D. Rissik · I. M. Suthers

Feeding in a larval fish assemblage: the nutritional significance of an estuarine plume front

Abstract Gut fullness of larval fishes was used to determine the nutritional significance of an estuarine plume front off Botany Bay, SE Australia, on three days in March/April 1990. Fishes were captured in three different water masses (estuarine plume, front and shelf water), each separated by >200 m, using a 260 μm mesh purse-seine net. Overall, the gut-fullness index (GFI) of 260 fish larval combined from eight families (Gerridae, Mugilidae, Mullidae, Sparidae, Blemnidae, Kyphosidae, Monodactylidae, Pomacentridae), was significantly greater in the plume and front water on two of the sampling occasions, but no difference was detected on the third occasion. Trends in GFI among families were inconsistent with respect to the front. The mugilid (Liza argentea) fed equally and abundantly in all water masses (gut fullness > 90%), while the kyphoid (Kyphosus spp.) had a significantly greater GFI in the plume compared to the shelf water. In general, the response of GFI to the front varied between dates and amongst taxa. Diet analysis showed that mugilids selected for copepod nauplii within the plume and shelf water [alpha selectivity index (ASI) of 0.22 to 0.98] and for harpacticoid copepods within the front (ASI = 0.92), representing characteristic diets identified by canonical discriminant analysis. Kyphodids selected positively for copepod nauplii in all three water masses on both occasions (ASI > 0.96). In general, diets of larval fish were taxon-specific, and responded variably to the three habitats. Comparison of diets across water masses was complicated by the large number of families, which rarely occurred in all water masses. The nutritional significance of an estuarine plume front varies between species of larval fish, and there are no obvious trends that can be applied to the larval fish community in general.

Introduction Starvation is considered to be a major source of mortality amongst fish larvae, acting either directly, or mediated by reducing larval growth rates and therefore increasing exposure to size-selective predation (Shepherd and Cushing 1980). Thus, feeding conditions and feeding success of larval fishes are important in the recruitment of fish larvae into higher year-classes (May 1974; Lasker 1973, 1981; Hunter 1981).

Zooplankton and larval fishes accumulate in the convergence associated with estuarine fronts (Govioli et al. 1989; Grimes and Finacane 1991; Govoni and Grimes 1992; Kingsford and Suthers 1994). The result- ant accumulation of zooplankton may provide above-average concentrations of food for associated fish larvae (Govioli et al. 1989). Munk (1993) found that larval sprat (Sprattus sprattus) from within a tidal front and mixed water masses achieved a higher growth rate than larvae from more stratified water masses. In contrast, fish larvae associated with the Mississippi plume front had no nutritional advantage compared to larvae from nearby oceanic and estuarine sites (Govoni and Chester 1990, Powell et al. 1990). More studies are therefore required to assess the nutritional significance of oceanographic features to fish larvae.

Off the southeast coast of Australia, an ebb-tide plume of estuarine water extends into the Tasman Sea from the mouth of Botany Bay. The front is often characterised by the presence of a slick indicated by the presence of drift algae and other flotsam. Kingsford and Suthers (1994) reported that larval fishes and zooplankton were more abundant in waters of the plume and front than in shelf waters most of the time. The simultaneous capture of fish larvae and zooplankton with a small-mesh purse seine provided an ideal

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opportunity to assess whether high concentrations of zooplankton in the front would lead to enhanced feeding by fish- associated larval fishes. No research has been published on the feeding ecology of larval fishes in the marine or estuarine waters of New South Wales, SE Australia. Studies on the feeding ecology of 20 species of larval fish have been carried out in Australian waters. These include six from the east coast (Young 1991), two of which were in the tropical waters off northern Queensland (Jenkins et al. 1986; Schmitt 1986), two of SE Tasmania (Thresher et al. 1992; Young and Davis 1992) and two in Port Phillip Bay, Victoria (Jenkins 1987). The large variety of larval fish taxa which occur along the Australian east coast (e.g. Gray 1993 reported 108 families, often resulting in relatively small numbers of individuals from each taxon being captured in larval fish samples (Kingsford and Sutters 1994). The nutritional significance of estuarine plumes to larval fishes cannot be determined by morphological or biochemical condition indices (e.g. Ferron and Leggett 1994), as these indices are species-specific and reflect changes in condition over at least 2 to 3 d (Morgan and Wright 1987), whereas a gut-fullness index (GFI) would match the 2 to 4 d temporal scale of frontal formation on the ebb tide. Furthermore, over 28 families were found about the plume fronts, but rarely did the same species occur in all three habitats (Kingsford and Sutters 1994). Fronts appear to restrict estuarine fishes from venturing from plume water; while larval of pelagic fishes may be prevented from entering estuaries by the presence of the more turbid, less dense estuarine water (Kingsford and Sutters 1994). A GFI could provide a short-term measure of feeding opportunity across a range of taxa.

Consequently, gut fullness was considered a possible measure comparing multihabitat feeding and to determine the significance of the front. The aims of this study were to determine whether larval fishes at the plume front had greater gut fullness than fishes caught within the estuarine or shelf waters on either side of the front, and to determine if certain prey types were preferentially selected in the different water masses. We also wished to determine if a variety of larval taxa responded similarly to the front. For the purpose of this study, it was assumed that larval fishes would feed constantly during the day and that the presence of food in the environment would be reflected in the relative gut fullness of larval fishes.

Materials and methods

Study area and sampling

Botany Bay is a large (56 km²) embayment near Sydney, New South Wales, Australia (Fig. 6). The bay is shallow, with a maximum depth of 19 m in the dredged shipping channel. Fresh water from rivers and stormwater drains discharges into the bay, resulting in the water being slightly less dense than shelf water, and thus promoting a composite estuarine plume on the ebb tide (Kingsford and Sutters 1994). A study of this ichthyoplankton and zooplankton of the Botany Bay plume was carried out over 8 d during March/April 1990 (Kingsford and Sutters 1994). Larval fishes caught in the plume front and shelfwater (1100 and 1500 hrs. on 21 March, 23 March and 10 April (when larval abundance was relatively high) were selected for comparison of gut fullness and stomach contents. On 23 March, the colour line of the ebb tide front off Cape Banks was associated with a slack, drift-elipse and (at times, while on 21 March and 10 April) there was no slack, and the front was located by the distinct colour line (Fig. 1). Sampling sites were located at the front end and at sites 200 m on either side of the front (i.e. plume and shelf). Fish and zooplankton were captured in each water mass by three replicate casts of a plankton purse-net box with a mesh size of 200 µm (Kingsford and Cho 1986; Kingsford and Sutters 1994). Each cast sampling was 30 m³ of water. Samples were fixed and stored in 5% formalin. Larval fishes were identified to the lowest possible taxa (Kingsford and Sutters 1994), including codlings, cyprinids and hermaphroditic copepods and copepodite stages which were referred to as this study. Eight abundant families in the front, which were present in the other two water masses, and with non-extravagant guts, were selected for gut analysis (Gerezeide, Mugilidae, Mullidae, Serranidae, Labridae, Kyphosidae, Myctophidae, Pleuronectidae). These taxa were divided into an estuarine guild and a rocky-shelf guild according to their adult habitats. Pelagic taxa (Chaparata and Gonostomidae) with long straight guts were empty (possibly due to gut evacuation during capture. Ashby 1976; and were not used for this study.

The standard length (SL) of each fish was determined with an optical micrometer. The gut content was dissected from the fish using a pair of fine dissecting needles. The gut was placed in glycine-citrate, open, and the stomach contents were insured. The stomach contents were stained with a solution of 5% buffered black F, 20% alcohol, 2% water and 1% lactic acid (Morisaki 1980). Care was
taken to ensure that all gut contents were removed from between the folds of the stomach wall. The contents were then identified to four broad taxa: calanoid, cyclopoid, harpacticoid, and nauplii.

In order to determine the general trends in gut feeding success of fishes in the plaice, flounder, and sole, the gut fullness data of all taxa from each of the sites were initially pooled and the mean gut fullness was compared before examining each family separately using a one-factor ANOVA and Sheffé’s post-hoc test. Sheffé’s test is a conservative comparison procedure which has demonstrated robustness to non-homogenous variances (Abbas-Caron 1992). The gut fullness rates were homogenous between water masses, and no transformation was required (Cochran’s test, p > 0.05).

Two taxa (Heteromastus, Magnidae and Kieffersia spp.) which were relatively abundant at each of the three sites were used to compare gut contents with data on zooplankton abundance in the water (Kjiiefred and Butter 1994) using the alpha index of selectivity (Chesson 1978; Marchand 1990, Asselmon 1994). The alpha index standardises selectivity for the relative abundance of all prey types, enabling samples with varying abundance to be directly compared. The L. argentiensis dip of 25 March was further analysed by a canonical discriminant analysis applied to the four dietary components.

The mesh size (25 μm) of the purse-seine net used to estimate zooplankton abundance precluded the capture of nauplii ≤70 μm in size. Table 1 indicates that nauplii in the gut contents of many fish larvae. The abundance of copepodite stages 150 to 100 μm in size was assessed to be in proportion to, and to be positively correlated with, the numbers of nauplii ≤70 μm in size in the surrounding waters (Frank 1992). There is no evidence to suggest that this is not the case in East Anglian waters.

Results

Two hundred and sixty fish larvae belonging to eight taxa (Table 2) were selected for gut-content analysis. Numbers were uniformly distributed across the three water masses (Fig. 2), reflecting the distribution and abundance of fish larvae at the three sampling stations.
Table 3 Results of one-factor ANOVA comparing gut fullness of larval fishes caught in plume-plume-front or shelf waters (MS: mean square value; * F-test value * significant difference)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 March (all taxa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>0.47</td>
<td>0.46</td>
<td>0.63</td>
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<tr>
<td>(error)</td>
<td></td>
<td>(44)</td>
<td>(1.01)</td>
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<tr>
<td>23 March (all taxa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>13.7</td>
<td>8.58</td>
<td>0.01*</td>
</tr>
<tr>
<td>(error)</td>
<td></td>
<td>(170)</td>
<td>(1.61)</td>
<td></td>
</tr>
<tr>
<td>10 April (all taxa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>2.41</td>
<td>2.54</td>
<td>0.09</td>
</tr>
<tr>
<td>(error)</td>
<td></td>
<td>(37)</td>
<td>(0.95)</td>
<td></td>
</tr>
<tr>
<td>Mullidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>0.02</td>
<td>0.04</td>
<td>0.96</td>
</tr>
<tr>
<td>(error)</td>
<td></td>
<td>(59)</td>
<td>(0.37)</td>
<td></td>
</tr>
<tr>
<td>Kyphosus</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>2.36</td>
<td>2.99</td>
<td>0.07</td>
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<tr>
<td>(error)</td>
<td></td>
<td>(180)</td>
<td>(0.79)</td>
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<td>K. phosphide</td>
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<tr>
<td>Hydrology (pH)</td>
<td>2</td>
<td>5.70</td>
<td>5.51</td>
<td>0.01*</td>
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<tr>
<td>(error)</td>
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<td>(280)</td>
<td>(1.05)</td>
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</tbody>
</table>

Comparison of the mean gut fullness of fish caught at each site on 23 March showed that the guts of fishes caught within the plume and front were significantly fuller (p < 0.01; Fig. 2; Table 3) than those of fishes caught within the surrounding shelf water (Schelle’s post-hoc test p < 0.05). On 10 April there was no significant difference in gut fullness between the three water masses (Table 3), although fishes (mostly Kyphosus) caught within the front tended to have a greater gut fullness.

A comparison of individual taxa from the three water masses on 10 April 1990 showed variable success for each water mass (Fig. 3), although trends were confounded by small sample sizes. Mullid fishes exhibited similar levels of gut fullness (mean = 4) in each water mass, while mullids, sparids and kyphoids exhibited no consistent trend.

A greater number of larvae were captured on 23 March, and comparison of individual taxa from the three sites revealed contrasting success for the individuals from the estuarine gill of fishes at each site (Fig. 4a). Fishes of this estuarine gill showed family-specific responses. Gireuids, although not captured within the plume, had similar levels of gut fullness within the front (mean GF1 = 2.3) and in shelf water (mean GF1 = 2.5). Mullids were highly successful feeders at each of the three water masses and no significant differences were found amongst water masses (Table 3), with mean GFIs of 4.4, 4.5, 4.5 at plume, front and shelf-water sites, respectively.

Mullids had half-full guts (mean GF1 = 3) within the plume and at the front (mean GF1 = 2.3), while those caught in shelf waters were unsuccessful feeders (mean GF1 = 1.5), although this trend was not statistically significant (Table 3).

Sparids were less successful feeders within the plume (mean GF1 = 2.3), than within the front (mean GF1 = 3.5), while no sparids were captured within the shelf-water-mass.

Fish taxa belonging to the rocky-reef guild had few representatives in each of the three water masses. Feeding generally appeared to be more successful within the plume, with individuals from the front and shelf waters being less successful (Fig. 4b).

Kyphoids fed significantly more within the plume (mean GF1 = 3.7) than in the shelf water (mean GF1 = 2.4, p < 0.04; Table 3), while individuals from the front (GF1 = 3.2) were not significantly different from either of the other sites (Schelle’s post-hoc test p > 0.05).

Monodactyl feeding incidence from within the plume (mean GF1 = 4.0) was similar to that within the shelf water-mass (mean GF1 = 4.1, p < 0.04; Table 3), while individuals from within the front (GF1 = 3.2) were not significantly different from either of the other sites (Schelle’s post-hoc test p > 0.05).

Feeding selectivity

Mugilid (Mugil anguillarum) diet

Mugilids were highly selective feeders, selecting against calanoid and cyclopoid copepods in the three water masses, and selecting for nauplii (Table 4; Fig. 5a). They
selected against harpacticoid copepods in plume and shelf waters (alpha values = -0.995 and -0.963, respectively), and selected for harpacticoid copepods within the front (alpha = 0.674). Calanoid copepods were three times more abundant than any other plankton type in the front, and harpacticoid copepods were only present in low numbers. In the 75 guts from Lica argentum that were dissected for this study, only three other food items were found: two cypsis larvae and one cladoceran.

The canonical discriminant analysis identified distinct diets of maglids in the three water masses on 23 March (Pillai’s trace $p < 0.001$, $n = 42$), and the result-
On 30 April, there was no slick associated with the front and no drift algae was apparent within the plume and front. Kyphosus within the plume, front and shelf water masses selected strongly for copepod nauplii (alpha values = 1.0, 1.0 and 0.946, respectively), and showed strong avoidance (alpha value = −0.62) of all other potential food items (Fig. 6).

There was no significant difference in (n = 62; p > 0.05) in the mean standard lengths of Kyphosus spp. between 23 March and 30 April sampling occasions, indicating that ontogenetic diet shift was not the cause of the different prey selectivity in the plume.

**Discussion**

Pooled data for the gut-fullness index of fish larvae in the three water masses, or that feeding was more successful within the plume and front than in shelf water. Slightly turbid water could enhance the contrast of transparent food organisms against background light, enabling fish to capture food more easily (Boshert and Morgan 1985; Breitburg 1988). Plume water and fronts may also contain fish eggs to which prey items can attach or around which they may aggregate. Convergence zones will also be areas of increased microturbulence. Increasing the contact rate between prey and larval fishes (Sundby and Fossum 1990), enabling fishes in a front to consume a greater number of food items than those in shelf waters. This overall trend did not continue across the eight families. The shortage of larvae captured in certain water masses made it difficult to compare suitable numbers of each taxon from each site. Nevertheless, the gut-fullness index comparisons seemed to be complicated by family-specific responses to feeding in the different water masses, and by day-to-day variability.

Data from the 21 March reflect the difficulty in conducting multi-taxon gut-fullness comparisons where the diversity of taxa is high but abundance is low (Gray et al. 1992; Gray 1993). The trends shown by individual taxa on this date did reflect those on 23 March when a greater number of individuals from each taxon within each water mass were captured.

The variation in gut fullness between individual taxa highlights the importance of not lumping taxa when assessing the nutritional significance of an oceanographic feature such as an estuarine plume front. The variation of gut contents between the same taxon captured in different water masses suggests that individuals captured in different oceanographic conditions should also not be lumped together when carrying out dietary studies.

Anatomical differences between species may have affected the results because of variation in evacuation time, shape and volume of the gut. Mugilids have large buoyant guts and are able to consume a relatively large volume of prey before their guts are full, whereas similar-sized Kyphosus larvae have small guts which become diseased after consuming a smaller volume of prey (Fig. 5).

The diverse breeding strategies of the taxa collected may result in the larvae having different feeding responses to different conditions. Estuarine-dependent fish either spawn within estuaries and carry out their entire life cycle within an estuary, or spawn in marine waters and the larvae then enter estuarine nursery habitats (Miskiewicz 1989; Whitfield 1989). The mugilid *Liza anguillarum* spawns at sea before its young are transported into estuaries (Miskiewicz 1989). While migrating from shelf water into estuarine water, the fish larvae must survive in water masses with vastly different physical characteristics. These larvae must be able to feed effectively in all physical regimes that they encounter.

Feeding periodicity of larval fishes has been reported to be species-specific and may have influenced these results. Although most fish larvae are visual feeders and feed during the day (Huntér 1981), larval *Trachurus* spp. (family Carangidae) are crepuscular feeders, feeding in the early morning and late afternoon (Young and Davis 1990).

**Diets of mugilids and kyphosids**

The diets of most larval fish studied in Australian waters have been dominated by various ontogenetic stages of copepods (Young 1991). The harpacticoid copepods in the larval guts were sufficiently large to ensure their capture in a 200 μm mesh net, yet their relative abundance was small in the plume, front and shelf waters. This high selectivity by the larva was not demonstrated in each water mass. Selection towards harpacticoid copepods has been reported in
Effects of frontal convergence

The dynamic nature of the front presents a highly variable feeding environment to larval fishes, and this could be a factor preventing consistently enhanced feeding from taking place. Small droplets placed up to 50 m on either side of the Botany Bay plume front were advected into the frontal gap (Crawford, Kingston and Sutters 1996), suggesting that strong convergence of the front could also result in0014 in fishes of varying condition being advected into the front from the surrounding water masses. A similar scenario was suggested by Govoni et al. (1989) as a contributing factor to the variation in nutritional condition and feeding rates of fishes at the Mississippi plume front. Gut evacuation times for larval fishes are between 4 and 12 h (Jenkins 1987), which often exceeds rates of convergence. A survey on a scale greater than 200 m on either side of the front may produce different results.

Conclusions

Fishes from the plume and front water-masses were generally more successful feeders than those caught in the shelf water-mass. However, the direct significance of plume fronts for feeding and survival in a larval fish assemblage is complex, due to taxon-specific trends in the gut fullness of larval fish. The gut-fullness index was not a "species robust" method for assessing the nutritional significance of oceanographic features across a range of taxa. Any significance is complicated by the opportunistic feeding nature of larval fishes, and the relative paucity of individuals of the same species in all three habitats for comparison, coupled with variable physical dynamics and convergence rates.

Gut fullness is a simple technique reflecting species-specific responses, but represents feeding over the previous 2 to 3 h when the fishes could potentially have been in a variety of different habitats depending on convergence rates. Future studies of this nature should attempt to sample larvae at increased distances from the front, or should consider caging larvae in each of the three water masses. Specific taxa should be targeted during sampling to ensure that sufficient sample sizes are obtained from each water mass.

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References

Archer DR (1976) Food and feeding of three fishes occurring in the Californian current. Sardinius pyela, Engraulis mordax and Thunnus thynnus. Fish Bull 72: 517-526
Govoni JI, Grimes CB (1992) The surface accumulation of larval fishes by hydrodynamic convergence with the Mississippi River plume. Trans Roy Soc Sel 12: 1265-1281