

D. Rissik · I. M. Suthers

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

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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 μ m mesh purse-seine net. Overall, the gut-fullness index (GFI) of 260 fish larvae combined from eight families (Gerreidae, Mugilidae, Mullidae, Sparidae, Blenniidae, 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 kyphosid (*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. Kyphosids 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 1975, 1981; Hunter 1981).

Zooplankton and larval fishes accumulate in the convergence associated with estuarine fronts (Govoni et al. 1989; Grimes and Finucane 1991; Govoni and Grimes 1992; Kingsford and Suthers 1994). The resultant accumulation of zooplankton may provide above-average concentrations of food for associated fish larvae (Govoni 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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D. Rissik (✉) · I.M. Suthers
Centre of Marine Science, the University of New South Wales,
Sydney, New South Wales 2052, Australia

Table 1 Mean (SE) carapace widths (μm) of copepod prey items in guts of larval fishes

	Calanoid	Cyclopoid	Harpacticoid	Nauplii
Mugilidae (<i>Liza argentea</i>)	195 (15)	129 (4)	142 (14)	58 (11)
Kyphosidae (<i>Kyphosus</i> spp.)	136 (26)	111 (11)	138 (10)	41 (6)

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 and harpacticoid copepods and nauplii. The carapace width of the various prey items, representing the smallest dimension for feeding by larvae, was measured using an optical micrometer (Table 1).

A gut-fullness index (GFI), estimated from the relative size of the alimentary canal and the gut contents, was used to score the fullness of each gut (Young and Davis 1990). The following criteria were used: 0, empty; 1, at least some form of gut contents; 2, gut less than half full; 3, gut half full; 4, gut greater than half full; 5, gut distended. A GFI between 4 and 5 classified a successful feeder, while a GFI of 0 or 1 classified an unsuccessful feeder.

Analysis

In order to determine the general trends in the feeding success of fishes in the plume, front and shelf water-masses, 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 Scheffé's post-hoc test. Scheffé's test is a conservative comparison procedure which has demonstrated robustness to assumption violations (Abacus Concepts 1992). The GFI variances were homogeneous between water masses, and no transformation was required (Cochran's test, $p \geq 0.05$).

Two taxa (*Liza argentea*, Mugilidae and *Kyphosus* spp., Kyphosidae) which were relatively abundant at each of the three sites were used to compare gut contents with data on the zooplankton abundance in the water (Kingsford and Suthers 1994) using the alpha index of selectivity (Chesson 1978; Murdoch 1990; Anderson 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. argentea* diet of 23 March was further analysed by a canonical discriminant analysis applied to the four dietary components.

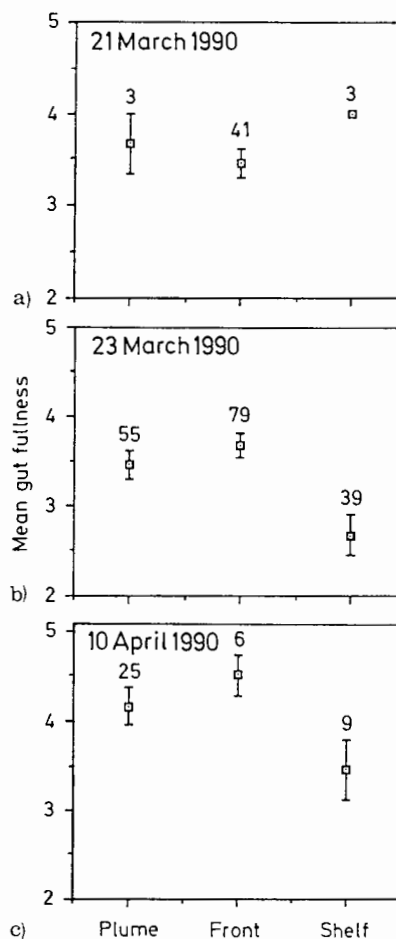
The mesh size (264 μm) of the purse-seine net used to estimate zooplankton abundance precluded the capture of nauplii (<90 μm carapace width, Table 1) that were found in the gut contents of many fish larvae. The abundance of copepodite stages (50 to 100 μm carapace width) is assumed to be in proportion to, and to be positively correlated with, the numbers of nauplii (10 to 70 μm carapace width) in the surrounding waters (Frank 1992). There is no evidence to suggest that this is not the case in east Australian waters.

Results

Two hundred and sixty fish larvae belonging to eight taxa (Table 2) were selected for gut-content analysis. Numbers were unevenly distributed across the three water masses (Fig. 2), reflecting the distribution and abundance of fish larvae at the three sampling sites.

Table 2 Length statistics of each taxon of fish larvae analysed for gut fullness (*ni* not identifiable to genus level, *SL* mean standard length, mm; *n* sample size)

Family	Genus	SL (SE)	Range	[<i>n</i>]
Gerreidae	<i>Gerres</i>	3.80 (0.17)	3.0–5.7	[8]
Mugilidae	<i>Liza</i>	5.20 (0.15)	3.2–8.1	[77]
Mullidae	ni	5.68 (0.60)	3.0–15	[28]
Sparidae	<i>Acanthopagrus</i>	5.64 (0.22)	3.3–8.2	[30]
Blenniidae	ni	5.93 (0.25)	5.1–7.0	[7]
Kyphosidae	<i>Kyphosus</i>	4.26 (0.11)	2.1–6.6	[90]
Monodactylidae	<i>Monodactylus</i>	3.90 (0.26)	2.7–5.1	[9]
Pomacentridae	ni	4.37 (0.52)	2.1–7.9	[11]

**Fig. 2** Mean \pm standard error (SE) of gut fullness of larvae for all taxa combined, captured from each of the three water masses in each sampling period (Number above each data point sample size)

Gut fullness

The pooled comparison revealed no significant difference ($p > 0.05$) between the mean gut fullness of fish larvae caught in each water mass (plume, front and shelf) on 21 March (Fig. 2; Table 3).

Table 3 Results of one-factor ANOVA comparing gut fullness of larval fishes caught in plume (p), front (f) or shelf (s) waters (MS: mean square values; F F-test value; * significant difference)

Source of variation	df	MS	F	p
21 March (all taxa)				
Hydrology (pfs)	2	0.47	0.46	0.63
(error)	(44)	(1.01)		
23 March (all taxa)				
Hydrology (pfs)	2	13.7	8.58	0.01*
(error)	(170)	(1.61)		
10 April (all taxa)				
Hydrology (pfs)	2	2.41	2.54	0.09
(error)	(37)	(0.95)		
Mugilidae				
Hydrology (pfs)	2	0.02	0.04	0.96
(error)	(59)	(0.57)		
Mullidae				
Hydrology (pfs)	2	2.36	2.99	0.07
(error)	(18)	(0.79)		
Kyphosidae				
Hydrology (pfs)	2	5.70	5.51	0.01*
(error)	(29)	(1.05)		

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 (Scheffé'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 Kyphosidae) 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. Mugilids exhibited similar levels of gut fullness (mean = 4) in each water mass, while mullids, sparids and kyphosids 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 guild of fishes at each site (Fig. 4a). Fishes of this estuarine guild showed family-specific responses: Gerreids, although not captured within the plume, had similar levels of gut fullness within the front (mean GFI = 2.3) and in shelf water (mean GFI = 2.5).

Mugilids 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 GFI = 3) within the plume and at the front (mean GFI = 2.3), while those caught in shelf waters were unsuccessful feeders (mean

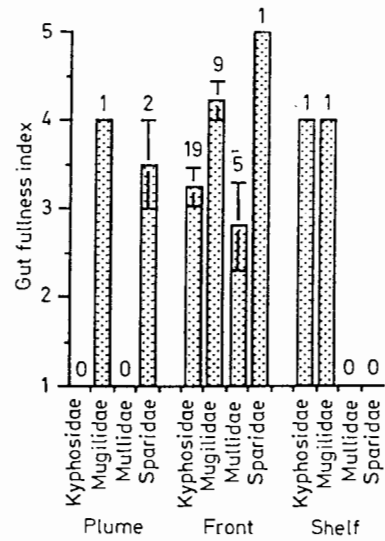


Fig. 3 Mugilidae, Kyphosidae, Mullidae and Sparidae. Mean gut fullness (\pm SE) of fish larvae from each of the three water masses on 21 March 1990 (Number above each column sample size)

GFI = 1.5), although this trend was not statistically significant (Table 3).

Sparids were less successful feeders within the plume (mean GFI = 2.3), than within the front (mean GFI = 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).

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

Monodactylid feeding incidence from within the plume (mean GFI = 4.0) was similar to that within the shelf water-mass (mean GFI = 3.5, Fig. 4b).

Pomacentrids within the plume (mean GFI = 4.6) tended to have greater feeding incidence than those in shelf waters (GFI = 1.7, Fig. 4b).

On 10 April, 90% of the catch consisted of kyphosids, and showed no significant differences in gut fullness between sites (Fig. 2c).

Feeding selectivity

Mugilid (Liza argentea) 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

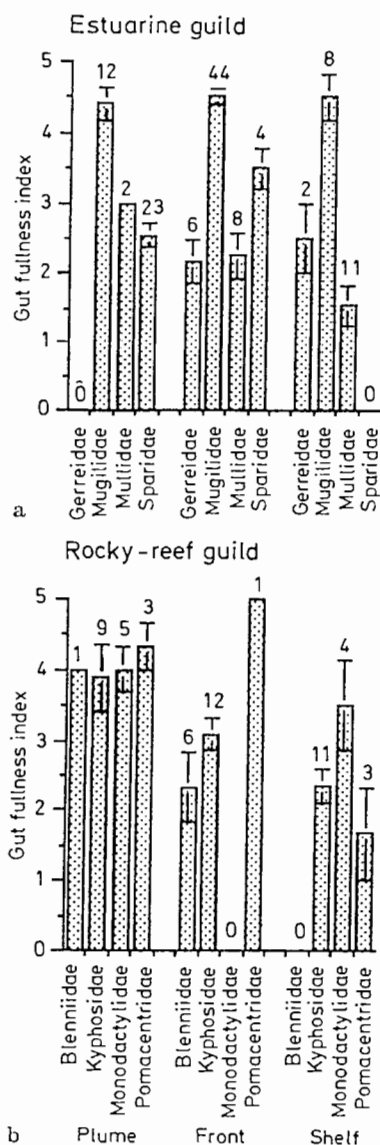


Fig. 4 Mean gut fullness (+ SE) of **a** estuarine guild of fishes (Gerreidae, Mugilidae, Mullidae and Sparidae), and **b** rocky-reef guild of fishes (Blenniidae, Kyphosidae, Monodactylidae and Pomacentridae) from each of the three water masses on 23 March 1990 (Number above each column sample size)

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 *Liza argentea* that were dissected for this study, only three other food items were found: two cypris larvae and one cladoceran.

The canonical discriminant analysis identified distinct diets of mugilids in the three water masses on 23 March (Pillai's trace $p < 0.001$, $n = 42$), and the result-

Table 4 Mugilidae and Kyphosidae. Alpha selectivity values calculated for four prey types at three sampling sites on 23 March 1990 (Fig. 5) (* positive selection)

Prey type	Plume	Front	Shelf
Mugilidae			
calanoid	-0.907	-0.927	-0.790
cyclopid	-0.981	-0.933	-0.963
harpacticoid	-0.995	0.674^*	-0.963
copepodite	0.986^*	0.224^*	0.966^*
Kyphosidae			
calanoid	-0.960	-0.989	-0.966
cyclopid	-0.986	-0.996	-0.987
harpacticoid	-0.782	-1.000	-1.000
copepodite	0.967^*	0.998^*	0.995^*

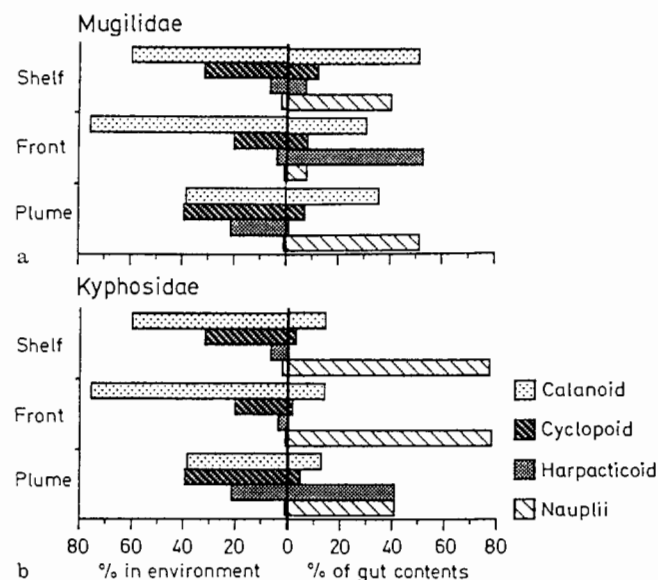


Fig. 5 **a** Mugilidae; **b** Kyphosidae. Percent of food items consumed in each of three water masses on 23 March 1990 [zooplankton data from Kingsford and Suthers (1994), for 264 μ m-mesh purse seine]. Abscissas compare nauplii in guts to copepodites in environment

ant discriminant function successfully reclassified 83% of fish to the water masses by the four dietary components.

Kyphosid (Kyphosus spp.) diet

On 23 March, when a slick of drift algae occurred, the diet of the kyphosids was dominated by nauplii at all sites, although similar numbers of harpacticoids and nauplii were consumed in the plume (Fig. 5b). They positively selected for copepod nauplii within the plume, front and shelf, and selected against all other potential food items. Harpacticoid copepods were present in the plume and were consumed, but were selected against (alpha value = -0.782 , Table 4).

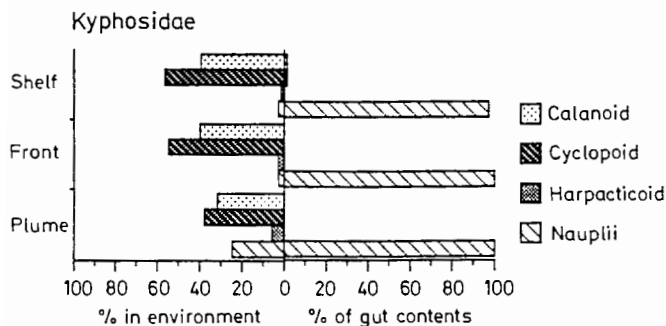


Fig. 6 Kyphosidae. Percent of food items consumed in each of three water masses on 10 April 1990 [zooplankton data from Kingsford and Suthers (1994) for 264 μ m-mesh purse seine]. Abscissa compares nauplii in guts to copepodites in environment

On 10 April, there was no slick associated with the front and no drift algae was apparent within the plume and front. Kyphosids 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 ($n = 62$; $p > 0.05$) in the mean standard lengths of *Kyphosus* spp. between 23 March and 10 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 plume, front and shelf water on all sampling dates indicated either no difference between feeding in the three different 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 (Boehlert and Morgan 1985; Breitburg 1988). Plume water and fronts may also contain flotsam 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 taxa from each site. Nevertheless, the gut-fullness index comparison 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 baggy guts and are able to consume a relatively large volume of prey before their guts are filled, whereas similar-sized kyphosid larvae have small guts which become distended 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 move into estuarine nursery habitats (Miskiewicz 1989; Whitfield 1989). The mugilid *Liza argentea* 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 (Hunter 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 260 μ m purse-seine net, yet their relative abundance was small in the plume, front and shelf waters. This high selectivity by the larvae was not demonstrated in each water mass. Selection towards harpacticoid copepods has been reported in

bottom-associated soleid larvae which consume bottom-associated zooplankton such as harpacticoids. Harpacticoid copepods may also be associated with driftweed. The mugilids and kyphosids may have encountered greater concentrations of these zooplankters in the driftweed that was present in large quantities in the plume and front on 23 March. Driftweed-associated harpacticoids were found in the guts of larval fishes captured in or near driftweed in the Irish Sea (Tully and Ceidich 1989).

In general, marine and estuarine larval fishes are copepodivores, and when there are differences in the diets of fish larvae between estuarine and marine waters they are due to either differences in the abundance and types of suitably sized prey, or differences in prey selection by the species of fish larvae which occur in each system (Gaughan 1991). In the present study, the abundance and types of prey available in the environment was not reflected in the diets of fishes. It may be possible that the fishes were selecting prey differently in each of the water masses according to taxon-specific responses by the surrounding zooplankton to different environmental conditions.

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 drogues placed up to 50 m on either side of the Botany Bay plume front were advected into the front within 90 min (Kingsford and Suthers 1996), suggesting that strong convergence of the front could also result 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 success 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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