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Relationship between gape size and feeding selectivity of fish larvae from a Neotropical reservoir

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Larvae feeding selectivity of *Iheringichthys labrosus*, *Hypophthalmus edentatus* and *Plagioscion squamosissimus* was assessed, examining the role of mouth gape in prey selection. Fish larvae were sampled in the Itaipu Reservoir (Brazil–Paraguay). *Iheringichthys labrosus* and *H. edentatus* larvae, with small and similar gape sizes, exhibited slightly different diets; *I. labrosus* preferred cladocerans (*Bosmina hagmanni*, *Bosmina huauriensis* and *Bosminopsis deitersi*) and the rotifer *Brachionus calyciflorus*. *Hypophthalmus edentatus*, however, primarily ingested the cladocerans *B. hagmanni*, *Ceriodaphnia cornuta*, *Daphnia gessneri* and *Diaphanosoma spinulosum*. *Plagioscion squamosissimus*, with a greater gape size, preferred Calanoida. The mechanistic processes that determine food selectivity of fish larvae in temperate aquatic systems were similar in the Neotropical system. The trophic spectrum of these species is characterized by small- to intermediate-sized prey. *Plagioscion squamosissimus* larvae, which have larger mouths, exploit primarily larger prey differing from the most abundant species or size classes; consequently, their diet is quite different from *I. labrosus* larvae and modestly similar to *H. edentatus* larvae, opportunistic feeders that they eat more abundant prey.

Key words: feeding selectivity; fish larvae; gape size; prey selection.

INTRODUCTION

Fish assemblages are strongly structured by size in a way that a variety of interactions, including competition and predation, can occur according to the life stages of the fishes (Ross, 1986). Competition can be especially important during the early stages of development, when larval survival is extremely dependent on size. Larger larvae are more resistant to starvation, have greater

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swimming ability and better visual capabilities, and thus are better foragers. They also are less vulnerable to predation and mortality.

Food selection by animals is based on size, abundance, and how easily prey can be detected and captured (Brooks & Dodson, 1965). Size dominates prey selection patterns for many fish larvae (Hunter, 1984); and mouth structure differences may lead to differences in feeding success (Bremigan & Stain, 1994). Co-occurring larvae of different species with similar-size mouths may therefore exhibit a higher rate of significant dietary niche overlap than those with mouth of different size. It also is important to examine mouth size and prey size when exploring feeding strategies of fish larvae. Some larvae, however, feed in such a way as to reduce prey capture costs (energy and time) by selecting the most abundant prey (Ponton & Muller, 1990).

Most of the studies on gape–prey size relationships have been conducted in temperate systems. For these systems, prey consumption can be affected especially by larvae size, form, predator vision and preference (Zaret, 1980; Teska & Behmer, 1981; Hartmann, 1986; Lazzaro, 1987), and feeding selectivity patterns are related to gape size (Hartmann, 1986; Gaughan & Potter, 1997; Mehner *et al.*, 1998).

Changes in abundance and distribution of zooplankton size throughout systems can directly affect planktonic fish populations. Therefore, knowledge of the influence of prey size and availability on larvae growth and survival are essential in understanding the recruitment process (Welker *et al.*, 1994).

Fishes in Neotropical aquatic systems such as *Iheringichthys labrosus* (Lűtken, 1874), *Hypophthalmus edentatus* (Spix, 1829) and *Plagioscion squamosissimus* (Heckel, 1840) are important to the bulk harvest of fisheries conducted in Upper Paraná River reservoirs. This is especially true for the Itaipu Reservoir. Larvae are pelagic and zooplanktivorous (Makrakis *et al.*, 2005), their peak abundances overlap seasonally (November to April), and they are the most abundant larvae species. Thus, feeding selectivity of the larvae of these species can be evaluated, as well as the role of the mouth in prey selection to produce the hypotheses (1) that similar mechanistic processes determine food selectivity of fish larvae in Neotropical aquatic systems and (2) that scarce resources create resource segregation. It can be verified if (a) the resources are abundant, (b) differences in gape size exist, such that (c) selectivity is determined by differences in gape size, whereas selectivity patterns are similar in similar-sized fishes.

MATERIALS AND METHODS

The Itaipu Reservoir (24°05′–25°33′ S; 54°00′–54°37′ W) (Paraná River, Brazil–Paraguay) is 150 km long and occupies an area of 1350 km^2, with an average depth of 21 m and a maximum depth of 170 m (Muller, 1987). Water hydraulic retention time is *c.* 40 days, with an 8200 m^3 s^{-1} discharge. Average concentration of total phosphorus is 22 mg m^{-3} and chlorophyll *a* is 3·6 mg m^{-3} (Miranda *et al.*, 2000). These values correspond to trophic state indices of 49 and 43, respectively, which suggest mesotrophic conditions (Carlson, 1977).

This reservoir presents a well-defined longitudinal gradient with three distinct zones: fluvial, transitional and lacustrine. Sampling (Fig. 1) was carried in the lacustrine zone. These sampling stations included the reservoir body (Paraná River) and east margin tributaries (São Francisco Falso and Ocoí Rivers).

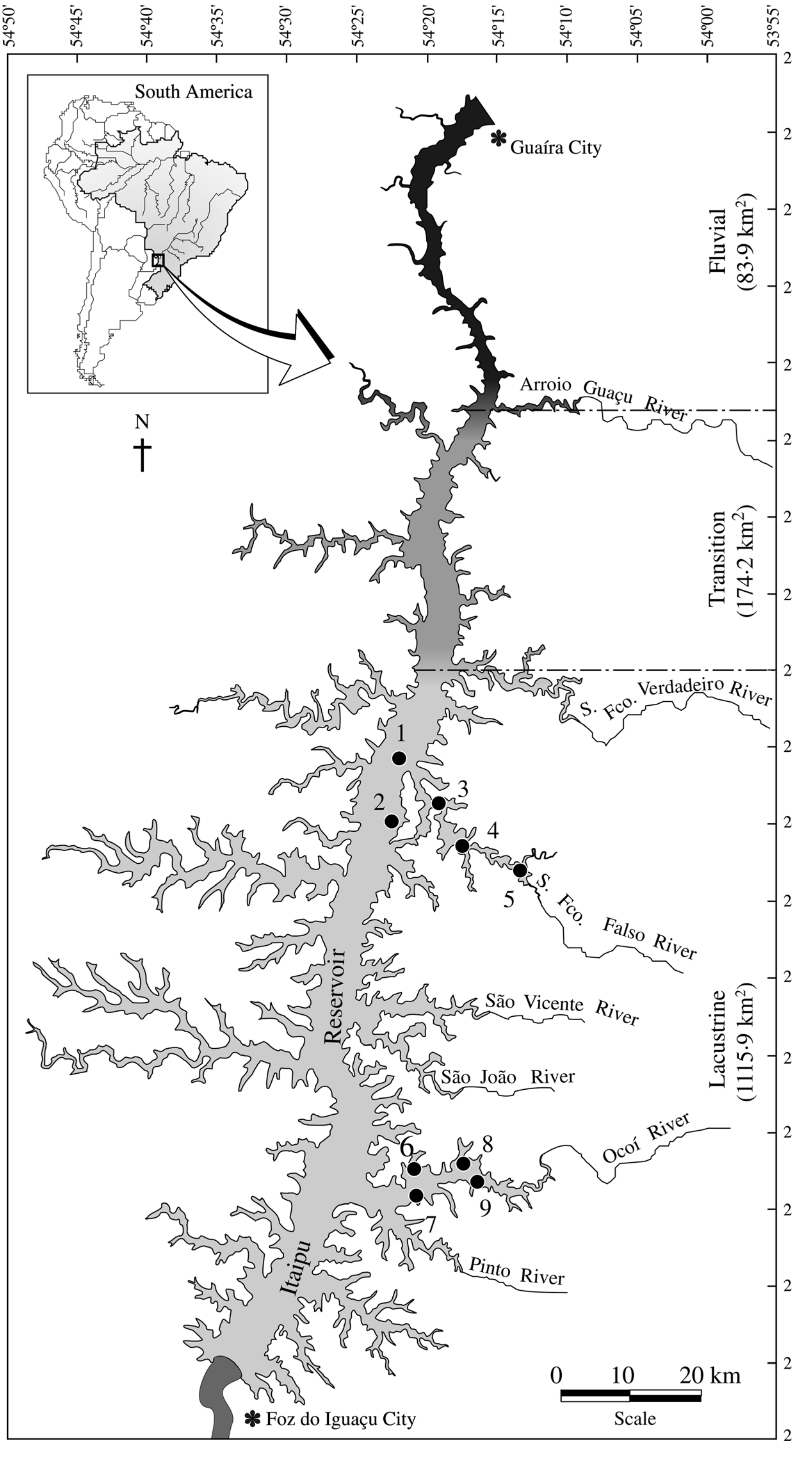

FIG. 1. Locations of the sampling sites (●) in the Itaipu Reservoir.

The samples were collected monthly between October 1996 and March 1997 using a conical–cylindrical plankton net (500 μm mesh) equipped with a flowmeter for surface collections. Tows were horizontal (200 mm deep), lasted 10 min, and were always between 1900 and 2300 hours. Fishes were anaesthetized in clove oil and fixed in buffered 4% formalin. They were counted and identified to the species level based on descriptions in Nakatani *et al.* (2001). Larval mean abundances were calculated according to Tanaka (1973), modified by Nakatani *et al.* (2001). These values were 262 larvae 10 m^{-3} for *H. edentatus*, 14 larvae 10 m^{-3} for *I. labrosus* and 12 larvae 10 m^{-3} for *P. squamosissimus*.

The zooplankton was collected in the same sampled locations using a plankton net with a suction pump. A total of 200 l of water was filtered in a 70 μm mesh net. Samples were fixed in buffered 4% formalin. Sub-sample counts were carried out using a Henson–Stempel pipette (at least 200 individuals of the most abundant taxa). The organisms were counted and identified based on Sendacz & Kubo (1982), Reid (1985), Matsumura-Tundisi (1986) and Segers (1995). At least 15 individuals of the most abundant taxa were measured (total body length, including spines and helmets; copepods: from head to caudal branch base). Taxa codes and zooplankton abundance in the environment are presented in the Appendix.

The upper jaw length (Shirota, 1978) was measured in order to analyse larvae species gape size (G_S) and the mouth opening at 90° calculated (Shirota, 1970). Analysis of covariance (ANCOVA) (Dowdy & Wearden, 1991) was applied to evaluate if the relationship between G_S and standard length (L_S) (co-variable) varied among the species. All bivariate pair-wise comparisons of slope and intercepts were made. A *t*-test was applied to verify significant differences ($P < 0.05$). ANCOVA was conducted using STATISTICA software, version 7.0.

The food items in the intestinal contents of *I. labrosus*, *H. edentatus* and *P. squamosissimus* were counted and identified under a stereoscopic microscope. The total length of the prey (zooplankton) was measured when they were intact (for the pre-flexion and flexion stages, total contents were analysed; for the post-flexion stage, two-thirds of the digestive tube was analysed due to the degree of food item digestion in its final portion).

The values of taxonomic feeding selectivity (Chesson, 1978, 1983) (monthly for each species) were obtained to differentiate larval prey selection through the zooplankton community. Prey size was obtained individually (for each class of species G_S). Selectivity (α_i) is calculated as follows: $\alpha_i = r_i n_i^{-1}\left(\sum_{j=1}^{m} r_j n_j^{-1}\right)^{-1}$, $i = 1, \ldots m$, with $r_i n_i^{-1}$ being the proportions of either prey species or size classes in the diet and environment, respectively, and m corresponding to the number of prey categories divided per available sizes. This index varies from 0 to 1, where α values $= 1\ m^{-1}$ indicate neutral selection, values $>1\ m^{-1}$ indicate positive selection and values $<1\ m^{-1}$ indicate negative selection.

Taxonomic feeding selectivity for *I. labrosus* during February 1997 and for *P. squamosissimus* during October 1996 was not calculated. This was because only one individual from each species was analysed. Similarly, feeding selectivity was not calculated for *I. labrosus* during March 1997 because larvae of this species were not captured.

The sizes of the ingested and available zooplankton were divided into eight size classes with 0·2 mm intervals to calculate feeding selectivity by prey size. To analyse ingested zooplankton size, larvae were divided into 12 G_S classes (0·3 mm intervals) to minimize the differences in each size class. This verified whether larvae with similar G_S consume similar prey sizes.

Non-metric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to highlight across the species diet. Sorensen distances were computed and the general NMS procedure outlined by McCune & Grace (2002) was followed. Random starting configurations were used, the number of runs with the real data was 10 and the stability criterion was S.D. ≤ 0.005 in stress over the last 10 iterations.

Multi-response permutation procedures (MRPP) (Mielke, 1984; Mielke & Berry, 2001) were used to test for significant separation in diet composition among groups. Pair-wise comparisons of diet among species (*I. labrosus* and *H. edentatus*, and *H. edentatus* and *P. squamosissimus*) and diet among the G_S classes for each species were calculated. Larvae of *I. labrosus* and *P. squamosissimus* were not compared due to low species co-existence. The Sorensen distance measure was used (McCune & Grace, 2002).

Indicator species analysis (ISA; Dufrêne & Legendre, 1997) was used to identify taxa that were indicative of diet for each group. An indicator value is provided that is representative of the concentration of taxon abundance and the fidelity of a taxon to a particular group (McCune & Grace, 2002). Significance is tested using a Monte-Carlo procedure (Fortin & Gurevitch, 1993).

Mantel test (Fortin & Gurevitch, 1993) was used to examine the association between ingested and available zooplankton, and ingested size and available zooplankton size for three species. The species diet matrix with the available zooplankton species matrix and the ingested zooplankton size class matrix with the available zooplankton size class matrix were correlated. All analyses were conducted using PC-ORD software, version 4.01.

RESULTS

Values of L_S and G_S were strongly related to three larvae species (Fig. 2). Slopes and intercepts differed between *P. squamosissimus* on the one hand and *H. edentatus* and *I. labrosus* on the other (Fig. 2 and Table I). In contrast, no differences were found in slope and intercept between *H. edentatus* and *I. labrosus*. *Plagioscion squamosissimus* larvae presented a larger G_S compared to *H. edentatus* and *I. labrosus*, which are species with a similar G_S. Differences in G_S were smaller for smaller larvae, increasing with ontogeny.

Taxonomic feeding selectivity patterns can be seen in Figs 3–5. *Iheringichthys labrosus* larvae strongly selected cladocerans, especially *Bosmina hagmanni*, *Bosmina huauriensis* and *Bosminopsis deitersi* (*Moina minuta*, only in January), and the rotifer *Brachionus calyciflorus* (Fig. 3).

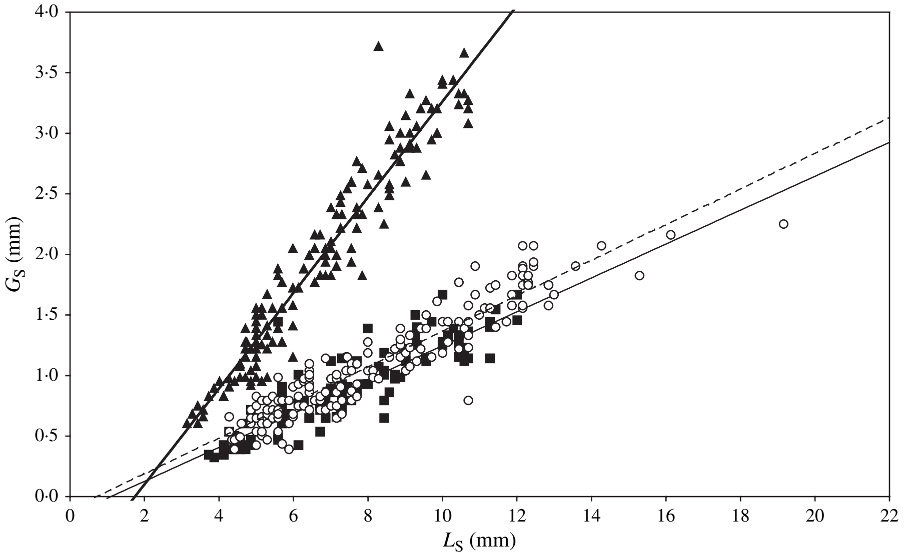

FIG. 2. Larvae gape size (G_S) in relation to standard length (L_S) for: *Iheringichthys labrosus* (■; $y = -0{\cdot}153 + 0{\cdot}140x$; $n = 112$), *Hypophthalmus edentatus* (○; $y = -0{\cdot}104 + 0{\cdot}147x$; $n = 178$) and *Plagioscion squamosissimus* (▲; $y = -0{\cdot}688 + 0{\cdot}395x$; $n = 152$).

TABLE I. Results of ANCOVA applied to verify differences between intercepts (*a*) and slopes (*b*) in the gape size and standard length linear relation. Different superscript lower case letters indicate significant differences ($P < 0{\cdot}05$) between coefficients estimated by *t*-tests

Species	*a* ± S.E.	*b* ± S.E.
Iheringichthys labrosus	$-0{\cdot}1529^{a} \pm 0{\cdot}0807$	$0{\cdot}1399^{x} \pm 0{\cdot}0078$
Hypophthalmus edentatus	$-0{\cdot}1038^{a} \pm 0{\cdot}0676$	$0{\cdot}1469^{x} \pm 0{\cdot}0049$
Plagioscion squamosissimus	$-0{\cdot}6880^{b} \pm 0{\cdot}0526$	$0{\cdot}3951^{y} \pm 0{\cdot}0076$

For *H. edentatus* larvae, a strong selection for the cladocerans *B. hagmanni*, *Ceriodaphnia cornuta*, *Daphnia gessneri* and *Diaphanosoma spinulosum*, and a weak selection for the cladocerans *B. huauriensis*, *B. deitersi* and *M. minuta*, and the rotifer *B. calyciflorus* (Fig. 4) was observed.

Plagioscion squamosissimus larvae strongly selected the copepod *Notodiaptomus* sp., whereas *Argyrodiaptomus* sp. and *Thermocyclops minutus*, as well as the cladocerans *B. hagmanni*, *B. huauriensis*, *B. deitersi*, *D. gessneri*, *D. spinulosum* and *M. minuta*, were weakly selected (Fig. 5).

Mean sizes of the ingested zooplankton differed among the species, especially between *I. labrosus* (mean = 0·3 mm) and *P. squamosissimus* (mean = 0·9 mm)

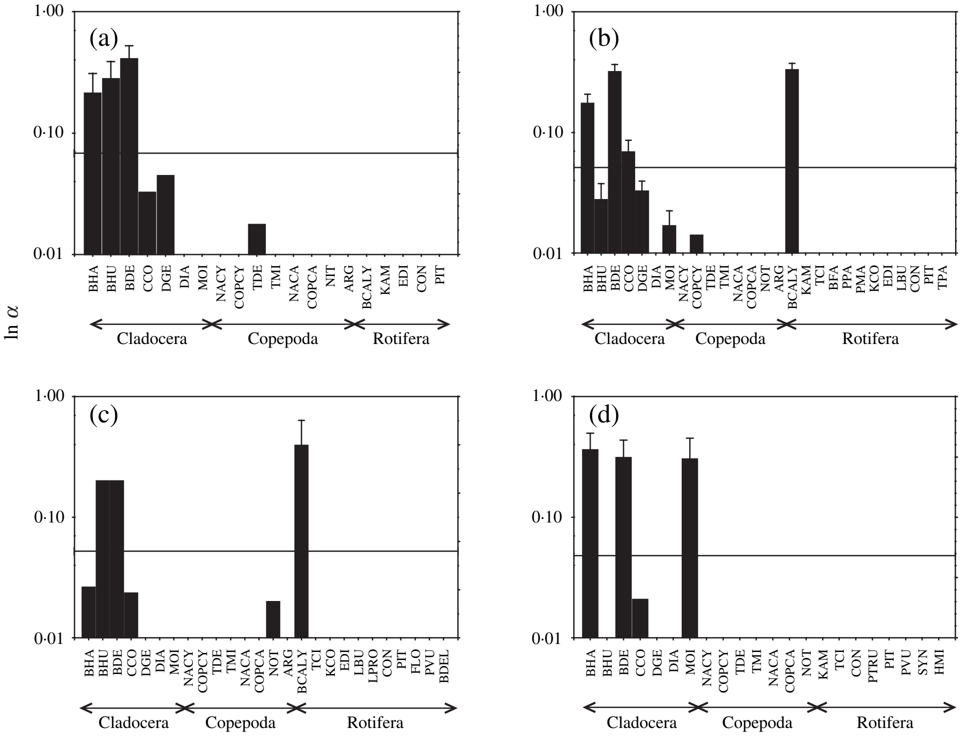

FIG. 3. Mean ± S.E. *Iheringichthys labrosus* larvae taxonomic feeding selectivity (α) in (see Appendix) (a) October, (b) November, (c) December and (d) January. ——, neutral line.

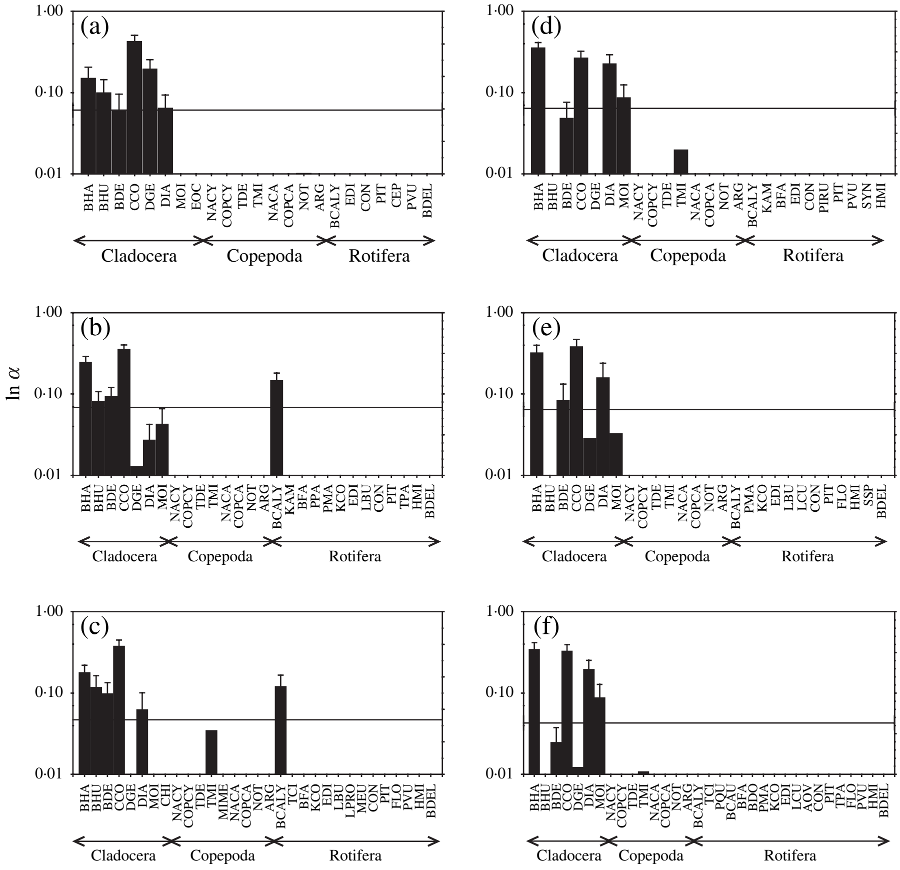

FIG. 4. Mean ± S.E. *Hypophthalmus edentatus* larvae taxonomic feeding selectivity (α) (see Appendix) in (a) October, (b) November, (c) December, (d) January, (e) February and (f) March. ——, neutral line.

(Fig. 6). Among G_S classes, average zooplankton length varied very little for *I. labrosus* (mean = 0·3–0·4 mm). For *P. squamosissimus*, however, an increase in the first G_S classes was verified (mean = 0·6–0·96 mm). Ingested zooplankton average length for *H. edentatus* increased in the last G_S classes (mean = 0·4–0·6 mm).

Feeding selectivity analysis by prey size showed that *I. labrosus* larvae preferentially selected prey between 0 and 0·6 mm, especially the 0·2–0·4 mm class (Fig. 7). For *H. edentatus* larvae, selection of prey between 0·2 and 0·6 mm was predominant (Figs 7 and 8). *Plagioscion squamosissimus* larvae strongly selected prey between 0·8 and 1·2 mm but weakly selected prey <1·4 and between 0·2 and 0·8 mm (especially in the first G_S classes) (Figs 7 and 8).

Non-metric multidimensional scaling ordination of dietary items separated the species (Fig. 9). After 33 interactions, the stability criterion was reached with a final stress of 24·32 (Monte-Carlo test: $P < 0·01$) for two-dimensional solution. Two prevalent gradients contained most of the variance in the diet groups with axes 1 and 2 encompassing 34·4 and 17·5%, respectively, of the

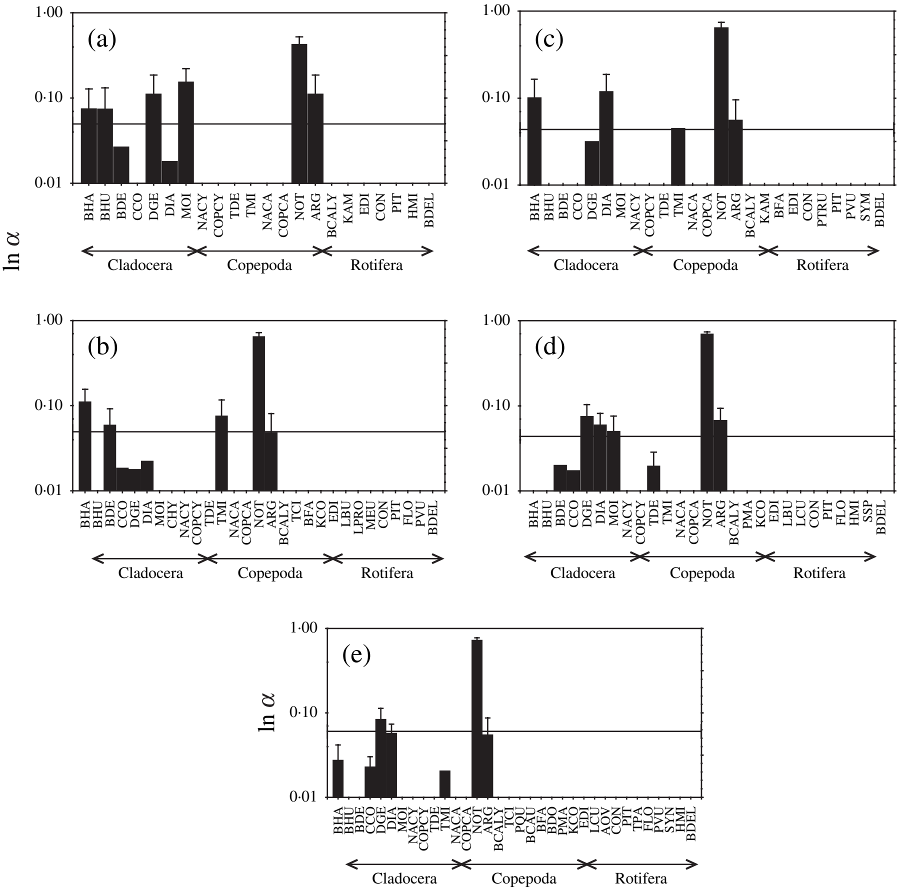

FIG. 5. Mean ± S.E. *Plagioscion squamosissimus* larvae taxonomic feeding selectivity (α) in (see Appendix) (a) November, (b) December, (c) January, (d) February and (e) March. ——, neutral line.

information in the analytical data set (cumulative = 51·9%). A comparison of axes 1 *v.* 2 indicated a prevalent Calanoida and Cladocera and Rotifera gradient driving the separation. *Plagioscion squamosissimus* diet was different especially from *I. labrosus*, and *H. edentatus* diet was intermediate to the two species.

Diet composition varied across all groups of species (MRPP: $n = 442$, $A = 0{\cdot}206$, $P < 0{\cdot}001$) and when examined pair-wise, all comparisons were significantly different. *Plagioscion squamosissimus v. H. edentatus* diet had the strongest separation (MRPP: $n = 330$, $A = 0{\cdot}224$, $P < 0{\cdot}001$) and *H. edentatus v. I. labrosus* had the weakest (MRPP: $n = 290$, $A = 0{\cdot}055$, $P < 0{\cdot}001$). For the G_S classes, the diet was different in *H. edentatus* (MRPP: $n = 178$, $A = 0{\cdot}093$, $P < 0{\cdot}001$) and in *P. squamosissimus* (MRPP: $n = 152$, $A = 0{\cdot}047$, $P < 0{\cdot}001$), and the diet was similar in *I. labrosus* (MRPP: $n = 112$, $A = 0{\cdot}017$, $P > 0{\cdot}05$).

Indicator species analysis (ISA) isolated indicative taxa of the species. *Plagioscion squamosissimus* indicators were *Notodiaptomus* sp., *Argyrodiaptomus* sp., *T. decipiens* and *D. gessneri* (ISA: $n = 151$, $P < 0{\cdot}05$). For *I. labrosus*, *B. deitersi*,

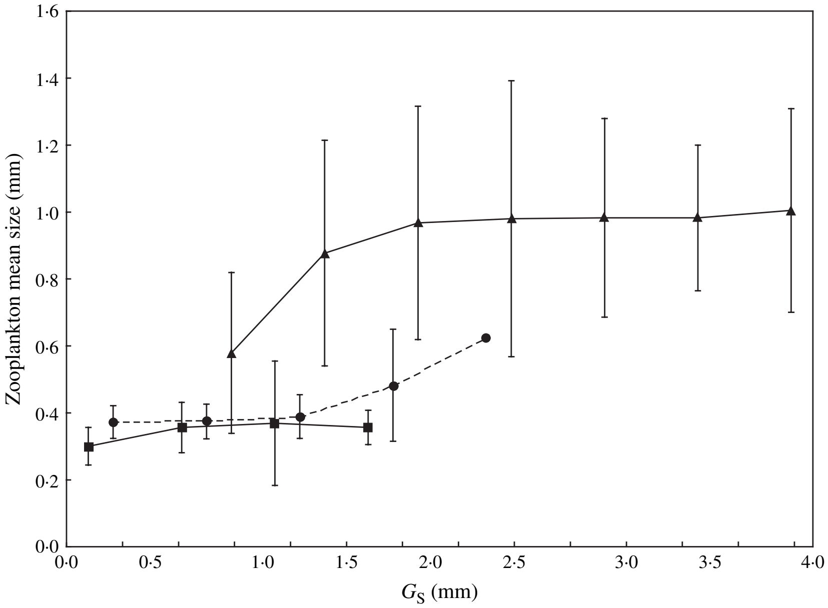

FIG. 6. Mean ± S.D. size of the zooplankton ingested by larvae per gape size (G_S) class: *Iheringichthys labrosus* (■), *Hypophthalmus edentatus* (●) and *Plagioscion squamosissimus* (▲).

B. calyciflorus, rotifer eggs, *B. huauriensis*, and *Keratella cochlearis* were indicators (ISA: $n = 112$, $P < 0{\cdot}05$). *Hypophthalmus edentatus* indicators were *C. cornuta*, *D. spinulosum* and *M. minuta* (ISA: $n = 178$, $P < 0{\cdot}05$). *Iheringichthys labrosus* and *H. edentatus* shared *B. hagmanni* as an indicator (Table II).

Mantel test indicated that the ingested and available zooplankton matrices were associated for *I. labrosus* (Mantel test: $n = 112$, $r = 0{\cdot}27$, $Z = 0{\cdot}315$, $P < 0{\cdot}001$) and *H. edentatus* (Mantel test: $n = 178$, $r = 0{\cdot}10$, $Z = 0{\cdot}797$, $P < 0{\cdot}01$), and they were not associated for *P. squamosissimus* (Mantel test: $n = 152$, $r = 0{\cdot}06$, $Z = 0{\cdot}511$, $P > 0{\cdot}05$). For ingested and available zooplankton size classes matrices, association was indicated for *I. labrosus* (Mantel test: $n = 112$, $r = 0{\cdot}12$, $Z = 0{\cdot}114$, $P < 0{\cdot}01$), and the matrices were not associated for *H. edentatus* (Mantel test: $n = 178$, $r = 0{\cdot}01$, $Z = 0{\cdot}313$, $P > 0{\cdot}05$) and *P. squamosissimus* (Mantel test: $n = 152$, $r = -0{\cdot}01$, $Z = 0{\cdot}397$, $P > 0{\cdot}05$).

DISCUSSION

Interactions between predator and prey can be of great importance in structuring freshwater zooplankton communities (Brooks & Dodson, 1965; Confer & Blades, 1975; Zaret, 1980). Additionally, adequate zooplankton prey densities can be important for larvae growth and survival where prey type availability for one predator can be the result of physiological and behavioural processes presented by both predators (Sipaúba-Tavares, 1983).

Prey consumption can be affected by larval size, form, pigmentation, contrast, movement and ability to escape, as well as by predator vision, preference, hunger and feeding behaviour (Zaret, 1980; Teska & Behmer, 1981; Hartmann,

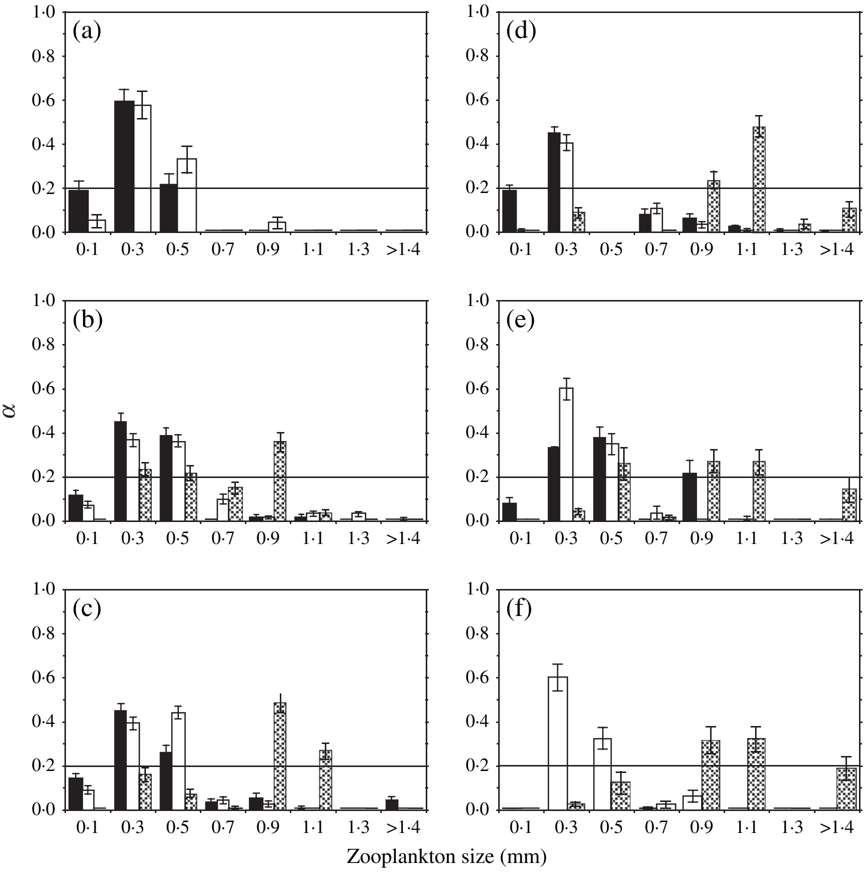

FIG. 7. Mean ± S.E. feeding selectivity (α) by prey size for fish larvae in different gape size classes (a) 0·3–0·6, (b) 0·6–0·9, (c) 0·9–1·2, (d) 1·2–1·5, (e) 1·5–1·8 and (f) 1·8–2·1 mm in *Iheringichthys labrosus* (■), *Hypophthalmus edentatus* (☐) and *Plagioscion squamosissimus* (▨). ——, neutral line.

1986; Lazzaro, 1987). In this study, *I. labrosus* and *H. edentatus* larvae, with small and similar gape sizes, exhibited slightly different diets; *I. labrosus* especially preferred the cladocerans *B. hagmanni*, *B. huauriensis*, *B. deitersi* and the rotifer *B. calyciflorus*, while *H. edentatus* primarily ingested the cladocerans *B. hagmanni*, *C. cornuta*, *D. gessneri* and *D. spinulosum*. Other abundant rotifers (*Euchlanis dilatata*, *Conochilus* sp. and *Ptygura* sp.), with size similar to *B. calyciflorus*, were not ingested. This is possibly due to their preferential habitat. These rotifers are classified by Bonecker *et al.* (1998) as non-planktonic (referring to periphitic and benthonic taxa). Yamanaka (1988) and Sipaúba-Tavares (1983) related the elevated rotifer consumption by initial pacu *Piaractus mesopotamicus* (Holmberg), tambaqui *Colossoma macropomum* (Cuvier) and tambacu (pacu and tambaqui hybrid) larvae in the laboratory. Sipaúba-Tavares (1983) attributed this to the small size and availability of these organisms. Rossi (2001) also found high consumption of rotifer and cladocerans in pre-flexion larvae of *Sorubim lima* (Bloch & Schneider) from the Paraná River. According

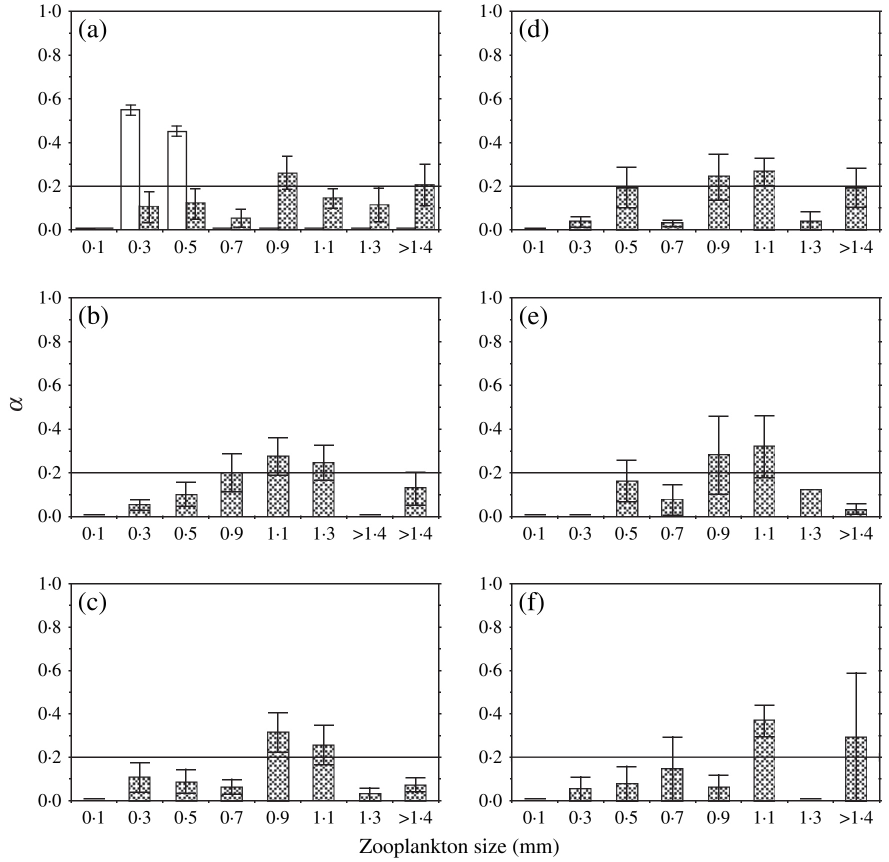

FIG. 8. Mean ± S.E. feeding selectivity (α) by prey size for fish larvae in different gape size classes (a) 2·1–2·4, (b) 2·4–2·7, (c) 2·7–3·0, (d) 3·0–3·3, (e) 3·3–3·6 and (f) 3·6–3·9 mm in *Hypophthalmus edentatus* (□) and *Plagioscion squamosissimus* (▩). ——, neutral line.

to Drenner *et al.* (1978, 1986), fishes prefer smaller sized groups (such as cladocerans) to larger sized groups (like copepods). This is explained by body form and the more efficient locomotion mechanism among copepods (Zaret, 1980), which makes prey escape easier. Confer & Blades (1975) explain, however, that larger zooplankton are more visible and, therefore, are more readily captured than smaller ones. In addition, fishes may prefer larger invertebrate prey (Brooks & Dodson, 1965), especially when they are in the last larval stage (Rossi, 2001).

Plagioscion squamosissimus larvae, with larger gape size in relation to the other two species, presented a distinct diet, preferring calanoid copepods (mainly *Notodiaptomus* sp.). Makrakis *et al.* (2005) associate *P. squamosissimus* diet, essentially made up of copepods during the larval period, with visual acuity, notable swimming ability and protraction of the jawbone. These attributes allow the fish larvae to capture these calanoid copepods, which are larger and faster than cladocerans and rotifers. Cyclopoid copepods, smaller than calanoids, however, were not ingested very much. Nauplii and copepodites (the

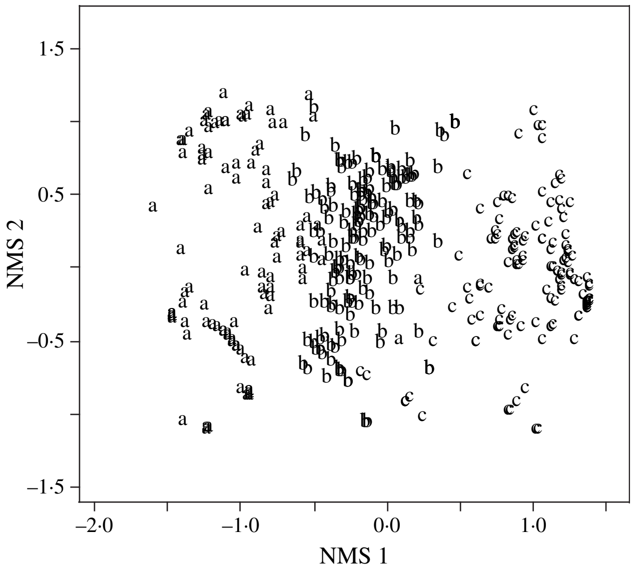

FIG. 9. Non-metric multidimensional scaling (NMS) ordination of the diet of fish larvae: *Iheringichthys labrosus* (a), *Hypophthalmus edentatus* (b) and *Plagioscion squamosissimus* (c).

TABLE II. Results from indicator species analysis. Indicator values are given for diet contributors under species groups: *Iheringichthys labrosus* (1), *Hypophthalmus edentatus* (2) and *Plagioscion squamosissimus* (3)

Taxa	1	2	3	*P*
Bosmina hagmanni	24*	26*	2	0·001
Bosmina huauriensis	11*	9	0	0·005
Bosminopsis deitersi	45*	5	0	0·001
Ceriodaphnia cornuta	6	60*	1	0·001
Daphnia gessneri	5	4	13*	0·039
Diaphanosoma spinulosum	0	22*	13	0·001
Moina minuta	4	13*	3	0·015
Copepodite of Cyclopoida	2	1	0	0·463
Thermocyclops decipiens	1	0	5*	0·021
Thermocyclops minutus	2	1	3	0·608
Copepodite of Calanoida	1	0	0	0·451
Notodiaptomus sp.	0	0	86*	0·001
Argyrodiaptomus sp.	0	0	28*	0·001
Brachionus calyciflorus	32*	4	0	0·001
Rotifer eggs	23*	4	0	0·001
Keratella cochlearis	3*	0	0	0·019
Lecane ludwigi ludwigi	2	0	0	0·071
Trichocerca capucina	1	0	0	0·267
Trichocerca cylindrica	2	0	0	0·065

*, significant values.

most abundant cyclopoid copepod stages) were not ingested at all by larvae. Perhaps this is because calanoid copepods are more visible. Teska & Behmer (1981) also verified that lake whitefish *Coregonus clupeaformis* (Mitchill) larvae prefer copepods (*Diaptomus sicilis*) to cladocerans and rotifers, even though they are faster swimmers. They ascribe this fact to the orange pigmentation found on these copepods that makes them more visible. Laroche (1982) considers body transparency a very important characteristic in the selection of various copepods by fish larvae. *Daphnia gessneri*, an abundant and slowly swimming cladoceran similar in size to calanoid copepods, did not constitute one of their favourite prey. Confer & Lake (1987) and Confer & O'Bryan (1989) believe that differences in handling time, intestinal course or assimilation efficiency can explain a more frequent pursuit of cyclopoid copepods than for *Daphnia* sp. by burbot juveniles *Lota lota* (L.).

Assuming the same spatial and temporal distribution for the different fish larvae, the species analysed presented a little distinct diets for those with similar gape sizes (*I. labrosus* and *H. edentatus*) and for those with different gape sizes (*H. edentatus* and *P. squamosissimus*), with no evidence of interspecific competition. It is possible that *H. edentatus* larvae have a forage behaviour distinct from *I. labrosus* larvae, that is, they are opportunists feeding on the most abundant prey. In addition, mouth position differences between both species may be related: the sub-terminal mouth of *I. labrosus* larvae (Makrakis *et al.*, 2005) can represent a greater limitation on prey types in comparison to *H. edentatus* larvae, which have terminal mouths and are able to explore distinct layers. Lack of a predictable relationship between gape size and diet has been noted by many authors (Laroche, 1982; Bremigan & Stain, 1994; Gaughan & Potter, 1997). Gaughan & Potter (1997) noted low feeding niche overlap for species with similar gape sizes and high overlap for species with distinct gape sizes. They ascribed this to the high concentration of available zooplankton.

Mouth size limitation is stronger during the initial life stages for planktivorous fishes (Zaret, 1980). In *P. squamosissimus* larvae, mouth limitation was more obvious in the early development phase (G_S classes between 0·6 and 1·5 mm L_S). In this period, their swimming capacity is possibly more restricted and does not allow the capture of larger and faster prey. Sizes of the zooplankton ingested by *H. edentatus* and *I. labrosus* larvae, however, were smaller compared to *P. squamosissimus*. According to Schmitt & Holbrook (1984), prey size selectivity patterns are related to the feeding apparatus size of the predator and the spectrum of available prey sizes. The preference of *H. edentatus*, and especially of *I. labrosus*, for smaller prey indicates that these species select prey smaller than the maximum size allowed by their mouths. The different feeding selectivity patterns are related to G_S, which limits the maximum size of potential prey (Hartmann, 1986), and mouth position. In addition to these factors, visual acuity, swimming ability and the filtering apparatus of *H. edentatus* should have an impact (Makrakis *et al.*, 2005). Gaughan & Potter (1997) explained that *Afurcagobius suppositus* (Sauvage) larvae ate larger prey than the other four fish species. *Afurcagobius suppositus* hatches at a more advanced stage with better developed fins than other species and are probably superior swimmers and thus more efficient at capturing larger prey. Wanzenböck & Schiemer (1989), Bremigan & Stain (1994) and Machácek & Matena (1997), however, highlighted the importance of visual acuity in prey selection by fish larvae.

The quality and quantity of food lead to the success of larval foraging, which may be the result of not only zooplankton abundance but also available size distribution. The high densities of zooplankton can ease, to a certain point, limitations that large extremes of zooplankton size exert on larval foraging. Gaughan & Potter (1997) commented that availability strongly influenced the sizes of the prey ingested by fish larvae in Wilson Inlet, Australia. The Mantel tests showed that larvae with small gapes (*I. labrosus* and *H. edentatus*) are rather opportunistic feeders that they eat more abundant prey, whereas *P. squamosissimus* actively selects prey types differing from the most abundant species or size classes.

Zooplankton community size structure can vary considerably throughout systems. This provides an explanation for the distribution patterns and abundance of planktonic fish species. In this manner, available zooplankton sizes could probably differentially affect the larvae of the three fish species studied in the Itaipu Reservoir. Environments dominated by large-sized zooplankton can represent ideal forage environments for *P. squamosissimus* larvae but can inhibit forage success and the growth, survival and recruitment of the larvae of both *H. edentatus* and *I. labrosus*. Therefore, low availability of small and intermediate-size zooplankton may lead to high diet overlap in *I. labrosus* and *H. edentatus*. This situation was observed in German estuaries by Thiel *et al.* (1996).

In conclusion, the mechanistic processes that determine food selectivity of fish larvae in temperate aquatic systems were similar in a neotropical system. *Iheringichthys labrosus* and *H. edentatus* larvae, with smaller and similar gape sizes, have selectivity patterns a little similar with slightly different diets (Fig. 10). The trophic spectrum of these species is characterized by small- to

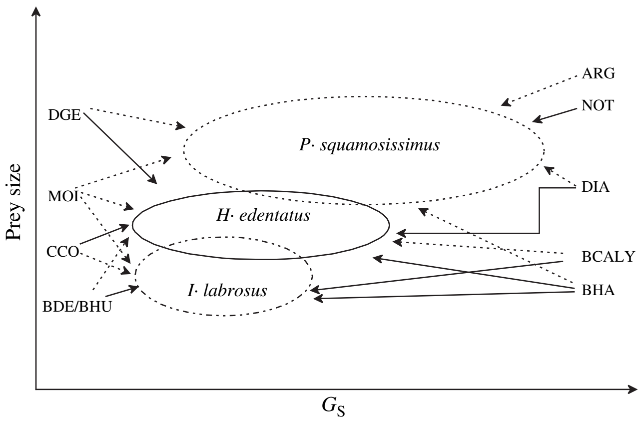

FIG. 10. Conceptual model showing relationships between gape size and prey size (see Appendix) observed for the fish larvae of *Plagioscion squamosissimus*, *Hypophthalmus edentatus* and *Iheringichthys labrosus*. Continuous arrows indicate strong selection whereas dotted ones indicate weak selection.

intermediate-sized prey. *Plagioscion squamosissimus* larvae, which have larger mouths, exploit primarily larger prey differing from the most abundant species or size classes. Consequently, their diet is quite different from *I. labrosus* larvae and modestly similar to *H. edentatus* larvae, which are opportunistic feeders in that they eat more abundant prey. It is probable that *P. squamosissimus* larvae are energetically more efficient. Therefore, the feeding resources used by the larvae of the three species are related to gape size, which impacts upon prey size, though not through a single or simple explanation. In addition, other factors are directly associated. Oral anatomy differences like mouth position, teeth and gill rakers, digestive tube morphology, visual acuity, forage behaviour and motility are also fundamental characteristics in determining the diet of these species.

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APPENDIX. Taxa codes and zooplankton abundance

Taxa	Code	Mean density (individual m^{-3})
Cladocera		
Bosmina hagmanni	BHA	187
Bosmina huauriensis	BHU	71
Bosminopsis deitersi	BDE	114
Ceriodaphnia cornuta	CCO	2016
Chydorus sp.	CHY	1
Daphnia gessneri	DGE	2547
Diaphanosoma spinulosum	DIA	754
Euryalona occidentalis	EOC	1
Moina minuta	MOI	73

APPENDIX. Continued

Taxa	Code	Mean density (individual m^{-3})
Copepoda		
Nauplius of Cyclopoida	NAUCY	1771
Copepodite of Cyclopoida	COPCY	951
Mesocyclops meridianus	MME	1
Thermocyclops decipiens	TDE	97
Thermocyclops minutus	TMI	162
Nauplius of Calanoida	NAUCA	824
Copepodite of Calanoida	COPCA	1383
Argyrodiaptomus sp.	ARG	329
Notodiaptomus sp.	NOT	506
Rotifera		
Ascomorpha ovalis	AOV	11
Bdeloidea sp.	BDEL	33
Brachionus calyciflorus	BCALY	400
Brachionus caudatus	BCAU	9
Brachionus dolabratus	BDO	4
Brachionus falcatus	BFA	12
Cephalodella sp.	CEP	1
Conochilus sp.	COM	670
Euchlanis dilatata	EDI	119
Filinia longiseta	FLO	27
Hexarthra mira	HMI	26
Keratella americana	KAM	12
Keratella cochlearis	KCO	19
Lecane bulla	LBU	8
Lecane curvicornis	LCU	13
Lecane proiyecta	LPRO	1
Manfredium eudactilota	MEU	1
Plationus macracanthus	PMA	25
Plationus patulus	PPA	1
Platyias quadricornis	PQU	4
Ploesoma truncata	PTRU	10
Polyarthra vulgaris	PVU	14
Ptygura sp.	PIT	3010
Sinantherina spinosa	SSP	9
Synchaeta sp.	SYN	40
Testudinella patina	TPA	7
Trichocerca cilindrica	TCI	5