Abstract.–Fish larvae and zoo-plankton were sampled during seven consecutive months from four regions of Wilson Inlet, an estuary in south-western Australia. Mouth size, prey size, and dietary composition of larvae of the gobiids *Afurcagobius suppositus*, *Pseudogobius olorum*, and *Favonigobius lateralis*, the blenniid *Parablennius tasmanianus,* and the syngnathid *Urocampus carinirostris* were determined. Dietary niche overlap (DNO) was calculated for co-occurring species pairs, both with and without incorporating a measure of relative prey (zooplankton) abundance. Significance of DNO was assessed 1) objectively, with boot-strapping of the dietary data and 2) subjectively, by assigning significance to values >0.6. The diet of *A. suppositus* was dominated by harpacticoids, poly-chaete larvae, and the calanoid *Gladioferens imparipes*, whereas diets of the other species were dominated by cope-pod nauplii and postnaupliar stages of the cyclopoid *Oithona simplex*, the proportions of the latter increasing with growth of the larvae. Small numbers of large and small prey items were found in the stomachs of *A. suppositus* (mean=2.5), which had the largest mouth, whereas large numbers (mean= 28.7) of small prey and no large items were found in the stomachs of *P. tasmanianus,* which had the second largest mouth. Between these ex-tremes, *P. olorum, U. carinirostris,* and *F. lateralis* each ate mostly small and intermediate-size prey, supplemented by a few large prey. The data did not support the hypothesis that an increase in the difference in gape size between species would decrease the prevalence of significant DNO. The lack of a con-sistent relation between mouth size and DNO among the five species is evidence that interspecific dietary differences reflect differences in feeding behavior. With bootstrapping, the prevalence of significant ($P<0.05$) DNO between spe-cies pairs was 32.6% when prey data were included in the analyses and 46.5% when prey data were not in-cluded. By subjectively assigning sig-nificance to DNO values >0.6, we ob-tained substantially less conservative estimates that indicated the prevalence of significant DNO was >53%.

Analysis of diet and feeding strategies within an assemblage of estuarine larval fish and an objective assessment of dietary niche overlap

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Starvation has been considered a major cause of mortality in larval fish (e.g. Hunter, 1984), although evidence from the field has been dif-ficult to obtain (Heath, 1992). If starvation occurs within an assem-blage of larval fish, competition for food is expected to contribute to that starvation. However, indications of any such competition may go unde-tected if the diet of only a single spe-cies is examined or if the influence of other planktivores (Fortier and Harris, 1989) is not considered. In the case of larval fish, relatively few studies have examined in detail the diets of several co-occurring species (e.g. Last, 1980; Laroche, 1982; Govoni et al., 1983; Watson and Davis, 1989). Furthermore, no study has objectively assessed the significance of dietary niche over-lap (DNO), where DNO refers to the amount of sharing of food resources among larval fish. Assessments of whether dietary overlap within or between species (including larval fish) is significant have been based on indices that range from 0 for no overlap to 1 for complete overlap, with values greater than 0.5, 0.6, or 0.7 considered to be significant (e.g. Harmelin-Vivien et al., 1989; Cervel-lini et al., 1993; Vega-Cendejas et al., 1994; Hartman and Brandt, 1995). However, because these cutoff points are arbitrary, they are not necessarily biologically significant, as in the case with fish larvae where individuals of co-occurring species may be confronted with large con-centrations of the same prey type and thus any similarities in diet may be due to chance encounters.

Although dietary compositions of larval fish have been considered in the context of the abundance of the zooplankton prey of those larvae (e.g. Dagg et al., 1984; Jenkins, 1987; Hirst and DeVries, 1994; Welker et al., 1994), no study of di-etary overlap between larval fish has incorporated data on their zooplank-ton prey. This analysis is necessary in order to assess whether there is a likelihood of competition for food.

Differences in mouth structure of fish may lead to differences in feed-ing success on particular prey types (Lavin and McPhail, 1986). Co-oc-curring larvae of different species with similar-size mouths may therefore exhibit a higher rate of significant DNO than those with mouths of different size. Because fish larvae usually swallow prey

whole, mouth size limits prey size; thus prey width is typically the limiting dimension for ingestion (e.g. Hunter, 1984, Heath, 1992). It is therefore important to examine mouth size and prey width when exploring the trophic relations of larval fish.

The first aim of this study was to examine the relation between mouth width, prey width, and dietary composition of the larvae of five teleosts in an estuary. The dietary data were then used to examine the extent of DNO between these species with a technique that takes into account relative prey concentrations. With this procedure we were able to test the hypothesis that divergence in gape size between species should be accompanied by a decrease in the prevalence of significant DNO between these species. Bootstrapping was used to assess whether species-pair DNO values were significant. The results of using this robust approach were compared with those obtained when relative prey concentrations were not included in the calculation of DNO and when a subjective level of >0.6 was considered to be significant for the DNO values.

Materials and methods

Sampling methods

This study was carried out in Wilson Inlet (35°00'S, 117°24'E), an estuary in southwestern Australia that comprises a 48 km^2 basin with two main tributaries, the Denmark and Hay rivers. Although samples were collected monthly between July 1988 and June 1989, the data used in this paper are restricted to those obtained between October 1988 and April 1989 when fish larvae were most abundant. Ichthyoplankton and zooplankton were sampled from open waters of the upper, middle, and lower basin, and the central channel of the lower saline reaches of the Denmark River, located 10.7, 8.3, 2.0, and 7.3 km, respectively, from the estuary mouth. The water depth in each region was between 2 and 3 m.

Sampling was initiated soon after sunset to reduce the likelihood of larvae avoiding the plankton nets. Fish larvae were collected with a pair of 500-μm-mesh conical nets, each with a mouth diameter of 0.6 m and a length of 2 m. The nets were attached to either side of a powerboat and towed for 10 min just below the surface of the water at a speed of 1.5 m/s. During each ichthyoplankton tow, three to five zooplankton samples were taken from the surface with a conical, 53-μm-mesh net with a mouth diameter of 0.35 m. The volumes of water filtered during each ichthyoplankton and zooplankton tow were measured with flowmeters. The zooplankton tows were 7–10 s

in duration. The flowmeter in the zooplankton net was closely observed during each tow. A tow was immediately terminated if the propeller speed suddenly decreased—a sign that the net was clogging. Samples were fixed in a 5% solution of formalin, which was replaced with 70% ethanol on the following day. The detailed results of the zooplankton sampling are given in Gaughan and Potter (1995).

Laboratory procedures and data analyses

Zooplankton were identified and counted under a dissecting microscope from subsamples of the replicate samples. Counts were standardized to numbers/m^3; thus mean concentrations of taxa at each region within each month were able to be calculated. Relative proportions of those zooplankton taxa that contributed to larval diets at any time during the study were calculated for each sample. These represented relative resource availability (R_i).

The gobiids *Pseudogobius olorum*, *Afurcagobius suppositus*, and *Favonigobius lateralis*, the blenniid *Parablennius tasmanianus*, and the syngnathid *Urocampus carinirostris* were chosen for the present study because their larvae are abundant in Wilson Inlet from late spring to early autumn (Neira and Potter, 1992), collectively contributing 70.8% of the total open-water assemblage of larval fish in this estuary between September 1987 and April 1989.

All larvae of each species in a sample were removed and counted. Body length (BL) of each larva (i.e. the distance from the snout to tip of notochord in preflexion and flexion larvae and from the snout to the posterior end of the hypural plate in postflexion larvae [Leis and Trnski, 1989]) was measured to the nearest 0.1 mm. Since a focus of this study was the comparison of mouth width with prey width, the diets of individual size classes of larvae were determined. However, because the analyses of DNO were undertaken for co-occurring species within individual samples, the dietary data for all size classes of each species were pooled (see below).

The smaller larvae of *P. olorum*, *P. tasmanianus*, *F. lateralis*, and *A. suppositus* were each grouped into 1.0-mm length classes. Because *P. olorum* and *P. tasmanianus* >5 mm BL and *F. lateralis* and *A. suppositus* >6 mm BL were rarely caught, larvae of these four species longer than these respective lengths were each grouped into single length classes. Because the length range of *U. carinirostris* was relatively wide, the larvae of this species were grouped into length classes with intervals of 3 or 4 mm, depending on the numbers caught.

Items in the gut were identified and counted. Maximum widths of intact dietary items, which typically

represent the limiting dimension for ingestion, were measured to 0.01 mm with an ocular micrometer in a compound microscope. Mouth width of larvae at the widest point of the upper jaw was similarly measured on a subsample of at least 50 larvae of each species. Widths of prey and mouth widths of larvae of each species were then plotted against body length of larvae.

Proportional utilization (p_i) of each prey type was calculated for length classes within each species with data pooled across regions and months. Proportional utilization was also calculated across length classes for the larvae of each species within a sample. Guts that were empty or contained only unidentifiable material were not included in these calculations.

Relative feeding prevalence of all larvae within samples were correlated against the corresponding estimates of zooplankton abundance to determine if there was any evidence that zooplankton abundance was limiting feeding success. The average DNO exhibited between all species within samples was likewise compared with zooplankton abundance.

Calculation of dietary niche overlap

Interspecific DNO was calculated for species-pairs within individual samples, i.e. for each site within a given month. Because this part of our study focused on examining niche relations between species, pooled diets for each species within a sample were considered to represent the average diet of each species. Furthermore, comparisons were limited to those samples in which ≥10 larvae of each of two or more species contained food. By pooling data across size classes we were able to compare more DNO data. Although the use of average diets would reduce the robustness of a parametric test of significance, we used nonparametric techniques for assessing the significance of DNO.

Sufficient numbers of larvae were obtained for analysis in 13 of the 28 ichthyoplankton samples (7 months × 4 regions) to allow 43 pairwise comparisons to be made between the diets of co-occurring species.

Besides the DNO values that were calculated and that incorporated prey abundance data, the results of this technique were also evaluated against calculations of DNO that did not incorporate such data. Because prey abundance data are incorporated into prey utilization data prior to calculating DNO (see below), the same formula was used to calculate DNO both with and without consideration of prey concentrations. DNO was measured with the symmetric niche overlap coefficient (Pianka, 1973)

$$\Phi_{ij} = \left(\sum p_{ij} p_{ik}\right) / \sqrt{\left(\sum p_{ij}^2 \sum p_{ik}^2\right)},$$

where p_{ij} and p_{ik} = the proportional utilization of prey type i by species j and k, respectively.

Using the p_i data directly, we were able to provide a basis for calculating DNO without prey abundance data. To incorporate prey abundance data, the geometric mean (g_i) of p_i and electivity (e_i) was used (Winemiller and Pianka, 1990), instead of p_i as in the original formula. The geometric mean gives a better indication of ecological similarity by reducing those biases within both p_i and e_i that can result from the presence of very abundant or very rare prey types (Winemiller and Pianka, 1990). Electivity is the p_i value that has been weighted by resource availability (R_i) as $e_i = p_i/R_i$. These values were calculated within the DNO algorithm and are not presented. Note that g_i can be used with other overlap indices because it is calculated prior to the calculation of the overlap value.

Bootstrapping of the resource matrix of a pair of species was used to obtain a null distribution of 1,000 pseudo-DNO values against which the significance of observed DNO could be assessed (Winemiller and Pianka, 1990). These calculations were performed for species pairs at sites within months. In each one of the 1,000 runs, the algorithm randomly reassigned the g_i values for each prey type (e.g. resource states $i...p$) within each larval species j and k, but among the resource types used by both j and k (e.g. amongst $g_{ij}...g_{nj}$ and $g_{ik}...g_{pk}$). A g_i value for one of the species pair may thus be reassigned to a resource state which was used only by the other species.

The null hypothesis (H_0) for each test was that the dietary compositions of the larvae of the two species were not the same. The null hypothesis was rejected if more than 95% of the 1,000 pseudo-DNO values were less that the observed DNO. Such cases indicated that the observed value was larger than would be randomly expected at $P<0.05$.

The prevalence of significant DNO calculated with g_i and bootstrapping was then compared with that obtained with p_i, i.e. when R_i was not taken into account. These results were also compared with those obtained when the significance of DNO was arbitrarily set at values >0.6.

Results

Zooplankton

Zooplankton were very abundant in Wilson Inlet between October 1988 and April 1989; there was a total mean monthly concentration of 342,746 organisms/m³ (range = 48,641–2,951,209/m³). Concentrations exceeded 100,000/m³ in 26 of the 28 zooplank-

ton samples. Mean monthly concentrations of zooplankton in Wilson Inlet were similar from October 1988 to April 1989; only January had a significantly ($P<0.05$) higher concentration (Gaughan and Potter, 1995).

All copepods, irrespective of stage, contributed 74.7% of the total mean concentration of zooplankton (Table 1). The cyclopoid *Oithona simplex*, the calanoids *Gladioferens imparipes* and *Acartia simplex*, and several species of harpacticoids were the only copepods that were common in Wilson Inlet (Gaughan and Potter, 1995). Considering just the copepods, adults of *A. simplex* and *G. imparipes*, which represented the largest prey types consumed by fish larvae in Wilson Inlet, contributed only 2.9% of the total mean concentration of this taxonomic group. The smaller species and developmental stages of copepods were thus approximately 33 times more abundant than the adults of *A. simplex* and *G. imparipes* collectively. The mean concentrations and relative contributions of other zooplankton taxa that were eaten by larval fish during this study are shown in Table 1.

Numbers of prey items consumed and dietary composition of fish larvae

The total number of larvae of each species examined during this study are shown in Table 2, and the numbers of larvae in size classes of each species which contained food are shown in Figure 1.

The mean number of prey items found in each larva was less than five for *A. suppositus* and *F. lateralis*,

between five and ten for *P. olorum* and *U. carinirostris* and 28.7 for *P. tasmanianus* (Table 2). Likewise, the maximum numbers of prey consumed were much lower for the first four species than for *P. tasmanianus* (Table 2). The number of prey ingested by larvae increased with body size only in the case of *U. carinirostris*.

Various developmental stages of copepods dominated the diets of larval fish in Wilson Inlet; the rotifer *Synchaeta* cf. *baltica* and the larvae of bivalves and polychaetes were also occasionally important (Fig. 1). Only the postnaupliar stages of copepods in the diets were identified to species. Each of the common types of copepod contributed to the diets of fish larvae.

During the growth of *P. olorum*, *F. lateralis*, *U. carinirostris*, and *P. tasmanianus*, the contribution of copepod nauplii declined while that of postnaupliar stages increased (Fig. 1). *Oithona simplex* was particularly important to *P. olorum* and *U. carinirostris*, representing over 30% of the diet of the three largest size classes of the former species and over 40% of the diet of all size classes of the latter species. By contrast, despite the increased contribution by *O. simplex* to larger size classes of *P. tasmanianus*, copepod nauplii dominated the diet of all size classes, contributing > 40% to each (Fig. 1). The diet of *F. lateralis* <4.0 mm BL consisted mainly of copepod nauplii and to a lesser extent of bivalve larvae and *O. simplex*. The main prey types of *F. lateralis* from 6.0–7.9 mm BL were harpacticoids (40.9%), calanoid copepodites (20.6%), and phytoplankton (15.6%).

Polychaete larvae, copepod nauplii, and harpacticoids each contributed over 25.0% of the diets of the smallest size class of *A. suppositus*, whereas harpacticoids alone contributed 60.0% to larvae >6.0 mm BL (Fig. 1). Harpacticoids also contributed 15.3 and 27.0% of the diet in the 4.0–4.9 and 5.0–5.9 mm length classes, respectively. *Gladioferens imparipes*

Table 1
Mean monthly concentrations and relative contributions of zooplankton in Wilson Inlet between October 1988 and April 1989.

Taxa	Mean concentration (no. organisms/m³)	Relative contribution (%)
Copepod nauplii	164,827	48.1
Calanoid copepodites	33,755	9.8
Oithona simplex	44,629	13.0
Acartia simplex	6,771	2.0
Gladioferens imparipes	719	0.2
Harpacticoids	5,523	1.6
Polychaete larvae	34,997	10.2
Bivalve larvae	18,435	5.4
Synchaeta cf. *baltica*	9,787	2.9
Other taxa	23,303	6.8
Total	342,746	

Table 2
Mean and maximum numbers of prey per larva for five teleost species in Wilson inlet. n = the total number of larvae of each species examined.

Species	n	Mean prey/larva	Maximum prey/larva
Pseudogobius olorum	1,946	7.7	30
Favonigobius lateralis	451	4.0	15
Afurcagobius suppositus	485	2.5	19
Parablennius tasmanianus	469	28.7	103
Urocampus carinirostris	434	9.7	23

was abundant only in the diet of the 4.0–4.9 and 5.0–5.9 mm length classes (Fig. 1).

Prey width and larval mouth width

Urocampus carinirostris had the smallest mouth, *P. tasmanianus* and *A. suppositus* the widest mouths (Fig. 2, A, D, E). The shapes of the mouths were most

Figure 1

Proportional utilization (p_i, %) for length classes of larvae of five species of fish caught at four sites in Wilson Inlet between October 1988 and April 1989. The numbers of larvae that contained food in each size class are shown above the bars.

similar in the case of *P. olorum* and *F. lateralis* (Fig. 2, B and C). Although mouth width of *U. carinirostris* increased linearly with body length (Fig. 2A), such an increase in the other four species was best described by a polynomial function (Fig. 2, B–E: Table 3). Mouth width of *U. carinirostris* increased slowly from 0.19 mm at 8 mm BL to 0.28 mm at 19 mm BL (Fig. 2A). The rate at which mouth width increased with body length was greater for the other four species (Fig. 2, B–E). In *A. suppositus*, mouth width increased from 0.33 mm at 3.5 mm BL to 0.68 mm at 6.0 mm BL (Fig. 2E). The smallest larvae of *P. olorum*, *F. lateralis*, and *P. tasmanianus* had narrower mouths (<0.15 mm) than both *A. suppositus* and *U. carinirostris*, owing to their smaller size upon arrival in the plankton (Fig. 2, A–E). However, mouth widths of the first three of these species exceeded the maximum recorded for *U. carinirostris* (0.28 mm) by the time each had attained 5 mm BL and approached 0.60 mm in larger larvae.

The slope describing the relation between prey width and larval length for each species was less than 0.03. The extent to which prey width increased with length was thus very small for each species. Minimum prey width for each species was about 0.04 mm (Fig. 2, A–E). The large numbers of prey of each species with widths of 0.04–0.08 mm were predominantly attributable to copepod nauplii. Prey widths of between 0.04 and 0.18 mm predominated in *U. carinirostris*, *P. olorum*, and *F. lateralis* (Fig. 2, A–C).

Parablennius tasmanianus ate mainly prey 0.04–0.13 mm wide, but with a maximum width of only 0.18 mm (Fig. 2D). *Afurcagobius suppositus* consumed the largest prey items, i.e. postnaupliar stages of *G. imparipes* and *A. simplex*, with widths of 0.12–0.30 mm and 0.10–0.16 mm respectively. As with the other species, *A. suppositus* also ate smaller items (0.04–0.10 mm) (Fig. 2E).

As *U. carinirostris*, *P. olorum*, *F. lateralis*, and *P. tasmanianus* grew, they continued to eat many prey <0.10 mm wide, even though the smaller larvae of each were capable of eating prey >0.10 mm (Fig. 2, A–D). Prey width was about 0.10 mm narrower than mouth width for most of the length range of *U. carinirostris* (Fig. 2A). The widths of the larger
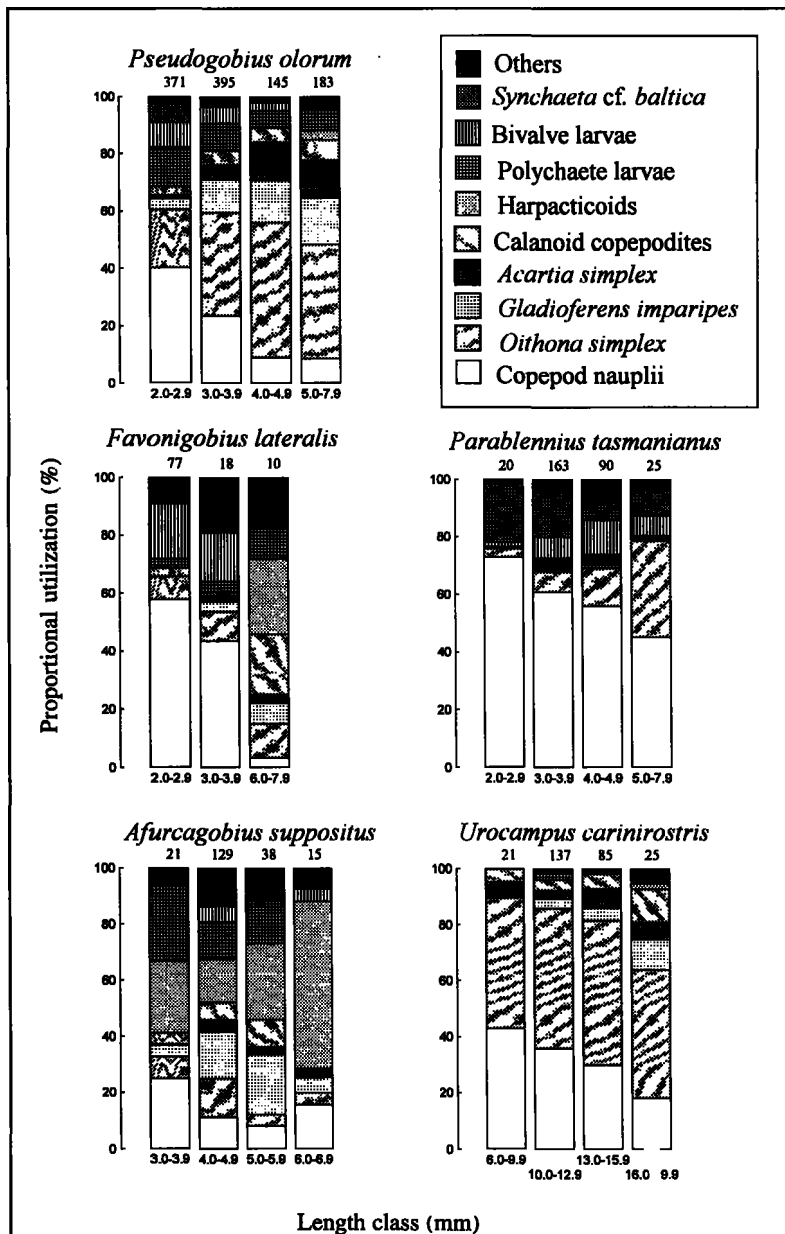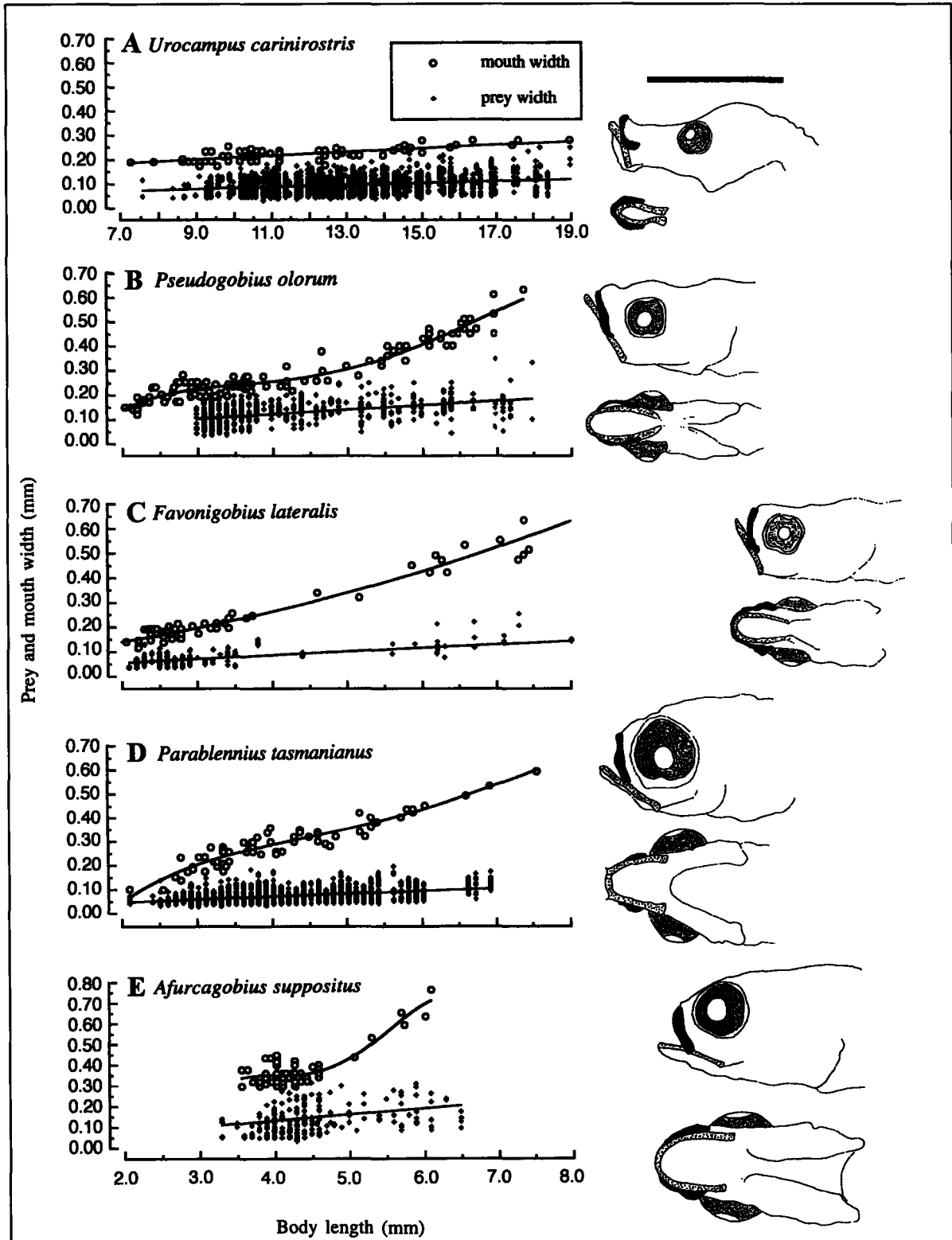
Figure 2
Prey width and larval mouth width for larvae of five species of fish caught in Wilson Inlet between October 1988 and April 1989. Lateral and ventral views of the head of a representative larva of each species are also given; the upper jaw is indicated in black, the lower jaw is indicated with stippling (scale bar equals 1.0 mm). The examples were each taken from a 5.0-mm-BL larva, except the example of *Urocampus carinirostris*, which was taken from a 10.5-mm-BL larva.

Table 3

The relations between mouth width (MW) and body length (BL) for the larvae of five teleost species in Wilson Inlet.

Species	n	Regression function	r^2
Urocampus carinirostris	69	$MW = 0.139 + 0.006(BL)$	0.453
Afurcagobius suppositus	50	$MW = -15.666 + 14.256(BL) - 4.687(BL^2) + 0.671(BL^3) - 0.035(BL^4)$	0.849
Pseudogobius olorum	98	$MW = -0.729 + 0.839(BL) - 0.273(BL^2) + 0.038(BL^3) - 0.002(BL^4)$	0.921
Favonigobius lateralis	50	$MW = 0.061 + 0.029(BL) + 0.005(BL^2)$	0.963
Parablennius tasmanianus	66	$MW = -0.517 + 0.411(BL) - 0.073(BL^2) + 0.005(BL^3)$	0.889

Table 4

The number of cases of significant dietary niche overlap (DNO) for larvae of five teleost species in Wilson Inlet between October 1988 and April 1989. Co-occurring species were compared only when ≥10 individuals of each contained food in their guts. The number of cases for which pairwise comparisons could be made is shown as n. The number of significant cases are presented for DNO calculations I) that used zooplankton concentrations and II) that did not use zooplankton concentrations. Within these categories, the number of significant cases were determined a) at $P<0.05$ from a null distribution derived from bootstrapping and b) with an arbitrary cutoff level for significance at an overlap value >0.6. DNO was measured with a modification of Pianka's (1973) symmetric niche overlap coefficient.

	Pseudogobius olorum n (I) (II) (a, b) (a, b)	*Afurcagobius suppositus* n (I) (II) (a, b) (a, b)	*Favonigobius lateralis* n (I) (II) (a, b)(a, b)	*Parablennius tasmanianus* n (I) (II) (a, b) (a, b)
Afurcagobius suppositus	5 (0, 2) (0, 0)	—		
Favonigobius lateralis	4 (1, 2) (1, 2)	1 (0, 0) (0, 0)	—	
Parablennius tasmanianus	8 (1, 4) (3, 6)	1 (0, 0) (0, 0)	4 (2, 4) (3, 4)	—
Urocampus carinirostris	8 (7, 7) (8, 8)	2 (1, 1) (0, 1)	4 (1, 2) (2, 3)	6 (1, 4) (2, 4)
Totals	n (I) (II) (a, b) (a, b) 43 (14, 23) (20, 28)			
Percent of total	(32.6, 53.5) (46.5, 65.1)			

prey items consumed by *P. olorum* <4.0 mm BL were similar to mouth width, as was also the case with *F. lateralis* of 2.0–2.5 mm BL and *A. suppositus* of 4.0–4.5 mm BL. For each of these three gobiid species, the maximum prey width of larvae >5 mm BL was far less than mouth width. This difference exceeded 0.20 mm in the larger gobiid larvae. Likewise, maximum prey widths for larval *P. tasmanianus* approached mouth width in smaller larvae but were much less for larger larvae (Fig. 2D).

Dietary niche overlap

Dietary niche overlap between *P. olorum* and *U. carinirostris* ranged from 0.543 to 0.983 and was significant on seven of the eight occasions in which these species co-occurred (Table 4). Although DNO ranged from 0.764 to 0.980 on the four occasions that *P.*

tasmanianus and *F. lateralis* co-occurred, overlap was significant only twice (Table 4). There were a few other cases of significant DNO amongst the larval fish assemblage; DNO was particularly low between *A.suppositus* and the other species, being significant only with *U. carinirostris* on one occasion.

Of the 43 pairwise comparisons that could be made between the diets of co-occurring larvae of the five species, there were 14 cases (32.6%) of significant DNO (Table 4). This increased to 20 (46.5%) if zooplankton data were not included in the calculations of DNO's. If DNO >0.6 had been considered significant, the number of significant cases increased from 32.6% to 53.5% for calculations which included zooplankton data and from 46.5% to 65.1% for those which did not include these data.

The magnitudes of the differences for the prevalence of significant DNO found by using bootstrap-

ping (18.6% and 20.9%) were greater than those obtained by accounting for zooplankton abundance data (11.6% and 13.9%, Table 4).

Relation between zooplankton abundance and both feeding prevalence and mean DNO

Zooplankton abundance at sites within months was not significantly related to either feeding prevalence ($P>0.05$, $r=0.346$, $n=26$) or mean DNO ($P>0.1$, $r=0.146$, $n=15$) of fish larvae within the corresponding samples.

Discussion

Numbers of prey consumed and prey size

Afurcagobius suppositus, because it ingested larger prey types, e.g. *G. imparipes*, consumed the least number of prey. The other species ate larger numbers of small and intermediate-size prey, e.g. copepod nauplii and *O. simplex*. The significant increase in numbers of prey with length for *U. carinirostris* only was probably attributable to the fact that the magnitude of the range of length of individuals examined for this species was 12 mm, whereas that of the other species was less than 6 mm.

Despite marked increases in mouth width during the growth of each species except *U. carinirostris*, average prey width of the five species increased only slightly with growth. Although smaller larvae consumed prey almost as wide as their mouths, larger larvae typically ate prey far smaller than their mouth size. Furthermore, the smaller larvae of each species consumed some prey items almost as wide as those eaten by larvae in the larger size classes. These data indicate that mouth width was not limiting the ingestion of larger prey types among larvae in the larger size classes.

The dominance of relatively small prey in the diets of larval fish in Wilson Inlet reflects the dominance of these types of zooplankton in the environment. During the study period, copepod nauplii, *O. simplex*, calanoid copepodites and harpacticoids were 33 times more abundant than the adults of *G. imparipes* and *A. simplex* collectively, the only common large prey. Thus, as has previously been found for other larval fish (e.g. Ware and Lambert, 1985; Kellermann, 1990), prey availability strongly influenced the sizes of prey consumed.

From an early age and size, *Afurcagobius suppositus* ate larger prey than the other four species. Since this species hatches at a more advanced stage and with better developed fins than the other four

species (Neira et al., in press), they were probably superior swimmers and thus more efficient at capturing larger prey. Greater mobility may have also resulted in *A. suppositus* searching a larger volume of water (Hunter, 1984), which would increase the rate at which the larger and less abundant zooplankton were encountered. The possession of a larger mouth apparently allows *A. suppositus* to take advantage of larger prey in presumably more frequent encounters.

Mouth size and DNO

Although *A. suppositus* had the largest mouth and consumed the largest and most diverse prey, the relative differences in mouth size of the other four species were not accompanied by corresponding differences in the size and composition of prey. A lack of a predictive relation between mouth size and diet has previously been recorded for fish larvae from another estuary (Laroche, 1982) and more recently for larvae of freshwater fish in an experimental situation (Bremigan and Stein, 1994). In Wilson Inlet, this situation was further highlighted by the lack of a relation between the prevalence of significant DNO and the mouth structure of the five species. Thus, the prevalence of significant DNO was not particularly high between *P. olorum* and *F. lateralis* (Table 4), the species with the most similar mouth structure, whereas *P. olorum* and *U. carinirostris* had very similar diets, as indicated by the high prevalence of significant DNO (Table 4), but had different-size mouths. Conversely, the diet of *A. suppositus* overlapped significantly only with that of *U. carinirostris*, the species with the smallest mouth. *Parablennius tasmanianus* and *F. lateralis*, the only other species-pair to exhibit more than one case of significant DNO, also had dissimilar mouths. Finally, *A. suppositus* and *P. tasmanianus* had the largest mouths but the most divergent diets.

Along with the general lack of a relation between mouth size and diet, the relatively frequent occurrence (32.6%) of significant DNO amongst the larval fish in Wilson Inlet, when prey abundance was taken into account, was also attributable to the high concentrations of relatively limited choices of acceptable prey types. The lack of a relation between concentrations of zooplankton and both feeding prevalence and mean DNO within samples was also probably a result of consistently high concentrations of zooplankton. Consequently, significant DNO among larval fish in Wilson Inlet provided no evidence of competition for food. Furthermore, Gaughan and Potter (1995) found that abundances of zooplankton and larval fish were significantly correlated at only two of the four sampling regions in Wilson Inlet. The lack of a rela-

tion at the other two regions was due to large fluctuations in the abundance of zooplankton between months. These fluctuations did not appear to influence monthly trends in the abundance of fish larvae, probably because concentrations of zooplankton typically remained high(>100,000/m³).

Because in this study we were limited to examining the diets of larval fish, a complete assessment of dietary relations and the potential for competition within the plankton community could not be undertaken. However, other zooplankton taxa (e.g. *Sagitta minima*) sufficiently large to have used the same food resources as larval fish were rare in Wilson Inlet, contributing less than 0.2% of the total numbers of zooplankton (Gaughan and Potter, 1995).

Feeding strategies

The diets of the fish larvae from Wilson Inlet may be viewed as representing a spectrum of feeding strategies.The diet of *A. suppositus* is distinguished from those of the other four species by its broader composition, the larger size of its prey items, and the smaller numbers of prey consumed. At the opposing end of the spectrum, *P. tasmanianus* larvae consumed large numbers of small prey items. The feeding strategies of the larvae of *P. olorum*, *F. lateralis*, and *U. carinirostris* lay between these extremes; these species consumed many small and intermediate-size prey which were occasionally supplemented with larger prey items.

Because the trophic character of a species may be influenced by both size and structure as well as behavior (Lavin and McPhail, 1986), the small influence of mouth width on the size of prey consumed by larval fish in Wilson Inlet indicates that the different feeding patterns among larval species probably resulted from behavioral differences (Bremigan and Stein,1994). These patterns, which occurred despite the high concentrations of zooplankton, may enhance survival, and hence recruitment, if marginally low concentrations of zooplankton were present at temporal or spatial scales beyond those sampled.

Evaluation of methods

In this study, we examined a technique for assessing DNO that consists of two parts (accounting for zooplankton abundance in the calculation of DNO and objectively assessing significance of DNO with bootstrapping). This technique was substantially more conservative than that which did not consider zooplankton abundance and which did subjectively assess significance. Prevalence of significant DNO thus doubled (32.6% to 65.1%) when zooplankton

data were not included in the calculations and an arbitrary cutoff point of 0.6 was used to test for significance. The less conservative techniques of measuring DNO and assessing its significance would have therefore overestimated the degree of DNO among fish larvae in Wilson Inlet.

A large overestimation of DNO would likely have led to a different interpretation of the data. For example, the higher rate of significant overlap may have led to the conclusion that competition for food was sufficiently high to influence markedly the survival rate of fish larvae in Wilson Inlet. In contrast, the lower prevalence of overlap is more consistent with our previous hypothesis that food is unlikely to be limiting for the open-water assemblage of larval fish in Wilson Inlet (Gaughan and Potter, 1995).

Although concentrations of potential zooplankton prey are not necessarily directly related to their availability, we suggest that inferences regarding competition for food among larval fish may be misleading if data on the abundance of the zooplankton are not considered when measuring DNO. In studies of other taxa, or even of adult fish, where the abundances of prey in the environment may be very difficult or impossible to estimate without bias, resource availability can be estimated in a circular manner with proportional-utilization data (see Winemiller and Pianka, 1990). However, because the majority of fish larvae and their potential prey are planktonic, small, and relatively immobile (thus highly susceptible to capture with plankton nets), estimates of prey concentrations in the environment should be used to calculate DNO for larval fish. Likewise, because a subjective assessment of the significance of DNO is inadequate, bootstrapping techniques may prove to be useful in making an objective examination of dietary relations,which are typically awkward to analyze statistically (Winemiller and Pianka, 1990; Baltanás and Rincón, 1992).

Finally, although the two parts of the technique used in this study, i.e. objectively assessing significance and accounting for zooplankton abundance, each contributed to the overall result, individually the former had a greater influence (18.6% and 20.9%) on the estimated prevalence of significant DNO than the latter (11.6% and 13.9%). Even though the direction and magnitude of the differences between the two parts of this technique may apply only to the current study, this finding further suggests that both the incorporation of prey abundance data and an objective assessment of significance need to be considered in an analysis of dietary overlap because either may have more influence on the apparent prevalence of significant DNO.

Acknowledgments

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