

# Variability in the trophic role of coral reef fish larvae in the oceanic plankton

Joel K. Llopiz\*, Robert K. Cowen

Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA

**ABSTRACT:** The transport of larval coral reef fishes to juvenile habitat inherently requires that they survive the planktonic journey; however, the processes governing survival—particularly those related to feeding—are not well known. Monthly sampling across the Straits of Florida allowed for analyses of the diets and diet variability of several co-occurring taxa of coral reef fish larvae from the families Serranidae, Lutjanidae, Mullidae, Pomacentridae, Labridae, Scaridae and Acanthuridae. The proportions of larvae with food present in the gut were high (0.94 to 1.0) for all taxa except scarids (0.04), and diets were generally narrow and predator-specific. *Serranus* spp. (Serranidae) diets changed little with growth and were composed almost entirely of calanoid copepods, while the labrids *Thalassoma bifasciatum* and *Xyrichtys* spp. consumed harpacticoid and cyclopoid (*Farranula* and *Oncaea*) copepods almost exclusively throughout ontogeny. Lutjanine and acanthurid larvae relied increasingly upon appendicularians with growth, and mullids exhibited an ontogenetic shift from nauplii to calanoid copepodites and appendicularians. Cluster analysis examining diet similarity among taxa yielded clear groupings: small acanthurids, labrids, appendicularian-feeders, and a fourth group consisting of subgroups of larvae with calanoid and mixed diets. Within larval taxa, canonical correspondence analysis indicated how diet varied with several environmental and larva-specific variables. The trophic niche breadth of 4 taxa decreased significantly with growth, while other taxa exhibited no significant change. These results highlight distinct differences between high- and low-latitude regions, most notably the taxon-specific trophic roles and the apparent niche partitioning of larval fishes within the diverse planktonic food webs of lower latitudes.

**KEY WORDS:** Coral reef fish larvae · Larval fish · Feeding · Diets · Niche partitioning · Canonical correspondence analysis

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

The early life history of most marine fishes is characterized by a planktonic larval stage that is highly vulnerable to both starvation and predation. Despite the potential influence of these 2 processes on total survival to later stages (Houde 1987), our understanding of them is limited; this is especially so for the larvae of coral reef fishes. As predation mortality is inextricably linked to growth (Cushing 1975) and, consequently, to feeding (Buckley & Lough 1987), a necessary step toward understanding survival in the early life stages of fishes is identifying the specific trophic roles of fish larvae in the complex planktonic food webs of the ocean.

The tropical/subtropical ocean is generally viewed as oligotrophic and unproductive, with fluctuations in productivity that are low in magnitude and temporally unpredictable (e.g. Longhurst & Pauly 1987). These conditions, which could represent a nutritionally constraining environment for planktotrophic larvae, differ from those of higher latitudes, where one of a few possible mechanisms influencing larval survival is the matching of the spawning periods of many fish species with distinct secondary productivity blooms (Cushing 1990). Additionally, the low-latitude open ocean, relative to higher latitudes, is habitat for a higher diversity of both larval fishes (Richards 2005) and their potential zooplankton prey (van der Spoel & Pierrot-Bults 1979,

\*Email: jllopiz@rsmas.miami.edu

Hillebrand 2004). High larval fish diversity in an unproductive yet diverse prey environment raises the evolutionary possibility of species-specific feeding niches, and while building evidence supports this hypothesis (Sampey et al. 2007, Llopiz & Cowen 2008), very little is known about the larval trophic ecologies of most coral reef fish larvae, especially over broad temporal, spatial and ontogenetic scales.

Though undocumented, it has been hypothesized that fish larvae that develop offshore may experience lower predation pressure relative to larvae in nearshore waters (e.g. Johannes 1978, Bakun & Broad 2003). However, as a result, offshore larvae could suffer from low food availability or unsuccessful transport to suitable juvenile habitat (Hare & Cowen 1991). While modeling studies in lower latitudes have provided insight into the transport success of larvae between spawning and settlement locations (Cowen et al. 2006), little is known regarding the possible nutritional tradeoff for offshore or oceanic larval development. Since the connectivity of marine populations is inherently tied to larval survival en route (which has been, in large part, a black box for modelers), the need for empirical work investigating the biological processes occurring during the planktonic larval phase is becoming increasingly apparent (Sponaugle & Grorud-Colvert 2006, Paris et al. 2007). Feeding studies are particularly important, since relating general zooplankton indices to larval fish survival is tenuous without knowledge of the specific diets of the larvae that are being modeled.

Empirical larval fish research in the tropics notably lags behind the extensive body of work in higher latitudes, presumably due to historical interest in understanding and maintaining the important fisheries in temperate regions. However, as the coral reef ecosystems of the world are increasingly threatened by anthropogenic pressures such as overfishing, habitat degradation and climatic effects (Hughes et al. 2003, Pandolfi et al. 2003), the steady increase in our understanding of the ecological processes governing coral reefs and their fish populations is critical to conservation efforts.

This study reports on the diets and diet variability of several taxa of coral reef fish larvae that occur in the tropical and subtropical oceanic waters of the western North Atlantic Ocean. In addition to taking a comparative approach, our goal was to maximize temporal, spatial and ontogenetic resolution of feeding variability by examining relatively large numbers of larvae collected throughout the year in the Straits of Florida (SOF). In this region, the oceanic waters of the Caribbean Sea and Gulf of Mexico become constricted between Florida and the Bahamas, allowing for the sampling of disparate water masses along a narrow 80 km transect. Due to the many physical and biological variables

inherent in our data, we also incorporated multivariate analyses to better understand the trophic ecologies of coral reef fish larvae and the factors that may influence their feeding variability. Overall, we addressed the following questions: (1) Are larval coral reef fishes generally successful feeders? (2) Do they exhibit taxon-specific diets, and if so, to what degree do diets differ among taxa? (3) Are there ontogenetic diet shifts in the types or sizes of consumed prey? (4) What variables of the environment and of the larvae themselves may influence prey type? (5) Do the larval taxa examined conform to the general assumptions regarding trophic niche breadth?

## MATERIALS AND METHODS

**Study area and field sampling.** The SOF encompass the waters between Florida and both Cuba and the Bahamas. The region is dominated by the rapid northerly flow of the Florida Current (nearer the Florida Shelf), which links the oceanic waters of the Gulf of Mexico and Caribbean Sea to the Gulf Stream of the western North Atlantic Ocean. In 2004, ichthyoplankton were sampled monthly along an east–west transect of 17 stations across the SOF (Fig. 1) between the Florida Shelf and Great Bahama Bank (Llopiz & Cowen 2008). For subsurface sampling, we utilized a multiple opening closing net and environmental sensing system (MOCNESS; Wiebe et al. 1985) with a 4 m<sup>2</sup> opening and 1 mm mesh nets. Discrete-depth sampling occurred at nominal intervals of 25 m from a depth of 100 m (~5 min interval<sup>-1</sup> and a speed of ~1.5 m s<sup>-1</sup>) at all but the shallower westernmost station

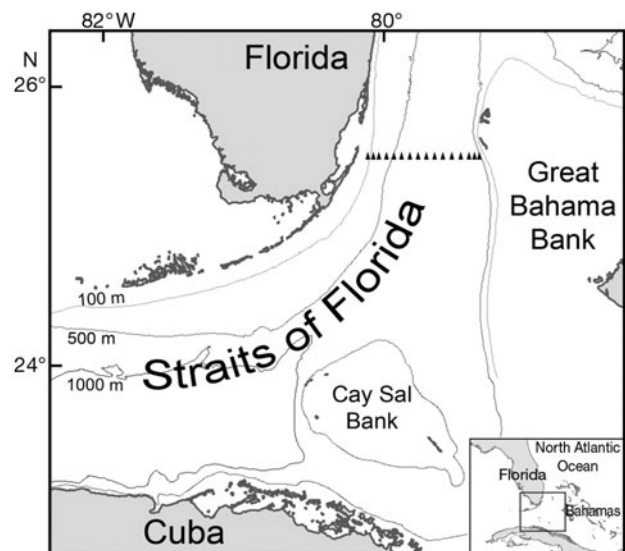


Fig. 1. Straits of Florida region and the transect of 17 stations (▲) sampled monthly in 2004 for ichthyoplankton

where sampling was from 50 m. A fluorometer attached to the MOCNESS continuously measured fluorescence. A rectangular neuston net (2 × 1 m, 1 mm mesh) sampled the surface waters to a depth of ca. 0.5 m. All sampling occurred during daylight hours. Plankton were preserved in 95% ethanol and later transferred to 70% ethanol.

**Laboratory procedures.** Fish larvae were sorted from plankton samples and initially identified to varying degrees of taxonomic resolution following Richards (2005). Ten taxa of coral reef fish larvae (generally those that are abundant as larvae or adults, or are of economic importance) were subsampled for gut content inspection (total  $n = 1266$ ). Taxa included the families Lutjanidae (snappers), Pomacentridae (damselfishes), Acanthuridae (surgefishes) and Mullidae (goatfishes); the serranid subfamilies Serraninae (seabasses) and Epinephelinae (groupers); the labrids (wrasses) *Halichoeres* spp., *Xyrichtys* spp. and *Thalassoma bifasciatum*; and the scarids (parrotfishes) *Sparisoma* spp. For most taxa, subsamples were taken from even-numbered stations of cruises taken in even-numbered months, and consisted of no more than 10 ind. from each of 3 regions of the SOF (west: Stns 1 to 5; central: Stns 6 to 11; east: Stns 12 to 17; for distributions of inspected larvae, see Fig. A1 in Appendix 1, [www.int-res.com/articles/suppl/m381p259\\_app.pdf](http://www.int-res.com/articles/suppl/m381p259_app.pdf)). If >10 ind. were collected within each region, larvae were selected proportionally to both horizontal and vertical total abundances, and, within each sample, to their size distributions. Exceptions were *T. bifasciatum*, which followed the same scheme described above but with a maximum of 20 ind. in each region–cruise combination, and epinepheline groupers, of which all individuals collected throughout the year and transect were inspected (due to low abundances). All taxa co-occurred in the SOF throughout the year, and most taxa co-occurred throughout the upper 100 m with the exception of the predominantly neustonic mullids (Fig. A1). Although we do not report on larval abundances, the use of 1 mm mesh nets may have resulted in the exclusion of the earliest stages (e.g. first-feeding) of some taxa.

Prior to inspection, most serranine and pomacentrid larvae were further identified to the genus level, and lutjanid larvae to subfamily. Larval body length (BL; notochord/standard length before/after flexion of the urostyle) and lower jaw length (LJL; mandible) were measured with the ocular micrometer of a stereomicroscope (Leica MZ15). Larvae were dissected with a microscalpel and minuten pins, and the contents of the entire alimentary canal were teased out and identified. Due to the increase in gut capacity with larval growth, gut fullness was estimated for each larva and assigned a value of 0 (empty), 1 (<half-full), 2 (>half-full) or 3 (full). Beginning at the anterior portion of the alimentary canal (where prey are least digested), up to

a maximum of 5 prey per larva were measured for length (prosome length for copepod copepodite stages except those of harpacticoids; carapace length for other relevant crustaceans; and the longest dimension in all other prey, including harpacticoid copepods but excluding the caudal rami). Appendicularians were not measured due to their soft bodies. Appendicularian enumeration became more difficult with the degree of digestion (posteriorly in the intestine), but was estimated by the distinctiveness of the trunk, tail and house regions of the organism and the repeatedly observed anterior to posterior gradient of digestion state. Reference to copepod orders follows Boxshall & Halsey (2004). If identified, only copepod genera are referenced, and no distinction was made between juvenile and adult copepodite stages.

**Data analysis.** The feeding incidence of a taxon of fish larvae was calculated as the proportion of individuals with food present in the gut. The overall diet of each taxon of larval fish was described using an index of relative importance (IRI) for each prey type observed, calculated as the product of the numerical percentage of a prey type and its frequency of occurrence (percentage of larvae) in feeding larvae (Govoni et al. 1983, Young & Davis 1990). Values were converted to a percentage of the sum of IRI values (%IRI). Although IRI values may be biased by prey size variability and length-frequency distributions of inspected larvae (Llopiz & Cowen 2008), their use here for several taxa allows for easier interpretation and comparison among taxa and with other studies. Values of numerical percentages and frequencies of occurrence of prey types are reported in Table A1 in Appendix 1 ([www.int-res.com/articles/suppl/m381p259\\_app.pdf](http://www.int-res.com/articles/suppl/m381p259_app.pdf)).

Indirect gradient analysis was used to examine diet similarity among larval fish taxa (Field et al. 1982). Both hierarchical clustering and non-metric multidimensional scaling (NMDS) were performed on a Bray-Curtis dissimilarity matrix (SYSTAT Software) constructed from the average arcsine-transformed numerical percentages of prey types for each taxon of larval fish. Taxa that exhibited distinct ontogenetic diet shifts or seasonal differences were further subdivided *a posteriori* into 2 size classes or 2 periods of the year. Prey categories used in the analyses were those constituting ≥5% of the prey items of at least one of the larval fish classes, and excluded unidentifiable prey. This yielded 12 prey categories (variables) and 18 larval fish classes (samples). Hierarchical clustering used the unweighted arithmetic average method (Legendre & Legendre 1998) and main groupings were chosen at the 55% similarity level with subgroups of the largest group at the 65% level. NMDS ordination was in 2 dimensions and used the Kruskal method with a monotonic regression. Cluster groupings were projected on the

NMDS ordination for visualizing the consistency between the methods; both methods were employed as generally recommended (e.g. Field et al. 1982) since they are not equivalent but complement each other.

To investigate diet variability within taxa and how it was related to variables of the environment and individual larvae, the direct gradient analysis technique of canonical correspondence analysis (CCA; ter Braak 1986) was employed. CCA is an ordination method that directly relates species or community composition to environmental or other explanatory variables. Here, within a taxon of larval fish, the prey type composition was related to the explanatory variables of larval BL, gut fullness, longitude (°W), collection depth, photoperiod (proxy for time of year) and fluorescence (proxy for chlorophyll concentration; uncalibrated voltages). Samples consisted of the prey consumed by larvae within the same cruise–station–depth–BL (1 mm interval) combinations containing at least 4 prey items. Collection depth and fluorescence were calculated as the means of the respective net sampled by the MOCNESS, and when multiple larvae were grouped, the mean gut fullness was used. Prey values were the arcsine-transformed numerical proportions within a sample. A forward stepwise selection method (ter Braak & Verdonschot 1995) determined which explanatory variables significantly contributed to explaining the variability in prey types (Monte Carlo permutation tests, 999 permutations,  $\alpha = 0.05$ ). Ordination diagrams allowed for interpretation of how the explanatory variables (arrows) were related to prey type consumption. Along the gradient for each explanatory variable (including in the opposite direction of the arrow), each prey type location, which represents its weighted mean, can be related to the distance along the gradient (with the origin being the mean for the explanatory variable). This allows the relative locations of all prey to be compared with each other, but for each prey type, it also illustrates how much above or below the average explanatory variable the prey type tended to be consumed. Additionally, arrow length relates to the importance of the variable, and the angle between any 2 arrows represents their correlation. CCA was performed with the computer program CANOCO (ter Braak & Simlauer 2002) incorporating biplot scaling with a focus on interspecies distances. The 5 larval taxa analyzed were those with sufficiently large sample sizes or diet variability, and prey classes included were those constituting  $\geq 1\%$  of the total diet within each taxon.

Taxonomic differences in the allometry of jaw development (linear in all taxa) were tested using ANCOVA (generalized linear model, SYSTAT). Pairwise differences in slope were tested using a Bonferroni correction and, if nonsignificant, further tested for differences in intercept. To better standardize morpholog-

ical differences between larval fish taxa in both jaw development and body shape, LJL (instead of BL) was related to prey size to examine the change and variability of prey size with larval growth. For each taxon, the lengths of consumed prey were grouped in LJL intervals of 0.1 mm (0.05 for acanthurids). Intervals contained  $\geq 10$  prey, and no more than 2 LJL intervals were combined to reach a minimum of 10 prey. Trophic niche breadth for each interval was calculated as the SD of the log-transformed prey lengths (Pearre 1986). It is generally hypothesized that the range of prey sizes increases with mean prey size (and larval growth), but the trophic niche breadth, which standardizes for the increase in mean prey size, should remain relatively constant throughout growth (Pearre 1986). However, evidence for an increase in trophic niche breadth has been shown in some taxa (Pepin & Penney 1997).

## RESULTS

### Feeding incidence, diets and ontogenetic variability

For nearly all taxa of coral reef fish larvae examined, the proportions of larvae with food present in the gut were high, ranging from 0.94 to 1.0 (Table 1). The only exception to this was *Sparisoma* spp., of which only 4% contained prey. The size ranges of larvae were broad and included some of the earliest stages; however, they may have excluded the first-feeding stage.

Diets of larvae were often narrow with clear distinctions evident among taxa (Table 2). *Serranus* spp. larvae consumed calanoid copepodite stages almost

Table 1. Larval coral reef fish taxa collected across the Straits of Florida and inspected for diet analyses. All taxa co-occurred throughout the year and across the sampled transect (see Fig. A1). Feeding incidence: proportion of larvae with prey present in the gut (all collected during daylight); n: no. larvae examined (total = 1266); BL: body length

Taxon	n	BL (mm)		Feeding incidence
		Range	Mean	
Serranidae				
Epinephelinae	61	2.8–12.8	5.7	0.98
Serraninae	140	2.9–10.4	5.1	0.97
Lutjanidae	107	2.9–9.4	4.8	0.98
Mullidae	153	2.7–22.8	7.6	1.00
Pomacentridae	95	2.4–8.8	3.9	1.00
Labridae				
<i>Halichoeres</i> spp.	71	3.3–9.8	5.9	1.00
<i>Thalassoma bifasciatum</i>	201	2.6–11.1	5.3	0.99
<i>Xyrichtys</i> spp.	139	3.4–13.5	6.8	0.94
Scaridae	156	2.8–10.9	7.0	0.04
<i>Sparisoma</i> spp.				
Acanthuridae	143	2.1–8.9	3.8	0.99

Table 2. Percent indices of relative importance (%IRI; calculated as the product of the numerical percentage of a prey type and its percent frequency of occurrence in feeding larvae) for the dominant prey of 13 taxa of coral reef fish larvae collected in the Straits of Florida. Epinepheline larvae were further divided by time of year collected due to noted seasonal differences in species composition and diet. Some prey types with low %IRI (<0.5%) were grouped into the 'other' category, including bivalve and gastropod larvae, cavolinid pteropods, small eggs, euphausiid calyptopes, tintinnids, radiolarians and foraminiferans. (-): values <0.1%. See Table A1 for numerical proportions and frequencies of occurrence of prey types. n<sub>i</sub> = no. fish larvae examined; n<sub>p</sub> = no. prey excised; crust.: crustacean

Prey category	Serranidae		Epinephelinae		Lutjanidae		Pomacentridae		Labridae		-Scaridae -		
	Serraninae (n <sub>p</sub> = 102)	Centropristis (n <sub>p</sub> = 244)	(Wint./Spr.) (n <sub>i</sub> = 40) <sup>a</sup>	(Sum./Fall) (n <sub>i</sub> = 19)	Lutjaninae (n <sub>i</sub> = 83)	Etelinae (n <sub>i</sub> = 20)	Chromis (n <sub>p</sub> = 333)	Stegastes (n <sub>p</sub> = 527)	Halichoeres (n <sub>p</sub> = 559)	Thalassoma (n <sub>p</sub> = 1293)	Xyrichtys (n <sub>i</sub> = 131)	Sparisoma (n <sub>i</sub> = 7)	Acanthuridae (n <sub>p</sub> = 1346)
Thecosomata:	-	0.1	4.5	0.7	-	-	-	0.8	0.1	-	0.1	-	41.1
<i>Limacina</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.6
Polychaete	-	-	-	-	-	-	-	-	-	-	-	-	-
trochophore	-	-	-	5.0	-	-	-	-	-	-	-	-	-
Cladocera:	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Evadne</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda	1.7	9.7	19.2	8.4	28.3	20.6	6.9	2.8	11.8	0.3	1.8	25.0	19.6
Nauplius	96.7	45.8	53.7	38.2	1.2	35.6	62.5	20.1	35.0	0.3	0.4	6.2	0.9
Calanoida	-	0.8	0.2	-	-	-	0.3	0.6	5.9	36.9	40.1	-	-
Harpacticoida	0.1	0.3	3.8	-	0.6	2.0	3.0	14.6	0.1	-	-	6.2	-
<i>Oithona</i>	0.1	19.2	2.4	0.1	0.1	-	2.1	29.0	12.7	16.6	38.3	-	1.3
<i>Oncaea</i>	-	1.4	0.3	-	-	-	0.4	2.0	1.0	1.5	3.5	-	-
<i>Corycaeus</i>	1.0	12.9	1.9	41.9	1.9	6.8	19.9	24.2	9.1	44.0	14.5	56.2	-
<i>Farranula</i>	-	1.5	1.0	0.1	0.1	2.0	2.6	3.4	7.8	0.1	-	-	-
Unknown/ remains	-	6.6	-	-	-	-	-	-	-	0.1	0.7	-	-
Ostracoda	-	-	-	-	0.1	0.1	-	-	-	-	-	-	-
Chaetognatha	-	-	-	-	58.3	14.6	-	-	3.1	-	-	-	18.1
Appendicularia	-	-	-	-	-	-	-	-	-	-	-	-	-
Fish egg	-	-	-	-	-	-	-	-	-	-	-	-	-
Other	-	0.1	0.3	0.3	0.2	-	-	-	-	0.1	0.1	-	1.0
Unknown crust.	0.5	1.5	12.5	5.3	4.3	17.1	2.4	2.1	9.6	0.1	0.3	-	3.1
Unknown item/ soft remains	-	-	0.2	-	5.1	1.1	-	0.5	3.0	0.1	0.3	6.2	14.3

<sup>a</sup>41 larvae used for frequency of occurrence calculation. <sup>b</sup>152 larvae used for frequency of occurrence calculation

exclusively while the confamilial *Centropristis* spp. consumed a mixture of ostracods and calanoid and cyclopoid copepodites. Winter- and spring-spawned epinepheline groupers consumed mostly calanoids, yet those occurring in the summer and fall added *Farranula* copepods to their diet. (Subsampling of these larvae for genetic species identification indicated these groups of epinephelines are largely composed of different species [D. Richardson et al. unpubl. data]). The labrids *Xyrichtys* spp. and *Thalassoma bifasciatum* relied heavily upon *Farranula*, *Oncaea* and harpacticoid (mostly *Microsetella*) copepods while consuming almost no calanoids or nauplii. Appendicularians, absent from many diets entirely, had high %IRI values in lutjanine snappers (58.3) and acanthurids (18.1), and they were consumed at lower levels by eteline snappers, mullids and *Halichoeres* spp. labrids. Acanthurid diets were also composed largely of *Limacina* pteropods and excluded copepodite stages of copepods. Pomacentrids consumed a mixture of copepodite copepods but few nauplii. Differences between pomacentrid genera included the greater importance of calanoids in the diet of *Chromis* spp. than of *Stegastes* spp., while the opposite pattern held for the cyclopoid genera *Oncaea* and *Oithona*.

Some larval fish taxa exhibited distinct ontogenetic changes in diet, while others consistently consumed similar prey types throughout development (Fig. 2). Appendicularian-feeding lutjanines and acanthurids fed increasingly on appendicularians with ontogeny to the gradual exclusion of copepod nauplii and pteropods, respectively. *Stegastes* spp. consumed fewer cyclopoids and more calanoids with growth, as did *Halichoeres* spp. The other labrids *Xyrichtys* spp. and *Thalassoma bifasciatum* continued to consume similar proportions of the same copepod taxa throughout most of the larval period, and *Serranus* spp. exhibited consistent feeding upon calanoid copepods with ontogeny. The smaller sample sizes of other taxa (Epinephelinae, Etelinae, *Centropristis* spp. and *Chromis* spp.) were deemed insufficient for illustrating ontogenetic changes in diet.

#### Diet similarity among taxa

Cluster analysis identified distinct larval fish groupings based on the degree of diet similarity (Fig. 3a). Small acanthurids (Group 1), consuming primarily copepod nauplii and *Limacina* pteropods, were grouped alone at the 55% similarity level. Lutjanines and larger acanthurids, which consumed high proportions of appendicularians, were grouped together (Group 2). The distinct diets of the labrids (except larger *Halichoeres* spp.) yielded their own grouping (Group 3), while the rest of the taxa (and their size and/

or seasonal subdivisions) made up Group 4. Within this group, there were 4 subgroups, including *Serranus* spp. (calanoid diet) and summer/fall-spawned epinephelines (calanoid and *Farranula* diet) that grouped separately. The 2 other subgroups exhibited diets that were more mixed; however, Subgroup 4a comprised mainly consumers of nauplii, calanoid copepodites and moderate proportions of appendicularians. The 2-dimensional NMDS plot (Fig. 3b) corroborated the results of the cluster analysis and yielded a low stress value of 0.12.

#### Prey consumption related to environmental and predator variables

The CCA for each of the 5 taxa of larval fish examined revealed several significant environmental and larval explanatory variables (Fig. 4). Larval BL was a significant variable for all taxa since diets often changed with growth. The number of significant explanatory variables ranged from 5 (*Thalassoma bifasciatum*) to 2 (*Xyrichtys* spp.) out of the 6 that were tested. For mullid larvae, 20.6% of the variation in prey types was explained by the CCA, with 90% of this accounted for by the first 2 canonical axes (CCA-I & -II). Acanthurid prey variability had 20.5% explained (95.6% by CCA-I & -II), *T. bifasciatum* 17.6% (82.4% by CCA-I & -II), *Halichoeres* spp. 17.3% (87.8% by CCA-I & -II) and *Xyrichtys* spp. 12.4% (100% by CCA-I & -II).

Several patterns can be discerned from the ordination diagrams of each larval taxon (Fig. 4). The change in diet with larval length was often the most prominent pattern for each taxon. Even for *Thalassoma bifasciatum* and *Halichoeres* spp., which had generally consistent diets with growth, some nuances emerged, including consuming a few nauplii at smaller sizes and ostracods, calanoids and *Corycaeus* copepods at larger sizes. Most informative was the use of CCA to help discriminate how diet differed with factors other than growth. Some examples include: mullids consuming calanoid and *Farranula* copepods when exhibiting greater gut fullness and consuming *Oithona* more in the winter and to the west, with *Corycaeus* consumed more in the summer and toward the east; *T. bifasciatum* consuming *Farranula* more in the east and during the summer, while *Oncaea* was consumed more in the west and during the winter; *Halichoeres* spp. feeding on *Farranula* when more full and calanoids when less full; and acanthurids consuming more nauplii when deeper and more *Limacina* pteropods closer to winter. Caution must be applied to some additional interpretations, due to the correlations of the explanatory variables, though such correlations may also be informa-

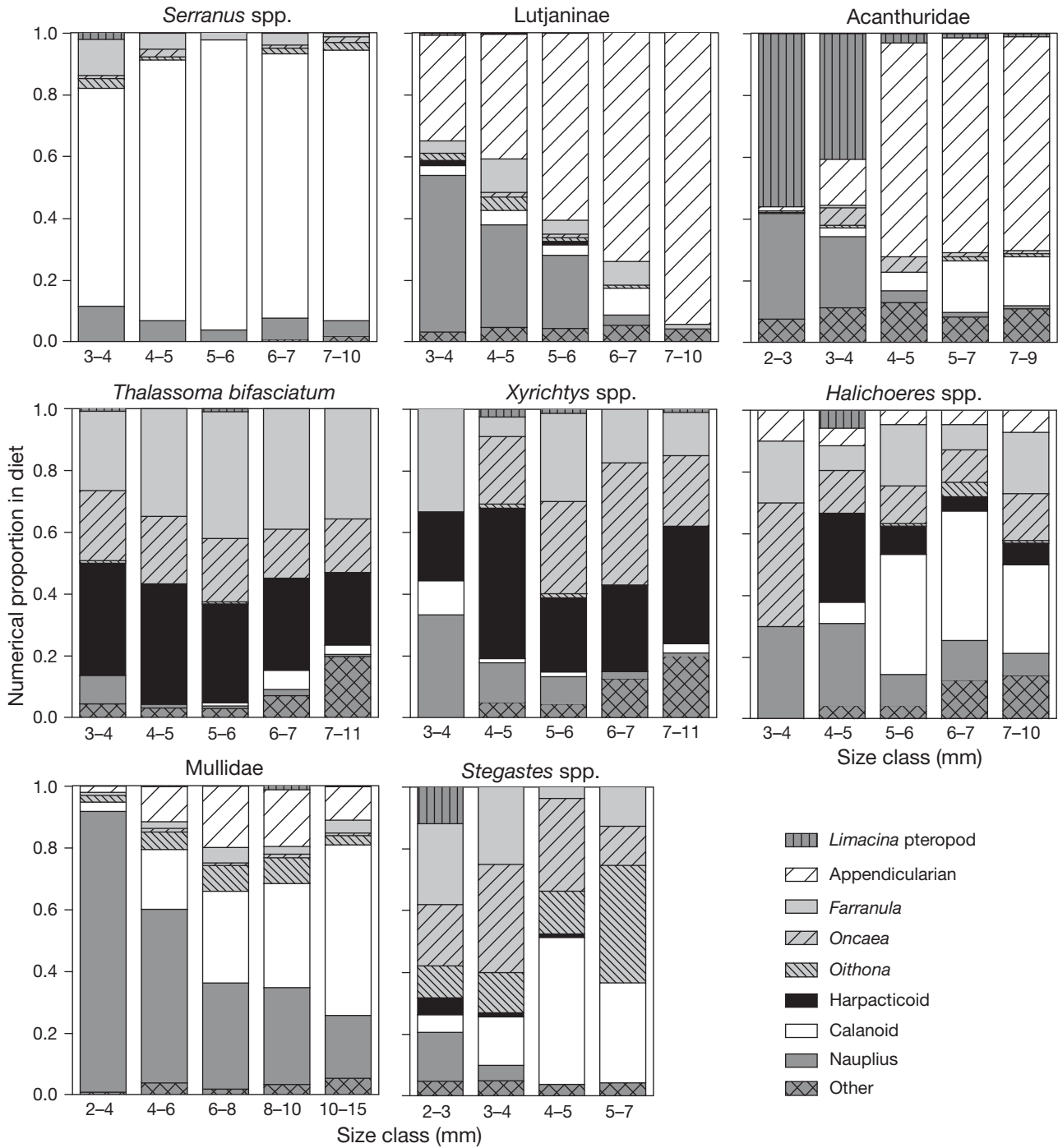


Fig. 2. Numerical proportions of prey types consumed by larval fish length class for 8 taxa of coral reef fish larvae collected in the Straits of Florida. Unidentifiable prey (see Table 1) were not included

For example, fullness in mullids and *T. bifasciatum* increased with larval length and, for *T. bifasciatum*, closer to summer. For mullids, the lack of correlation between length and longitude suggests that the increase in gut fullness with longitude (i.e. toward the west) is real; for *T. bifasciatum*, the apparent increase

in fullness toward the east is likely a result of inspected larvae from the east being slightly larger on average. Depth was a significant explanatory variable for *Xyrichtys* spp., which consumed *Farranula* and calanoids at shallower and deeper depths, respectively; and for acanthurids, which had less clear patterns. It is

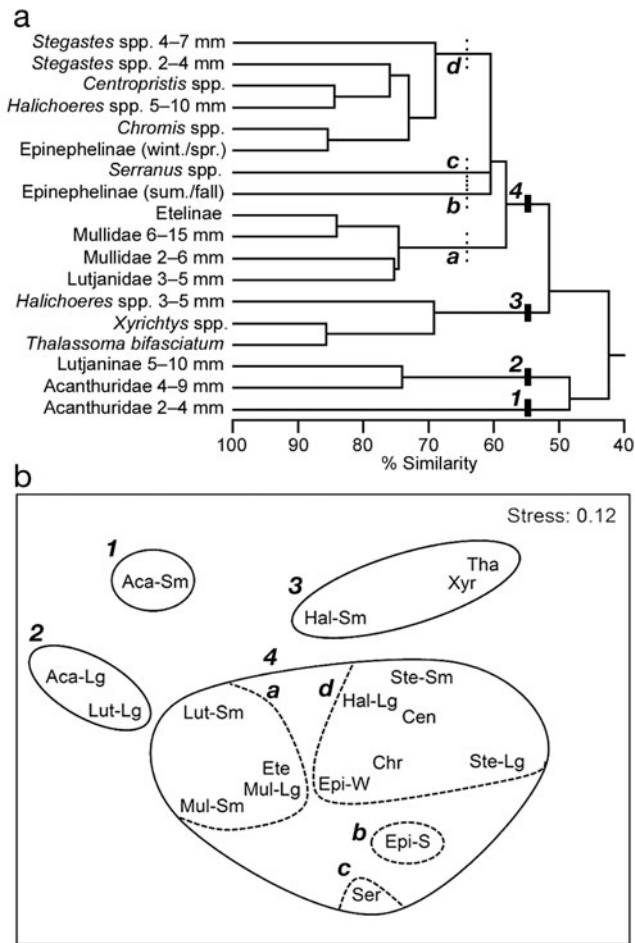


Fig. 3. (a) Cluster analysis and (b) non-metric multidimensional scaling (NMDS) results assessing diet similarity among larval fish taxa and subdivisions of some taxa based on observed ontogenetic changes in diet (Fig. 2) or seasonal differences (Epinephelinae; Table 2). Main groups from the cluster analysis (55% similarity level and numbered) are circled with a solid line on the NMDS plot, and subgroups of Group 4 (65% level and lettered) are circled with a dotted line. Labels in (b) are the first 3 letters of the taxon. Sm: smaller BL class; Lg: larger BL class. For Epinephelinae, S: summer/fall class, W: winter/spring class

worth noting that since diets were often consistent (temporally, spatially and often with ontogeny), some distinctions observed in the CCA were for the less prevalent prey types, while the more abundant prey often occurred closer to the means of the explanatory variables (e.g. with *T. bifasciatum*).

#### Jaw morphology, prey size and trophic niche breadth

Many of the LJL–BL relationships for larval fish taxa ( $r^2 = 0.78$  to  $0.96$ , mean =  $0.90$ ) were significantly different (Fig. 5), but they also formed 2 general groupings

of taxa with similar slopes (i.e. relative growth rates of the jaw). As expected, the more slender (shallow-bodied) taxa had relatively small jaws, with the exception of acanthurids. Despite the similarities within the 2 groups, there appeared to be no patterns in prey types consumed or the degree of diet similarity between taxa within each group.

Mean prey sizes increased significantly with LJL interval for all larval taxa ( $p < 0.05$ ) except *Halichoeres* spp. (Fig. 6). Among taxa, prey sizes were similar despite the distinct differences in types of prey consumed. For 7 of the 11 taxa, trophic niche breadth exhibited no significant change with growth (Fig. 6d–i,k). However, 4 taxa had significantly decreasing trophic niche breadths with increasing LJL ( $p < 0.05$ ) (Fig. 6a–c,j).

## DISCUSSION

The large-scale sampling of the present study afforded a thorough investigation on the planktonic feeding of several co-occurring larvae of coral reef fishes. Noteworthy was the prevalence of diets that were both narrow and taxon-specific despite the co-occurrence of these taxa both temporally and spatially. While copepods were the dominant prey overall, there were distinct differences in the stages and taxa of copepods consumed, not only among larval fish families but also among genera of the same families. Within the family Labridae, *Halichoeres* spp. larvae had a more mixed diet, consuming some calanoids and appendicularians, while *Thalassoma bifasciatum* and *Xyrichtys* spp., exhibiting similar diets, excluded these prey and instead consistently consumed 3 non-calanooid copepod taxa. Among the serranids, there were clear differences among and within subfamilies (including the temporal-, and likely species differences within Epinephelinae). Similarly, the pomacentrid genera exhibited clear differences in their relative consumption of calanooid and cyclopid copepods. With regard to the stages of copepods consumed, some larval taxa, including *T. bifasciatum*, *Xyrichtys* spp., *Serranus* spp. and pomacentrids, had diets that largely excluded nauplii. In other taxa (e.g. lutjanines and mullids), nauplii constituted a substantial portion of the diet throughout larval development.

Contrary to work in higher latitudes (e.g. Economou 1991, Pepin & Penney 1997), there was no overall dominance of calanoids in the diets, as cyclopid and even harpacticoids were common copepod prey. In addition to copepod-dominated diets, high reliance upon appendicularians was exhibited by some families (e.g. lutjanids, mullids and acanthurids). This particular strategy has been observed in other regions for some



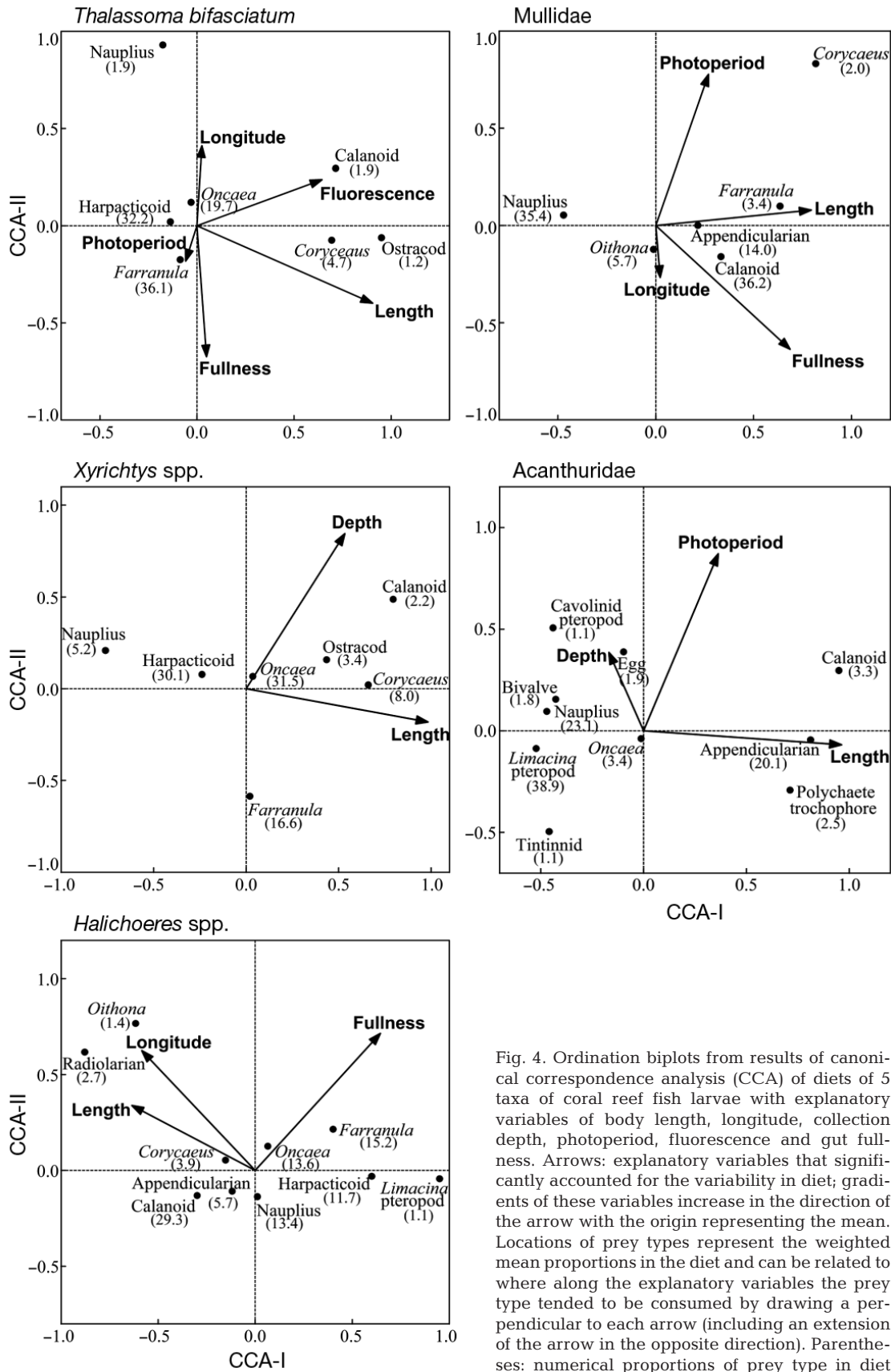


Fig. 4. Ordination biplots from results of canonical correspondence analysis (CCA) of diets of 5 taxa of coral reef fish larvae with explanatory variables of body length, longitude, collection depth, photoperiod, fluorescence and gut fullness. Arrows: explanatory variables that significantly accounted for the variability in diet; gradients of these variables increase in the direction of the arrow with the origin representing the mean. Locations of prey types represent the weighted mean proportions in the diet and can be related to where along the explanatory variables the prey type tended to be consumed by drawing a perpendicular to each arrow (including an extension of the arrow in the opposite direction). Parentheses: numerical proportions of prey type in diet

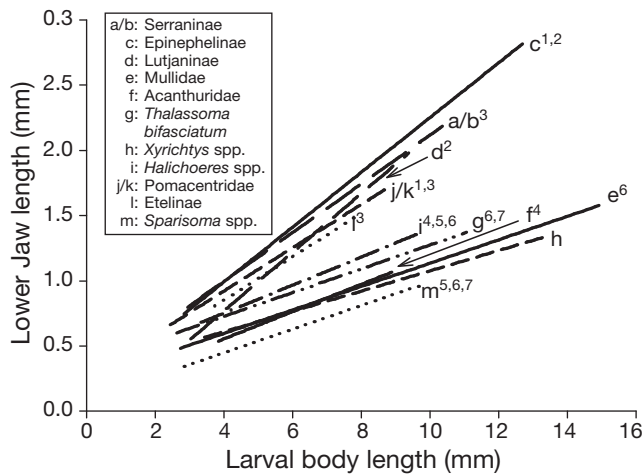


Fig. 5. Relationships of lower jaw length and body length for 11 taxa of larval coral reef fishes. Letters denote taxon and also correspond to each taxon's panel letter in Fig. 6. Relationships sharing the same superscripted number do not have significantly different slopes but have significantly different intercepts (ANCOVA,  $\alpha = 0.05$ , Bonferroni-corrected)

taxa (Purcell et al. 2005) and within the SOF by 3 genera of scombrids that consumed appendicularians almost exclusively (Llopiz 2008). The high diversity and typical relative abundances of zooplankton prey in the SOF (Llopiz & Cowen 2008, S. Smith unpubl. data), in conjunction with the clear distinctions in diet among larval taxa despite the temporal and spatial co-occurrence of the larvae, suggest feeding is highly selective in many of the groups examined. However, since direct comparisons to environmental abundances of zooplankton prey were not performed, a formal analysis of prey selectivity is warranted.

Aside from prey-type differences, the degree to which ontogenetic diet shifts occurred also differed among larval taxa. In mullids, lutjanines and acanthurids there were clear diet shifts with growth. Mullids switched from nauplii to copepodites and appendicularians, lutjanines (bypassing a copepodite-feeding period) shifted from nauplii to appendicularians, and acanthurids began feeding on pteropods and nauplii before consuming appendicularians. Such changes in diet over only a few mm in BL highlight the importance of developmental state when describing, classifying or comparing the trophic roles of these organisms. Not all taxa, however, exhibited ontogenetic diet shifts; the diets of *Serranus* spp., *Thalassoma bifasciatum* and *Xyrichtys* spp. were generally consistent throughout development. This latter behavior has also been shown in other studies in lower latitudes (Schmitt 1986, Østergaard et al. 2005), including those on billfishes and tunas (Young & Davis 1990, Llopiz 2008, Llopiz & Cowen 2008) in which diets were con-

sistent with growth until a single shift to piscivory. Even more precocious are the *Scomberomorus* spp. mackerels that can be piscivorous from the first-feeding stage (Jenkins et al. 1984, Shoji & Tanaka 2001). Such rigid and consistent diets throughout larval development may be more common nearer the tropics since there are few examples of this behavior in high-latitude larvae (but see Last 1978, Runge & de Lafontaine 1996). Consuming the same prey types throughout larval ontogeny may be a strategy that allows larvae to maintain a single trophic niche among a high diversity of potential competitors and a limited number of niches.

The analysis of several larval taxa, some of which did exhibit changes in diet with growth or season, was enhanced by the use of cluster analysis and NMDS to obtain quantitative measurements of diet overlap. These analyses confirmed some of the more qualitative conclusions drawn by describing the diets individually, and allowed for visualization of all patterns of diet similarity. A similar use of cluster analysis and NMDS has been employed for myctophid larvae (Conley & Hopkins 2004) and in a study on a high diversity assemblage of shore-fish larvae in Australia, which included some coral reef fish families (Sampey et al. 2007). Despite the low samples sizes and taxonomic resolution of the latter study, some consistencies with our observed taxon-specific diets were evident, which highlights the possible ubiquity of such feeding behaviors in low latitudes. The extensive spatial and temporal coverage of the present study in the SOF affords greater confidence that the observed diets and among-taxa differences in diet are likely representative of those occurring throughout the region and throughout the year.

The large-scale sampling of the present study also inherently results in several potentially confounding variables (both environmental and larva-specific) that could mask the patterns occurring in the ecosystem. The use of CCA helped account for these factors and aided in the interpretation of how diets changed or did not change along the gradients of each variable. The result of seemingly low values for percent variance explained is generally expected for ecological research (ter Braak & Verdonschot 1995), but, although no larval fish diet studies have employed CCA, the percentages of variance explained by our analyses were relatively high compared to work on adult fishes (Garrison & Link 2000, Jaworski & Ragnarsson 2006). Aside from the ontogenetic changes in diet that the CCAs corroborated, the variability in diet with other factors (e.g. space and time) is likely due to differences in the relative abundances of available prey, although this cannot be confirmed without a thorough analysis of environmental prey availability. However, the variability in

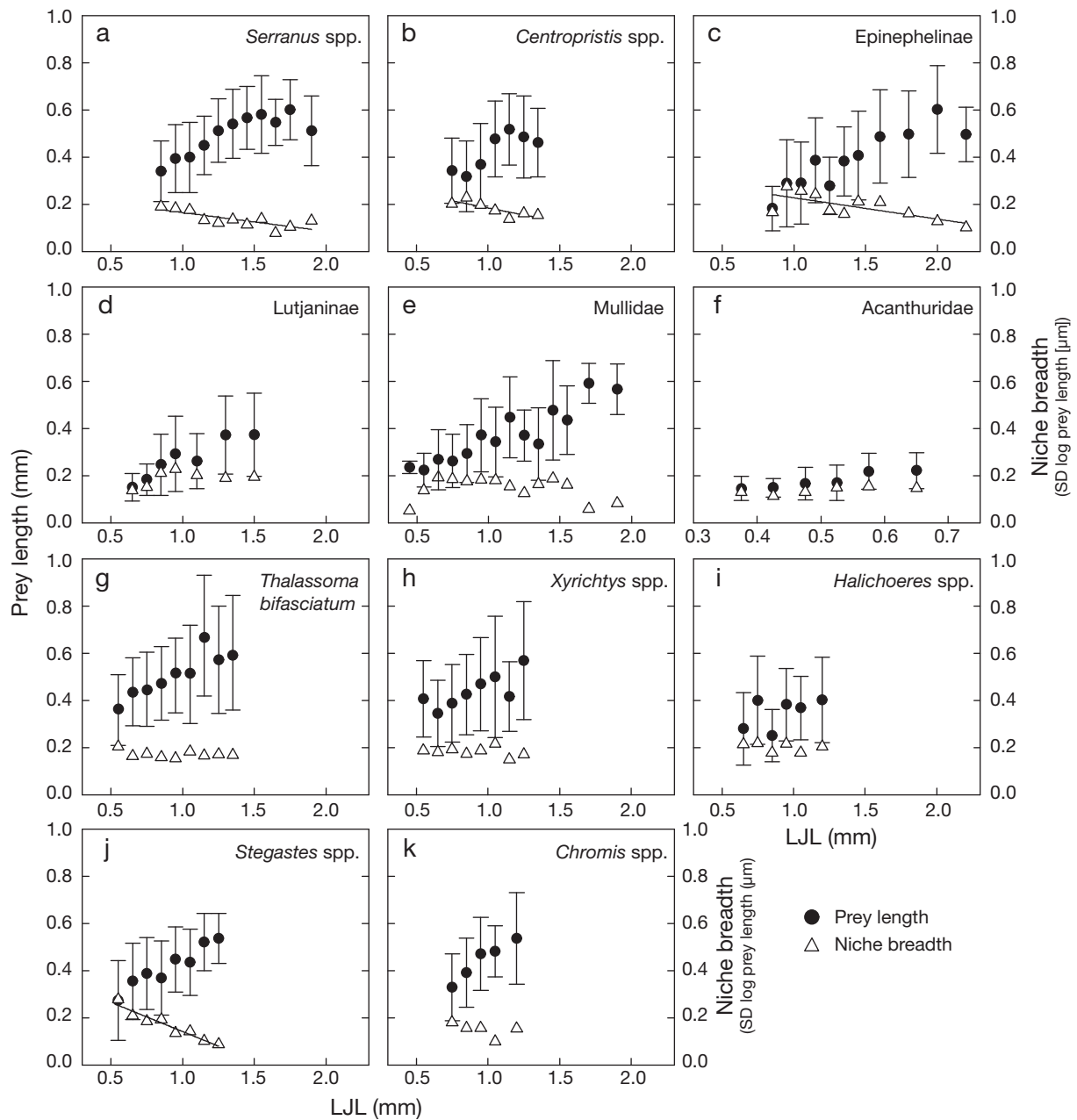


Fig. 6. Relationships of mean prey length ( $\pm$ SD) within lower jaw length (LJL) intervals ( $\bullet$ ) and trophic niche breadth (measured as the SD of the log-transformed prey lengths) within LJL intervals ( $\Delta$ ) for 11 taxa of coral reef fish larvae. Regression analysis of trophic niche breadth values that yielded slopes significantly differing from zero ( $p < 0.05$ ) have regression lines. For comparison, all axis scales are the same except for acanthurids (LJL axis)

diet alone, along with the inherent variability in larval distributions, illustrates that the structure and energy pathways of the planktonic food web in the SOF are not static.

Feeding incidence, though basic in its nature, is a useful parameter in larval fish studies for describing, at least qualitatively and for comparative purposes, the degree of feeding success. High feeding incidences

(near 100%) were observed for nearly all taxa examined with the exception of *Sparisoma* spp. While parrotfish larvae could be poor feeders, they often occurred at high abundances during the late larval stage, which suggests previously successful feeding. Some possible explanations for the observed low feeding incidence are prey regurgitation upon capture due to a straight gut (Hay 1981), defecation upon capture

(Canino & Bailey 1995) and feeding on items not observable by gut inspection (Pepin & Dower 2007).

In the literature, feeding incidences are quite variable among taxa at both high and low latitudes. Inshore of the SOF in Biscayne Bay, the average feeding incidence of several taxa was 46%, and that of perciform taxa was 51% (Houde & Lovdal 1984). Such values are substantially lower than the feeding incidences observed in the present study for larvae that are presumably in a much poorer feeding environment. Since nighttime feeding does not occur and gut evacuation rates in the SOF are rapid (Llopiz 2008, Llopiz & Cowen 2008), larvae in this region likely have to withstand an empty gut during the majority of every night. This ability, coupled with the observation of nearly no empty guts during the daytime, suggests that starvation mortality could be much lower than expected when considering the presumed nutritional constraints of the warm and oligotrophic open ocean. Our results alone, however, do not confirm that starvation is not occurring, and considering the high temperatures of tropical and subtropical waters, some food in the gut may not be enough to meet the greater demands of growth and metabolism in lower latitudes (Houde 1989). As such, future work with techniques specifically addressing nutritional status or energy requirements would be necessary to support any general inferences drawn here regarding levels of starvation mortality.

If the SOF region is less nutritionally constraining for larval fish than presumed, this result may be unique to the region and not typical of the tropical ocean. Although the open waters of the SOF are oceanic, the region may exhibit higher productivity than other low-latitude regions due to submesoscale eddies (Lee et al. 1991) and a shoaling thermocline in the west that is driven by the physics of the system (Olson 2001). However, our knowledge of total secondary production in the oligotrophic tropical ocean remains limited despite the increased understanding of the role of microzooplankton (Landry & Calbet 2004), the microbial food web (Landry 2002) and primary production variability and patchiness (Marañón et al. 2003) as energy sources for the prey of larval fish. Regardless, prey concentrations in the SOF are indeed much lower than in higher latitudes (Llopiz & Cowen 2008). Additionally, *Thalassoma bifasciatum* has been observed to exhibit differing growth rates across the SOF that were correlated to gut fullness (Sponaugle et al. in press), suggesting the occurrence of growth-limiting prey conditions.

Another key question our results raise concerns the driving force behind the specific diets and likely selective feeding of larval fishes, both of which appear to be more prevalent and pronounced than in higher lati-

tudes. If high larval diversity and low prey availability are influential factors in these characteristics, this would imply that competitive exclusion has occurred and prey would be limiting if trophic niches did not exist. Yet larvae can be rather dilute in relation to their prey (Cushing 1983, Dagg & Govoni 1996), which would make density-dependent feeding success unlikely. Therefore, if a larva was experiencing prey at less than optimal abundances, there should be no advantage to feeding selectively and bypassing suitable prey. There is some supporting evidence for scombrid larvae, however, for the possibility of density-dependent growth (Jenkins et al. 1991) and the potential for prey depletion if spatial and trophic niches do not exist (Llopiz 2008). It is also evident from almost all studies that larvae are not always feeding optimally, regardless of prey presence in the gut. This raises questions regarding the likelihood of prey-type switching occurring if a larva's preferred prey were absent but other types were present, and whether there are intrinsic capacities to detect, strike and capture only some of the many types of zooplankton prey in low latitudes.

Among the high diversity of perciform fishes in low latitudes, there exists a wide variety of larval morphologies. For the taxa in the present study (all perciforms), the allometric relationships of L<sub>JL</sub> and BL produced 2 general groupings of taxa with differing rates of jaw development. Using L<sub>JL</sub> for comparisons of prey size as a function of growth (e.g. Pepin & Penney 1997), mean prey sizes increased with L<sub>JL</sub> (except in *Halichoeres* spp.) as expected from most other larval feeding studies. However, most relationships were not very steep relative to the increase in L<sub>JL</sub>. This pattern, in part, contributed to the result of trophic niche breadth significantly decreasing with growth in 4 taxa (and trending negative in 4 others). Such findings contradict Pearre's (1986) general conclusion based on a meta-analysis of 45 datasets that trophic niche breadth remains constant with growth. Additionally, the observed decreases in the present study are opposite to the findings of Pepin & Penney (1997), which largely rejected the generalization of Pearre (1986) by showing an increase in trophic niche breadth with size for a majority of species examined. If more prevalent in lower latitudes, a declining trophic niche breadth with growth (meaning a narrowing of the niche and a relative increase in prey size selectivity) is further support for greater niche separation in these regions. However, making generalizations of prey consumption based on prey size, while convenient for modeling or synthesizing overarching patterns (Woodward et al. 2005), would largely be inappropriate for larval fishes in the SOF due to their distinct taxon-specific diets. Although a narrow and likely preferred size range of prey (e.g.

Munk 1992) exists for coral reef fish larvae, these taxa clearly do not consume prey based solely on size.

The comparative approach utilized in the present study has allowed for the observation of several distinctions among taxa, but the ability to make comparisons to other work is limited due to a lack of focus on the ecology of coral reef fishes during their planktonic larval phase. As a whole, the oceanic planktonic ecosystem remains relatively poorly understood, largely due to its enormity and the many interactions of diverse organisms that differ in size by several orders of magnitude. Within these interactions, larval fishes are often regarded as minor and ephemeral components of the ecosystem; if they are not ignored completely, they are often grouped together as one link in the food web. However, with year-round or protracted spawning by a high diversity of fishes, tropical and subtropical fish larvae are essentially permanent members of the oceanic planktonic food web and, as shown here, perform a variety of taxon- and size-specific trophic roles within these webs.

*Acknowledgements.* Several individuals made this research possible, including D. Richardson, C. Guigand, A. Exum, L. Gundlach, A. Shiroza, P. Lane, K. Leaman, P. Vertes, S. Smith and many others that participated in the cruises, sorted samples and provided other logistical and intellectual support. Very special thanks are given to the captain and crew of the RV 'F. G. Walton Smith'. Manuscript drafts were greatly improved by the suggestions of M. Hauff, S. Sponaugle, C. Paris and 3 anonymous reviewers. Funding was provided by grants from the National Science Foundation (OCE-0136132) and the Gulf States Marine Fisheries Commission (Billfish-2005-017) to R.K.C., with additional support from a gift from Arthur B. Choate to the University of Miami's Billfish Research Program, the Harding Michel Memorial Fellowship, NOAA-LMRCSC, the Capt. Bob Lewis Billfish Challenge Scholarship and the YCMBT/Capt. Harry Vernon Jr. Scholarship.

#### LITERATURE CITED

- Bakun A, Broad K (2003) Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fish Oceanogr* 12:458–473
- Boxshall GA, Halsey SH (2004) An introduction to copepod diversity. The Ray Society, London
- Buckley LJ, Lough RG (1987) Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. *Can J Fish Aquat Sci* 44:14–25
- Canino MF, Bailey KM (1995) Gut evacuation of walleye pollock larvae in response to feeding conditions. *J Fish Biol* 46:389–403
- Conley WJ, Hopkins TL (2004) Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. *Bull Mar Sci* 75:361–379
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527
- Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, Cambridge
- Cushing DH (1983) Are fish larvae too dilute to affect the density of their food organisms? *J Plankton Res* 5:847–854
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Dagg MJ, Govoni JJ (1996) Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? *Mar Freshw Res* 47:137–144
- Economou AN (1991) Food and feeding ecology of five gadoid larvae in the northern North Sea. *ICES J Mar Sci* 47:339–351
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Garrison LP, Link JS (2000) Diets of five hake species in the northeast United States continental shelf ecosystem. *Mar Ecol Prog Ser* 204:243–255
- Govoni JJ, Hoss DE, Chester AJ (1983) Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. *Mar Ecol Prog Ser* 13:189–199
- Hare JA, Cowen RK (1991) Expatriation of *Xyrichtys novacula* (Pisces, Labridae) larvae: evidence of rapid cross-slope exchange. *J Mar Res* 49:801–823
- Hay DE (1981) Effects of capture and fixation on gut content and body size of Pacific herring larvae. *Rapp Cons Int Explor Mer* 178:395–400
- Hillebrand H (2004) Strength, slope and variability of marine latitudinal gradients. *Mar Ecol Prog Ser* 273:251–267
- Houde E (1987) Fish early life dynamics and recruitment variability. In: Hoyt RD (ed) 10th Annu Larval Fish Conf, Miami, FL, 18–23 May 1986. *Am Fish Soc Symp* 2:17–29
- Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish Bull* 87:471–495
- Houde ED, Lovdal JA (1984) Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. *Estuar Coast Shelf Sci* 18:403–419
- Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Jaworski A, Ragnarsson SA (2006) Feeding habits of demersal fish in Icelandic waters: a multivariate approach. *ICES J Mar Sci* 63:1682–1694
- Jenkins GP, Milward NE, Hartwick RF (1984) Food of larvae of Spanish mackerels, genus *Scomberomorus* (Teleostei, Scombridae), in shelf waters of the Great Barrier Reef. *Aust J Mar Freshw Res* 35:477–482
- Jenkins GP, Young JW, Davis TLO (1991) Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii*. *Can J Fish Aquat Sci* 48:1358–1363
- Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environ Biol Fishes* 3:65–84
- Landry MR (2002) Integrating classical and microbial food web concepts: evolving views from the open-ocean tropical Pacific. *Hydrobiologia* 480:29–39
- Landry MR, Calbet A (2004) Microzooplankton production in the oceans. *ICES J Mar Sci* 61:501–507
- Last JM (1978) The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. *Mar Biol* 45:359–368
- Lee TN, Yoder JA, Atkinson LP (1991) Gulf Stream frontal eddy influence on productivity of the Southeast United States continental shelf. *J Geophys Res* 96:22191–22205

- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Llopiz JK (2008) The trophic ecologies of larval billfishes, tunas, and coral reef fishes in the Straits of Florida: piscivory, selectivity and niche separation. PhD dissertation, University of Miami, Coral Gables, FL
- Llopiz JK, Cowen RK (2008) Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida. *Mar Ecol Prog Ser* 358:231–244
- Longhurst AR, Pauly D (1987) Ecology of tropical oceans. Academic Press, San Diego, CA
- Marañón E, Behrenfeld MJ, González N, Mouriño B, Zubkov MV (2003) High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure. *Mar Ecol Prog Ser* 257:1–11
- Munk P (1992) Foraging behavior and prey size spectra of larval herring *Clupea harengus*. *Mar Ecol Prog Ser* 80: 149–158
- Olson DB (2001) Biophysical dynamics of western transition zones: a preliminary synthesis. *Fish Oceanogr* 10:133–150
- Østergaard P, Munk P, Janekarn V (2005) Contrasting feeding patterns among species of fish larvae from the tropical Andaman Sea. *Mar Biol* 146:595–606
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar Ecol Prog Ser* 347:285–300
- Pearre S (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Mar Ecol Prog Ser* 27:299–314
- Pepin P, Dower JE (2007) Variability in the trophic position of larval fish in a coastal pelagic ecosystem based on stable isotope analysis. *J Plankton Res* 29:727–737
- Pepin P, Penney RW (1997) Patterns of prey size and taxonomic composition in larval fish: Are there general size-dependent models? *J Fish Biol* 51:84–100
- Purcell JE, Sturdevant MV, Galt CP (2005) A review of appendicularians as prey of invertebrate and fish predators. In: Gorsky G, Youngbluth MJ, Deibel D (eds) Response of marine ecosystems to global change: ecological impacts of appendicularians. Contemporary Publishing International, Paris, p 359–435
- Richards WJ (ed) (2005) Guide to the early life history stages of fishes of the western central North Atlantic. CRC Press, Miami, FL
- Runge JA, de Lafontaine Y (1996) Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish–*Calanus*–microplankton interaction. *Fish Oceanogr* 5: 21–37
- Sampey A, McKinnon AD, Meekan MG, McCormick MI (2007) Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. *Mar Ecol Prog Ser* 339: 243–257
- Schmitt PD (1986) Feeding by larvae of *Hypoatherina tropicalis* (Pisces: Atherinidae) and its relation to prey availability in One Tree Lagoon, Great Barrier Reef, Australia. *Environ Biol Fishes* 16:79–94
- Shoji J, Tanaka M (2001) Strong piscivory of Japanese Spanish mackerel larvae from their first feeding. *J Fish Biol* 59: 1682–1685
- Sponaugle S, Grorud-Colvert K (2006) Environmental variability, early life history traits, and survival of new recruits of a coral reef fish. *Integr Comp Biol* 46:623–633
- Sponaugle S, Llopiz JK, Havel L, Rankin TL (in press) Spatial variation in larval growth and gut fullness in a coral reef fish. *Mar Ecol Prog Ser*
- ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179
- ter Braak CJF, Simlauer P (2002) Canoco for Windows, version 4.5. Center for Biometry, Wageningen, and Microcomputer Power, Ithaca, NY
- ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat Sci* 57:255–289
- van der Spoel S, Pierrot-Bults AC (eds) (1979) Zoogeography and diversity of plankton. Bunge Scientific Publishers, Utrecht
- Wiebe PH, Morton AW, Bradley AM, Backus RH and others (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar Biol* 87: 313–323
- Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. *Trends Ecol Evol* 20:402–409
- Young JW, Davis TLO (1990) Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. *Mar Ecol Prog Ser* 61:17–29

Editorial responsibility: Alejandro Gallego, Aberdeen, UK

Submitted: October 8, 2008; Accepted: February 4, 2009  
Proofs received from author(s): April 7, 2009