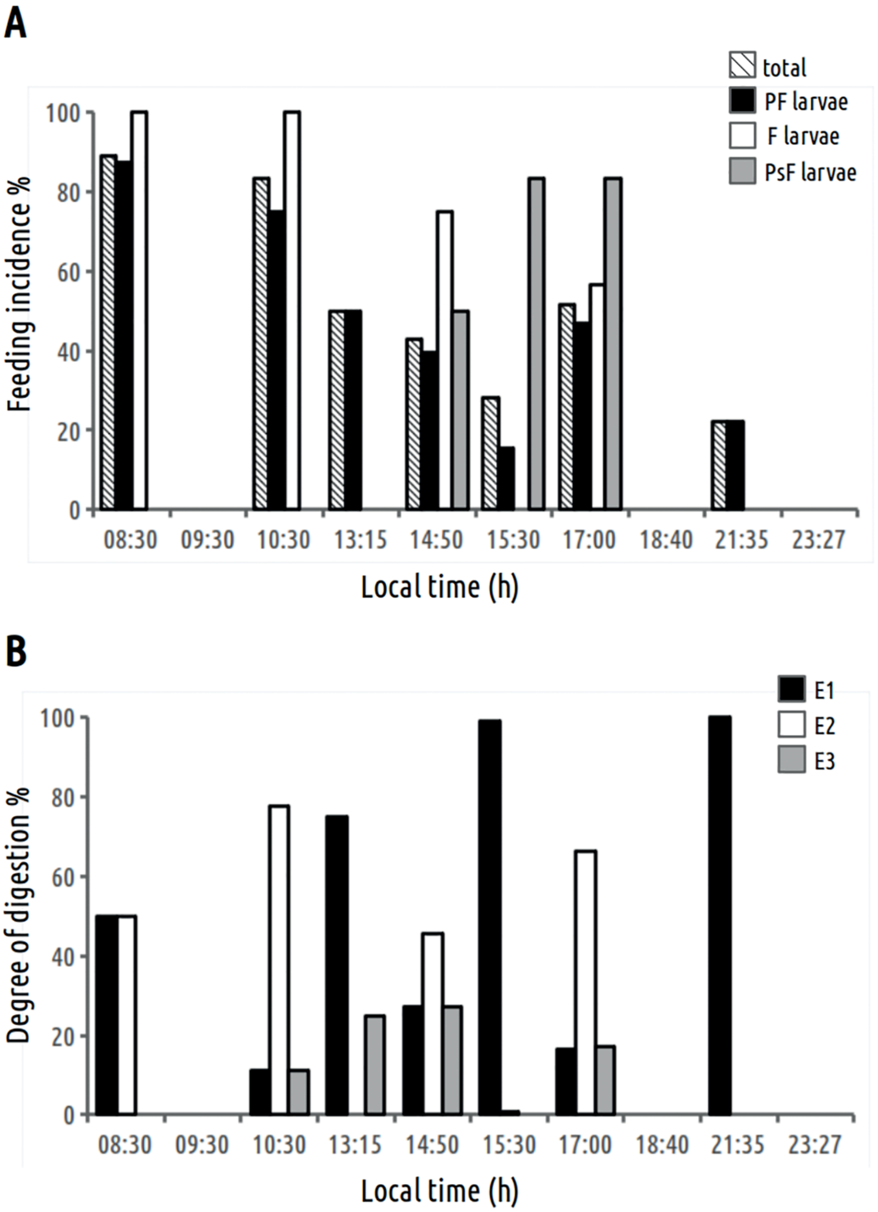

Figure 3. *Brevoortia aurea* in November 2001 off Río de la Plata. A) Feeding incidence (%) as a function of time of day and larval stage: PF = preflexion larva, F = flexion larvae, PsF = postflexion larvae; and B) Degree of digestion of ingested prey in larval guts as a function of time of day: undigested (black bars, E1), half-digested (white bars, E2), highly digested (gray bars, E3).

The dietary overlap (D index) between stages based on the type of prey evolved from high overlap between PF and F stages (D = 0.85) to low overlap between PF and PsF stages (D = 0.56; Table 2). Diet overlap followed a similar trend according to the size of the ingested prey: PF and F larvae evidenced a high overlap as they tended to consume prey in similar size ranges (D = 0.79), but low overlap was found between PF and PsF larvae (D = 0.20; Table 2).

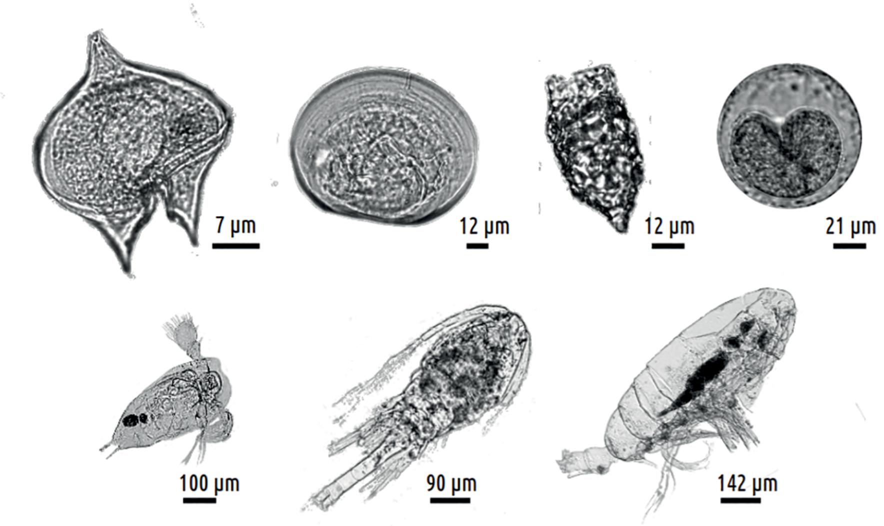

Figure 4. Examples of ingested prey by *Brevoortia aurea* larvae collected at Río de la Plata estuary photographed under microscope with digital camera. From left to right and top to bottom: dinoflagellate, bivalve larva, tintinnid, invertebrate egg, copepod nauplii, adult copepod Oithona in cursive spp., adult copepod *Acartia tonsa*. Images were processed with Inkscape 0.92® and Gimp 2.8.22® free software.

Table 1. *Brevoortia aurea*. Prey composition and index of relative dietary importance (IRI, %) expressed as total number (N%) and frequency of occurrence (FO%) of items in the diet discriminated by larval stages: preflexion (PF), flexion (F) and postflexion (PsF). n/i = not identified, Inv. = invertebrate.

	PF larvae (n= 65)			**Flarvae (n= 19)**			**PsF larvae (n= 11)**		
Prey item	**FO%**	**N%**	**IRI%**	**FO%**	**N%**	**IRI%**	**FO%**	**N%**	**IRI%**
Bivalvia larvae	1.5	0.8	0.03	-	-	-	9.1	0.8	0.1
Copepods (*)	53.8	54.2	81.45	73.7	65.9	87.3	100	98.5	99.9
Cladocerans	9.2	4.6	1.18	10.5	7.3	1.4	9.1	0.8	0.1
Diatoms	3.1	1.5	0.13	-	-	-	-	-	-
Dinoflagellates	3.1	1.5	0.13	-	-	-	-	-	-
Phytoplankton n/i	13.8	6.9	2.65	15.8	7.3	2.1	-	-	-
Gasteropod larvae	1.5	0.8	0.03	-	-	-	-	-	-
Invert. eggs	23.1	16.0	10.32	31.6	14.6	8.3	-	-	-
Nauplii	13.8	9.9	3.83	10.5	4.9	0.9	-	-	-
Ostracods	3.1	1.5	0.13	-	-	-	-	-	-
Tintinnids	1.5	2.3	0.10	-	-	-	-	-	-

* copepod species were represented by *Acartia tonsa* (60,4%), *Oncaea* sp. (4.4%), *Oithona* sp. (0.9%), *Paracalanus* sp. (0.9%), *Corycaeus* sp (0.4%). Percentage represents the occurrence of each copepod taxa from a total copepods present in the guts of all larvae analysed.

MORPHOMETRIC RELATIONSHIPS AND PREY SIZE

Body size of *B. aurea* larvae collected at RPE ranged from 2.44 to 27 mm (mean: 6.20 ± 3.13 mm) and mouth width ranged from 0.12 to 1.51 mm (mean: 0.39 ± 0.18 mm). Mean body size and mouth diameter discriminated by stage are shown in Table 3. Mouth width correlated strongly to body length according to an isometric pattern (Fig. 5, Table 4).

The size spectrum of ingested prey ranged between 7 to 378.2 µm (mean 188.1 ± 116.9 µm). Prey width increased non-linearly with both larval body size and larval mouth width. The maximum and minimum size of prey ingested at different

Table 2. *Brevoortia aurea*. Dietary overlap index (D) between preflexion larvae and flexion larvae (D PF-F), preflexion larvae and posflexion larvae (D PF-PsF), and flexion larvae and posflexion larvae (D F-PsF) based on two criteria: prey type and total prey size (above). Number of preys ingested discriminated by prey size classes (µm) and larval stages (below).

Dietary overlap			
Category	**DPF-F**	**DPF-PsF**	**DF-PsF**
Prey Type	0.85	0.56	0.67
Prey Size	0.79	0.20	0.22

Number of prey ingested						
	Prey size classes					
Larval stage	**≲ 50**	**51 - 100**	**101 - 150**	**151 - 200**	**201 - 300**	**> 300**
PF	16	45	26	5	4	2
F	2	12	12	4	0	1
PsF	0	1	11	11	42	59

Table 3. *Brevoortia aurea* larvae body length and mouth width mm, mean ± standard deviation (mm) discriminated by larval stage.

	Pre flexion larvae	**Flexion larvae**	**Postflexion larvae**
Body length	6.29 ± 1.56	7.13 ± 1.78	14.14 ± 6.0
Mouth width	0.34 ± 0.10	0.42 ± 0.16	0.72 ± 0.39

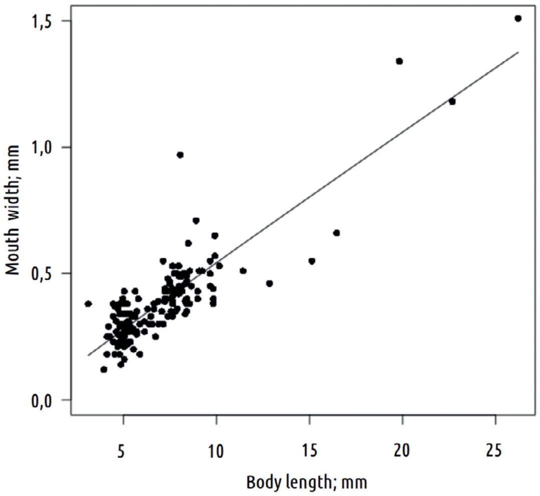

Figure 5. *Brevoortia aurea*. Relationship between body size (mm) and mouth width (mm). Regression details are shown in Table 4.

larval sizes followed very similar patterns along the larval body size range, as indicated by non-linear quantile regression (Fig. 6A, Table 4). In turn, some differences were observed in the increase of maximum and minimum prey sizes along the larval mouth width range: the minimum prey size increased faster at the lower end of the mouth width range, and the maximum prey size grew at a lower pace compared to both minimum and median prey sizes, and particularly at small values of mouth width (Fig. 6B, Table 4).

DISCUSSION

Brevoortia aurea larvae in the RPE were omnivore and showed a variety of prey items within a wide size range, and fed mostly at sunlit hours; however, this feeding behaviour did not show an homogeneous trend along ontogeny. The larval stages of *B. aurea* exhibited differences in terms of feeding incidence, preferences in type, and size of ingested prey linked to morphological changes along ontogeny.

Overall feeding incidence was low or moderate in relation to other species from the same region (Rodríguez-Graña et al., 2018) but within similar to other clupeids (Kurtz and Matsuura, 2001), and feeding incidence increased from smaller to larger individuals. Low FI could result from the

Table 4. *Brevoortia aurea*: Regressions fit to characterize morphometric relationships. On top: Mouth width vs Body length. Fitted equation: $Y = a * X^b$. Number of observations is 159. Middle: Prey width vs Body length. Fitted equation: $Y = a + X^b$. Number of observations is 254 τ = percentile for regression fit (5% and 95%). Bottom: Prey width vs Mouth width. Fitted equation is: $Y = a + X^b$. Number of observations is 204. τ = percentile for regression fit (5% and 95%).

Parameter	Estimate	Standard error	p
a	0.0589	0.0046	<< 0.001
b	0.9648	0.0345	<< 0.001
Variance explained; %	74.4		
Parameter	**Estimate**	**Standard error**	**p**
a	-1.1539	0.0109	<< 0.001
b	0.1172	0.0031	<< 0.001
Variance explained; %	76.9		
	Estimate	**Standard error**	**p**
τ = 0.05			
a	-1.2111	0.0177	<< 0.001
b	0.1102	0.0068	<< 0.001
τ= 0.95			
a	-1.0321	0.0321	<< 0.001
b	0.1101	0.0082	<< 0.001
Parameter	**Estimate**	**Standard error**	**p**
a	-0.7515	0.0038	<< 0.001
b	0.1792	0.0068	<< 0.001
Variance explained; %	76.9		
	Estimate	**Standard error**	**p**
τ = 0.05			
a	-0.8317	0.0154	<< 0.001
b	0.1427	0.0188	<< 0.001
τ= 0.95			
a	-0.6625	0.0090	<< 0.001
b	0.0929	0.0261	<< 0.001

combination of the effect of sampling (artifact factor) with the anatomical characteristics of the larvae of this family. That is, clupeiform larvae have a tendency to regurgitation during sampling (Llopiz, 2013) due to an elongated body and straight digestive tube, where chances for the prey to be retained are lower in comparison to species with a looped gut type (Arthur, 1976; Govoni et al., 1983; Canino and Bailey, 1995). However, FI increased with advancing stage, probably linked to an increase in body length and mouth width, and associated physiological and ethological changes that improve feeding efficiency, as noted for other *Brevoortia* species (Higgs and Fuiman, 1996) (see next section).

Most fish larvae are visual predators during daylight hours, depend on a minimum illumination level (light intensity threshold) and thus exhibit feeding rhythms on a circadian scale. Feeding rhythms change during ontogeny related to -among other factors- the development of sensory abilities. In fish larvae, vision evolves during ontogeny as the structural development of the eye progresses, particularly with the appearance of cones and rods, the photosensitive cells in the retina (Evans and Browman, 2004). During early

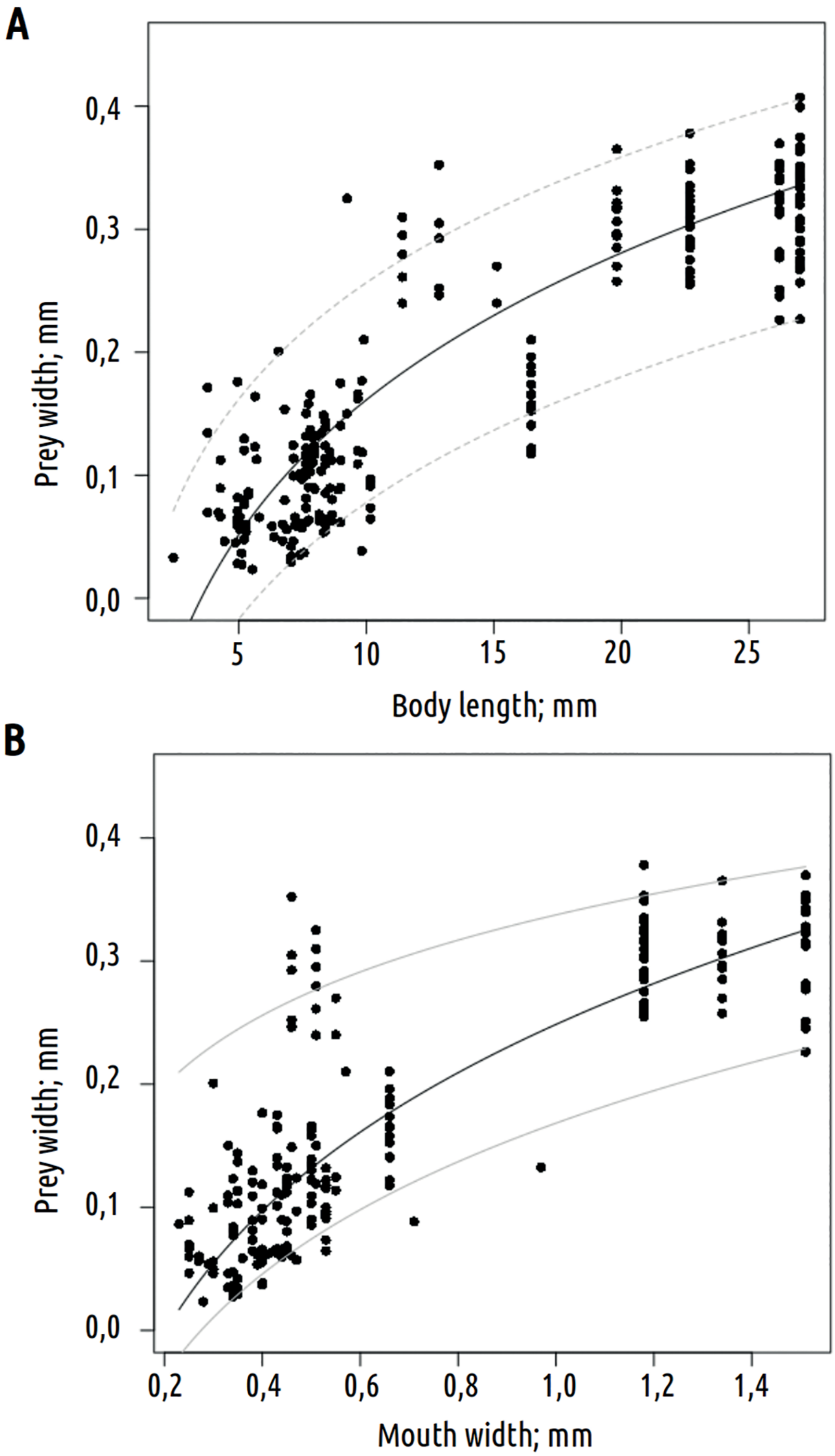

Figure 6. *Brevoortia aurea*. Quantile relationship between prey width and body length (A) and between prey width and mouth width (B). Black lines represent the 50% quantile, and grey dashed lines represent 5% and 95% quantile regression lines (upper and lower, respectively). Regression details are shown in Table 4.

development the retina is dominated by cones, the vision capacity is very restricted and proper object detection relies on sharp contrast under bright light. In more advanced stages the retina acquires rods, improving its sensory capacities and allowing larvae to detect prey at twilight, or even at night (Evans and Browman, 2004 and references therein). In the Northern Hemisphere, congeneric species *Brevoortia tyrannus* cone density is almost constant from hatching until 10 mm total length (TL), after which rods appears and gradually increase in number until 14 mm TL (Higgs and Fuiman, 1996). If a similar development pattern is valid for *B. aurea*, that could explain why larvae in PF stages showed high FI mostly during the early morning hours, while PsF larvae (14.1 mm SL ± 6.0) were able to feed efficiently (high FI) also late in the afternoon. However, low number of larvae captured at night do not allow to infer a nocturnal feeding behavior, and this issue deserves further investigation.

High digestive enzyme capacity has been recorded at night hours in larvae of certain clupeid and gadid species (Ueberschär, 1995). In this study, prey exhibited different degrees of digestion along the daily feeding cycle. The observed pattern was one of mostly undigested prey at daytime hours, preferentially early in the morning and early in the afternoon (with exception of two PF individuals captured at night). Taken together, results on feeding incidence and degree of prey digestion reinforce the idea that the earliest stages of *B. aurea* in the RPE feed during daylight hours, as most clupeids do (Arthur, 1976).

The ontogenic change in food selection is a well known pattern in fish larvae (e.g. González-Queiroz and Anadon, 2001; Robert et al., 2011). These changes and the degree of prey selectivity are attributable to factors which may be inherent to the species or functional groups to which they belong. In our study, the diet of larval *B. aurea* shifted from small microplankton, mostly copepod eggs and nauplii during earlier stages, towards copepodites, and adults of small (*Oncaea, Paracalanus*) and larger-sized (*Acartia tonsa*) copepods during mid- and late-larval stages. Use of different prey (e.g. copepods) by larger larvae may also have a bioenergetic basis: increased energy requirements of larval metabolism as development progresses is sustained by an active selection of prey with higher quality composition, for example in terms of lipids (Salhi et al., 1997; Bessonart et al., 1999, Cutts et al., 2006). Observations compatible with such pattern were made for a multi-species larval assemblage from a temperate microestuary at the same latitude (Machado et al., 2017).

Copepods were the most consumed prey, and specifically *Acartia tonsa* was strongly consumed (60.4 % of copepods ingested), well beyond other species present at higher abundances (see Fig. S1, supplementary material). That finding suggests a preference for *A. tonsa* over other potential prey, probably arising from its high nutritional quality. However, a rigorous analysis of prey selectivity is impeded due to lack of quantitative data on field abundance of microplankton prey categories. The relatively high nutritional quality of copepods in comparison to other zooplankters is well known (Kainz et al., 2004; Gonçalves et al. , 2012; Tiselius et al., 2012; Leu et al., 2013; Machado et al., 2017). That characteristic, together with their high abundance and year-round occurrence in a wide range of sizes, makes copepods suitable preys for fish larvae (see supplementary information). Consistent results were found for other fish larvae in the RPE (Rodríguez-Graña et al., 2018) and in other ecosystems, including subtropical and temperate estuaries and nursery areas (e.g. Pepin and Penney, 2000; Robert et al., 2011; Llopiz, 2013; Temperoni and Viñas, 2013). In particular *A. tonsa* matches well all such qualities as prey features, i.e., size range, quality as food, abundance in estuaries (Calliari et al., 2004; Calliari et al., 2019; Derisio et al., 2014; Machado et al., 2017; Rodríguez-Graña et al., 2018). In fact, the high abundance of copepods and in particular of *A. tonsa* in the RPE (up to 10,000 ind. m^{-3}, Calliari et al., 2004; Derisio et al., 2014; Marrari et al., 2004; Fig. S1, supplementary material) contributes to make that ecosystem a high quality nursery area for fish larvae, including *B. aurea*.

Diet shifts along ontogeny also generally contribute to decrease inter-cohort competition. Strong diet overlap between PF and F stages of *B. aurea* larvae according to both prey type and size could be interpretated as indicative of a potential competition between younger stages. The actual occurrence of competition and concomitant ecologically relevant density-dependent effects requires a significant impact of predation pressure on prey populations. No evidence exists so far on that matters, and given the typically high prey densities and planktonic production rates in the RPE (Ferrari and Pérez, 2002; Calliari et al., 2018, 2019), the emergence of competition seems unlikely. In any case, the likeliness of any potential competition decreases as development advances and dietary overlap diminishes.

During ontogeny larvae gradually shift their diet to larger prey items as they grow (Pepin and Penney, 1997). Differences in physiological abilities and morphology between stages or cohorts, -for example in terms of mouth and jaw size- lead to differences in prey selection. *B. aurea* exhibits deep changes in morphology during early development (Cassia and García de la Rosa, 1993; Gianglobbe and Sánchez, 1993; Bonecker and Castro, 2006). Larvae smaller than 30 mm have teeth and rudimentary gill rakers in the form of rounded protuberances. After 30 mm of body length (at the beginning of metamorphosis), they lose the former and the gill rakers elongate and increase their number and its morphology resembles the mesh-like structure of adults where they become preferentially phytoplanktivorous. (Giangiobbe and Sánchez, 1993). In our study, *B. aurea* exhibited an isometric development where the increase in mouth width and body length proceeded at equal pace; this is to say, as larvae grow they are (potentially) able to ingest proportionally larger prey like copepods. But interestingly, changes in the size of ingested prey (and therefore prey type) occurred at different paces for minimum and maximum prey sizes along larval development. Unlike other species, where the minimum prey size increases gradually and almost constantly (Rodríguez-Graña et al., 2018), here an acceleration or pronounced change in minimum prey size was evident early in development (below ca. 9 mm body length; 0.5 mm gape size). Instead, maximum prey size increased more gradually as the larvae grow (Fig. 6) and largest prey were much smaller than the mouth gape would allow. That is consistent with previous studies performed in *Sardinops sagax* and *Engraulis mordax* (Arthur, 1976). The slow increase in prey size means that gape size alone may not be the limiting factor for prey choice, and particularly for maximum prey size. Instead, other factors may have limited prey consumption of larger prey such as poor larval swimming capabilities as described for this Order, combined with strong escape responses of larger prey (Hunter, 1972; Lasker, 1984), and/or the timing in the development of feeding structures involved in prey-capture (Hunt Von Herbing, 2001). Studies focused on the mechanisms of prey capture and their development along ontogeny will contribute to elucidate the role of different processes in larval feeding performance and their implications for the recruitment of this species.

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AUTHOR CONTRIBUTIONS

D. C.: conceptualization; formal analysis; methodology; visualization; writing-review & editing.

G. C.: conceptualization; methodology; funding acquisition; writing-review & editing.

L. R. G: conceptualization; writing original draft; formal analysis; methodology; visualization; writing-review & editing.

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SUPPLEMENTARY MATERIAL

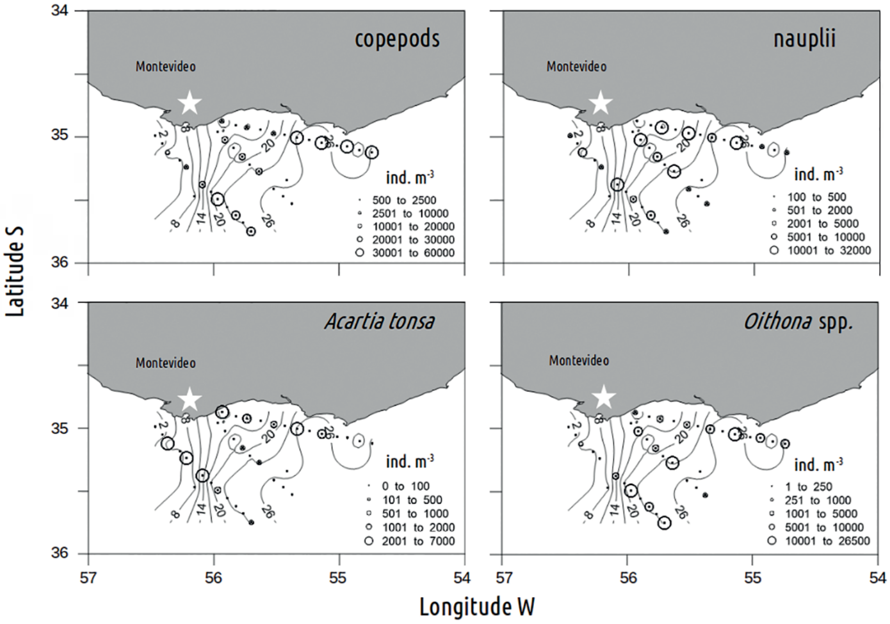

Figure S1. SM- Abundance (individuals m^{-3}) of total copepods (up-left), nauplii (up-right), *Acartia tonsa* (bottom-left) and *Oithona* spp. (bottom-right) sampled at RPE from november 17 to 19, 2001. Zooplankton samples were collected by oblique tows (from 1 to 2 m above the bottom and upwards) with a 19 cm diameter net fitted with a 68 µm mesh and a General Oceanic® flowmeter. Samples were preserved in buffered formaldehyde (~5% final concentration), and at the laboratory copepods were identified, staged and counted.