

Spatial variation in larval growth and gut fullness in a coral reef fish

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ABSTRACT: Successful feeding and fast growth is thought to be critical for surviving the pelagic larval stage of benthic marine fishes, yet few measures of these processes are available for tropical reef fishes. We tested the hypothesis that larvae experience faster growth in more productive coastal waters due to increased prey availability. We examined spatial patterns in larval growth and gut fullness for a common coral reef fish, the bluehead wrasse *Thalassoma bifasciatum*. During 2 ichthyoplankton cruises (September 2003 and October 2004), larvae were collected using a coupled MOCNESS at 17 stations along an 80 km east–west transect (25.5° N) across the Straits of Florida between Florida, USA, and the Bahamas. For a subsample of larvae collected at different distances along the transect, we examined sagittal otoliths to estimate growth rates and we inspected gut contents and estimated gut fullness for the same individuals. We also identified and enumerated the available prey of *T. bifasciatum* from a subsample of zooplankton samples collected simultaneously with the larvae. Larval *T. bifasciatum* collected at the western stations grew significantly faster, were larger-at-age, and had fuller guts than those collected at the central and eastern stations. Further, gut fullness of larvae was directly related to cross-straits prey abundance. Despite these repeatable patterns of growth and gut fullness, larval *T. bifasciatum* were consistently more abundant at the central and eastern stations, possibly reflecting particular transport processes or differential predation mortality. These results begin to bridge the gaps in our understanding of pelagic processes and the successful recruitment of nearshore populations.

KEY WORDS: Fish larvae · Larval growth · Early life history · Larval trophic ecology · Otolith microstructure · Zooplankton prey

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INTRODUCTION

For most benthic marine fishes, surviving the pelagic larval phase requires that larvae successfully find food, grow and develop, avoid predation, and eventually locate a suitable settlement habitat. These tasks are inherently intertwined and can have far-reaching population effects. For example, larval growth not only influences survival in the plankton (Meekan & Fortier 1996, Hare & Cowen 1997, Takasuka et al. 2003, Nielsen & Munk 2004), but also successful recruitment into the benthic population (Bergenius et al. 2002, Wilson & Meekan 2002, Jenkins & King 2006, Sponaugle

et al. 2006). Further, larval growth and condition at settlement can carry over to contribute to juvenile success (Searcy & Sponaugle 2001, Shima & Findlay 2002, McCormick & Hoey 2004, Sponaugle & Grorud-Colvert 2006, Gagliano et al. 2007). Although numerous studies have focused on the growth and survival of larvae of temperate fish species, there are fewer efforts to directly characterize larval growth of tropical coral reef species. In addition, most of the above studies on reef fishes have used hindcasted otolith records of settled juveniles to examine relative larval growth.

Similar to temperate species, growth of tropical fish larvae is influenced by water temperature (McCormick

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& Molony 1995, Benoît et al. 2000, Meekan et al. 2003, Sponaugle et al. 2006) and prey availability (Booth & Alquezar 2002, Wexler et al. 2007). Most reef fish larvae prey on zooplankton (Østergaard et al. 2005, Sampsey et al. 2007, Llopiz & Cowen 2009), which in turn feed on microzooplankton and phytoplankton (Landry & Calbet 2004). Because primary production depends on sufficient nutrient levels (Howarth 1988), phytoplankton and consequently zooplankton abundances are related to oceanographic processes, such as upwelling and mesoscale eddies, and terrigenous runoff that introduce nutrients into surface waters. These processes typically result in higher nutrients in nearshore relative to offshore waters both along continents and in the vicinity of islands (island mass effect; Sander & Steven 1973). Spatially heterogeneous distributions of prey in the coastal ocean thus have the potential to substantially influence larval growth and survival of coral reef fish larvae. Interactions between larval prey availability, nearshore adult spawning, the distribution of larval fish predators, and biophysical transport by currents (Pineda et al. 2007) potentially result in patchy areas of high and low larval growth and survival. Such patchiness has implications for successful larval transport and recruitment and, ultimately, population connectivity (Cowen & Sponaugle 2009).

Direct measurement of spatial variation in larval growth of temperate species has demonstrated that growth can be higher at coastal fronts (Munk 2007)

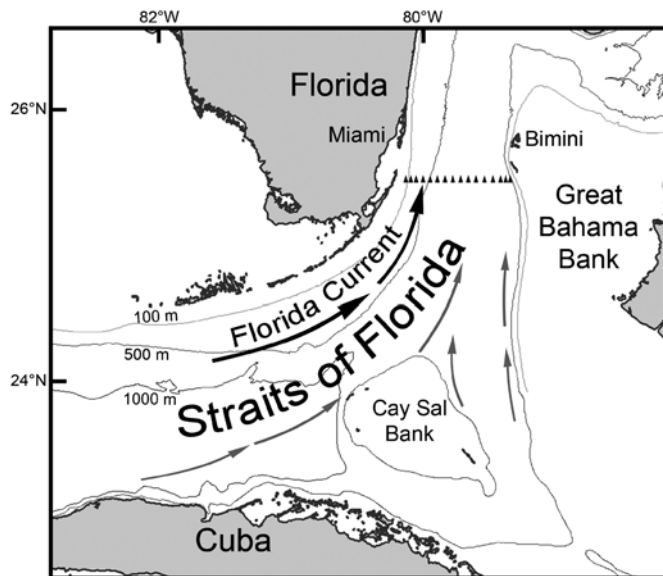


Fig. 1. Straits of Florida region and the sampled transect of 17 stations between Miami, FL, USA, and the Great Bahama Bank (indicated by triangles). The Florida Current flows N–NE through the Straits of Florida crossing the transect (black arrows). Gray arrows indicate upstream flow and thus potential sources of water (and larvae) passing through central and eastern stations

and in nearshore versus offshore waters (Takahashi et al. 2001, Chen & Chiu 2003). Indirect measurements based on otolith records of juvenile coral reef fishes have indicated that larval growth of a reef fish is higher in oceanic versus low salinity eddies (Sponaugle & Pinkard 2004) and in nearshore versus offshore waters (Hamilton et al. 2008). In cohorts settling during different months, larval encounter with different water temperatures can explain significant variation in larval growth (Sponaugle et al. 2006), but where water temperature does not vary substantially, relative onshore-offshore position of larvae during development may underlie observed variation in larval growth (Searcy & Sponaugle 2000). Meekan et al. (2003) examined settlement-stage larvae of a tropical damselfish during high temperature/low prey availability and low temperature/high prey availability conditions and found that temperature was more important in determining larval growth.

Offshore of the southeast coast of the USA, a major western boundary current, the Florida Current (FC), flows through the bathymetrically constrained Florida Straits located between the Florida Shelf and the Bahamas Bank (Fig. 1). The FC flows through this oceanographically dynamic area towards the northeast at speeds of up to 2 m s^{-1} as it tracks the coast and becomes progressively more northward flowing, eventually transitioning into the Gulf Stream. Along the western front of the FC, coastal upwelling of deep nutrient-rich waters and frequent formation of meso and sub-mesoscale frontal eddies that entrain nearshore waters result in higher primary and secondary productivity in western FC waters relative to eastern waters (Hitchcock et al. 2005, Llopiz 2008).

A suite of western Atlantic/Caribbean reef fish fauna live and reproduce on coral reefs of the Florida Keys. Different species reproduce in the vicinity of adult habitat or migrate along the reef to spawn at reef promontories. Larvae hatching from pelagic or demersally spawned eggs range in their ability to actively control their position in the water column (reviewed in Leis 2006) and in their susceptibility to being transported along the frontal boundary by mesoscale features (D'Alessandro et al. 2007), with many potentially advected into offshore waters.

We tested the hypothesis that reef fish larvae in more productive near-coastal waters grow faster than larvae in oligotrophic oceanic waters by estimating the daily growth rates of larvae of a common reef fish collected at various distances offshore of Florida. *Thalassoma bifasciatum* is a western Atlantic/Caribbean reef fish that spawns pelagic eggs on a daily basis. Larvae hatch after 2 d and spend ~50 d in the plankton before settling to the reef in pulses associated with lunar and tidal amplitude cycles. Growth during the larval phase

is naturally variable within and among cohorts (Searcy & Sponaugle 2000, Sponaugle et al. 2006), and the effects of variable growth and condition can carry over to influence juvenile survival (Searcy & Sponaugle 2001, Sponaugle & Grorud-Colvert 2006, Hamilton et al. 2008). Although many early life history studies have selected *T. bifasciatum* as a model study species, most efforts have focused on the early juvenile stage and hindcasted events (via otolith analysis) occurring during larval life. Here, we directly examined *T. bifasciatum* growth in larvae collected at various distances offshore of Florida reefs. Substantial cross-straits movement of larvae prior to collection is not likely due to the dominant northward along-straits flow and low cross-straits flow of the FC. We also examined the gut contents of the aged larvae to test whether growth was related to prey consumption and measured concurrent prey availability. With increasing interest in larval dispersal and connectivity among marine populations (reviewed in Cowen & Sponaugle 2009), quantifying variation in larval growth and survival in different water masses is an essential component of obtaining realistic data on dispersal kernels.

MATERIALS AND METHODS

Field sampling. Ichthyoplankton samples were collected along a transect across the Straits of Florida between Miami, Florida, and the Bahamas at 25.5° N (Fig. 1) that was sampled over 2 d at the beginning of every month for 2 consecutive yr (2003 to 2004) by the RV 'Walton Smith.' Seventeen stations (Stns 1 to 17, W to E; spaced ~2 km apart at both ends of the transect and ~5.5 km apart in the center) along the transect were sampled during daylight hours by MOCNESS. This system was modified to simultaneously sample ichthyoplankton and their prey by joining 2 sets of nets with different opening and mesh sizes (4 m², 1 mm mesh and 1 m², 150 µm mesh) and was used to obliquely sample discrete depth bins (0 to 25, 25 to 50, 50 to 75, 75 to 100 m; see Llopiz & Cowen 2008). The upper surface layer to ~0.5 m was sampled with a similarly designed double neuston net (2 × 1 m, 1 mm mesh and 0.5 × 1 m, 150 µm mesh). MOCNESS and neuston nets were outfitted with flowmeters to estimate the volume of water sampled. Water temperature data were collected by the MOCNESS during sampling. Ichthyoplankton samples were fixed in 95% ethanol and stored in 70% ethanol. Samples were sorted in the laboratory to remove fish larvae, and these were identified using standard identification guides; *Thalassoma bifasciatum* larvae can be easily identified to species based on their unique morphology (Jones et al. 2006). Larval abundance data are from the

1 mm mesh nets and exclude 3 mo (December 2003, January and November 2004) when weather conditions precluded the sampling of all 17 stations.

Otolith analysis and growth comparisons. We were able to use otolith increment analysis to obtain estimates of daily growth of *Thalassoma bifasciatum* because daily deposition of increments has been validated (Victor 1982) and the width between successive otolith increments is a proxy for somatic growth rate (Searcy & Sponaugle 2000). Additionally, otolith radius is typically highly correlated with fish length (Sponaugle & Cowen 1997). Thus, to compare growth rates among *T. bifasciatum* larvae distributed at different distances offshore, we selected the 2 replicate months with the highest numbers of *T. bifasciatum* larvae collected over the transect (September 2003 and October 2004, n = 203 and 181, respectively; Fig. 2) and most similar temperature profiles. During these 2 mo, sufficient numbers of *T. bifasciatum* larvae were collected from each of 3 zones (western zone: Stns 1 through 6; central zone: Stns 7 through 12; and eastern zone: Stns 13 through 17). For each of the 2 mo, larvae were selected from all stations to yield a total of 25 larvae from each of the 3 zones. However, in October 2004, only 16 larvae were available from the western zone, so the total number of larvae aged across the 3 zones for that month was 66. Standard length (SL) of each larva was measured to the nearest 0.01 mm using a Leica MZ12 dissecting microscope. Both sagittal otoliths were dissected from each larva and kept in medium viscosity immersion oil on microscope slides for 7 to 21 d to 'clear' and facilitate increment interpretation. The clearer of the 2 sagittae was read at 400× using a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. The image was captured with a Dage MTI video camera and framegrabber and analyzed using Image Pro Plus 4.5 image analysis software (Media Cybernetics). Individual increments were enumerated along the longest axis from the core (primordium) of the otolith to the outer edge to determine larval age. The distance between each pair of increments provided a measure of daily growth for each fish. Each otolith was read blind (i.e. with no size or collection location information available) by a single reader, and when all otoliths were completed, the process was repeated. If the difference in age between the 2 readings was <5%, one was chosen randomly as the final read. If there was a discrepancy in age of ≥5% difference between the 2 readings, the otolith was read a third time. If after a third read a high discrepancy in the readings remained, the otolith was discarded. In total, 4 fish were rejected from each month due to high variance in interpretation after the third read (final n = 71 for September 2003, n = 62 for October 2004).

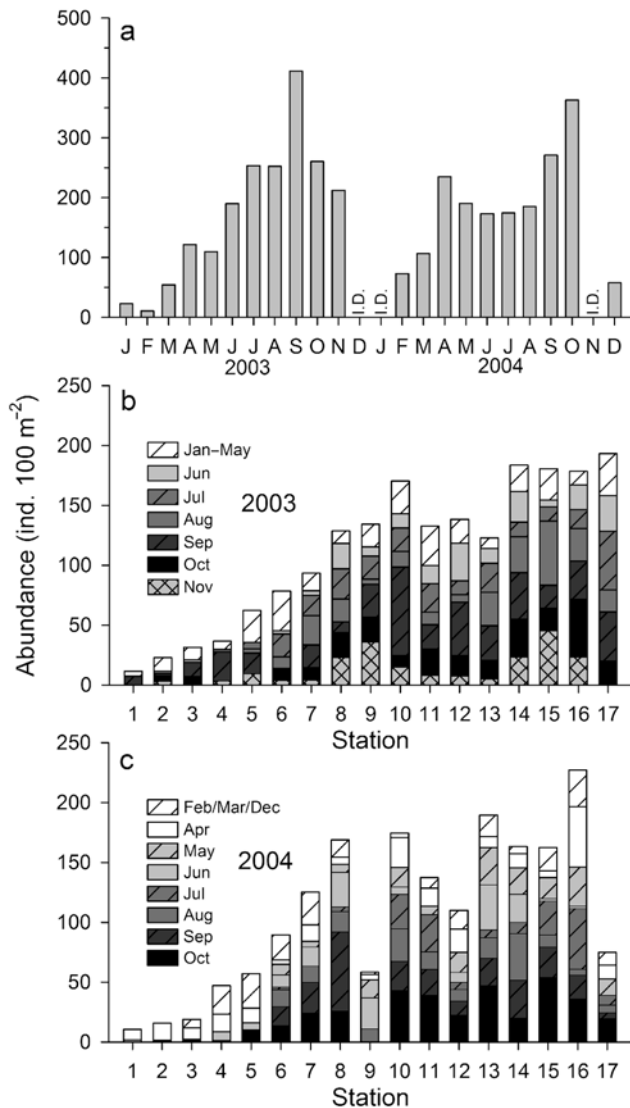


Fig. 2. *Thalassoma bifasciatum*. (a) Monthly abundance and (b,c) cross-straits spatial distribution of larvae collected during 24 monthly cruises (b = 2003, c = 2004) along a transect between Miami, FL, USA, and the Bahamas (n = 1810). Months where few larvae were collected were combined to simplify the presentation. Stn 1 was closest to Miami and Stn 17 closest to the Bahamas. I.D.: incomplete data

To ensure that otolith deposition rates remained consistent over the 2 study periods (months), the relationship between SL and otolith radius was defined for each month using standard least-squares regression. Only larvae between the ages of 16 and 28 d were used in the analysis of growth to minimize the influence of differential age on growth while maintaining a sufficiently large sample size (n = 106). Initial analyses were made to determine whether larval age and growth differed with sampling depth. All but 5 larvae were collected in the 0 to 25 or 25 to 50 m

depth bins. Although these 5 larvae collected at 50 to 75 m depth in September 2003 were older than the others (Kruskal Wallis: $p = 0.018$), larval growth was unrelated to depth of collection (ANOVA: $p > 0.05$); thus, larvae were pooled among depth bins for further analysis.

Growth rates were examined at specific age intervals. Mean growth rates (otolith increment widths) and mean size (otolith radii) at 10, 15, and 20 d were compared between months and among the 3 zones using a 2-way, mixed-model ANOVA for each day with zone as a fixed factor and months as a random factor. The mean square for the interaction of factors was pooled with the residual mean square when appropriate ($p > 0.25$). However, as we were largely interested in specific comparisons (i.e. spatial differences within months and temporal differences within zones), for all scenarios (interaction pooled, not pooled, or significant) we utilized Student-Newman-Keuls tests for pairwise comparisons (Underwood 1997). Due to the limited power of mixed model ANOVAs when the pooling of variability is inappropriate, such multiple comparisons can yield significant results without the main factors themselves being significant.

Gut contents analysis. A detailed inspection of the gut contents of *Thalassoma bifasciatum* larvae (n = 93) was made for all 16 to 28 d old larvae used in the otolith growth analysis, with the exception of 10 damaged larvae and 3 that were collected exactly at sunrise. Since *T. bifasciatum* larvae were observed to feed only during daylight, larvae collected at sunrise would have had insufficient time to reach typical daytime gut fullness levels (Llopiz & Cowen 2008). For each larva, the entire alimentary canal was removed and individual prey items were excised using a microscalpel and minuten pins (see Llopiz & Cowen 2008). In total, 468 prey were excised, of which only 5 unidentifiable prey items and 4 small, non-copepod prey were excluded from analyses. All remaining prey were copepods, identified to the lowest taxonomic level practical for utilizing published length–weight conversions. Prosome lengths were measured with an ocular micrometer (Leica MZ15) and lengths were converted to dry weight (following Chisholm & Roff 1990, Webber & Roff 1995, Hopcroft et al. 1998) to obtain estimates of prey biomass at time of ingestion. Sixty-eight prey (often damaged) were assigned lengths that were either the taxon-specific average length within the same larva, or if not possible, the average length within the larva's 1 mm size class.

To obtain quantitative estimates of gut fullness, values of ingested prey biomass for each larval *Thalassoma bifasciatum* (sums of individual prey weights within each larva) were regressed against larval

length to account for the increase in gut capacity with growth. The residuals from this linear relationship were used as an estimate of gut fullness (Dower et al. 1998), and were tested for differences between months and among the 3 zones of the transect using a 2-way, mixed-model ANOVA as performed above for the growth data.

Prey availability and selectivity. A subset of plankton samples from the 1 m² MOCNESS nets was used to examine the relationship of environmental copepod abundance to larval gut fullness, and for performing prey selectivity analyses. Subsamples (5 ml) were taken from the 1 l plankton/ethanol sample with a Hensen-Stempel pipette until at least 100 individuals of the 3 dominant *Thalassoma bifasciatum* copepod prey (harpacticoids and the cyclopoids of the genera *Farranula* and *Oncaea*) were enumerated (Postel et al. 2000). One sample with relatively high numbers of *T. bifasciatum* larvae was selected from near the center of each of the 3 zones each month. Prey selectivity analyses followed Manly et al. (2002) and, as specifically applied to fish larvae, Llopiz & Cowen (2008). Briefly, selection ratios were calculated as the ratios of proportions of prey types consumed to those available. Selection for a prey type is indicated by values >1, with selection against the type by values <1. Statistical significance of selection for or against a prey type is determined by confidence intervals (Bonferroni-adjusted) not overlapping with 1 and, since dependent upon the sample size of prey consumed, is not easily obtained for low consumed-prey sample sizes, including prey that are rarely consumed. Selection ratios were calculated for each sample by pooling the prey consumed by all larvae collected in the sample.

RESULTS

Larval abundance and age distribution

In total, 1810 *Thalassoma bifasciatum* larvae were collected across the transect over the 2 yr of monthly sampling. Patterns of overall abundance were similar each year, with winter lows increasing to late summer peaks (Fig. 2a). Larvae were collected most frequently from the central and eastern zones, where overall zone-specific *T. bifasciatum* abundances were each about 3 times greater than in the western zone (Fig. 2b,c). We used the 2 mo of peak abundance to compare growth across the transect. Larval ages ranged from 14 to 36 d (23.31 ± 4.29 d, mean \pm SD) in September 2003 and 13 to 48 d (22.53 ± 7.47 d) in October 2004. The majority of the collected larvae were 16 to 28 d old, so all remaining analyses focused on these.

Otolith radii and somatic size

Larvae ranged in size from 3.30 to 7.40 mm SL in September 2003, and 3.48 to 5.99 mm SL in October 2004, with corresponding otolith radii of 41.82 to 122.59 μ m and 44.90 to 95.22 μ m, respectively. Variation in otolith radii accounted for 80 to 89% of the variation in SL (least squares regression: September 2003: $y = 0.0553x + 0.7773$; $r^2 = 0.89$; $n = 71$; October 2004: $y = 0.0516x + 1.1302$; $r^2 = 0.80$; $n = 62$; both $p < 0.001$).

Growth rates

Overall, growth and size-at-age of larval *Thalassoma bifasciatum* varied by region at specific ages, but there was no significant effect of month (Table 1). More informative were pairwise tests that revealed daily growth was frequently higher at western zone stations relative to eastern zone stations, resulting in consistently larger sizes-at-age for fish collected at western zone stations (Table 1 & Fig. 3). There were few significant temporal differences and these only occurred at eastern zone stations (Table 1).

Diet and gut fullness variability

Larval *Thalassoma bifasciatum* consumed varying proportions of *Farranula*, *Oncaea*, and harpacticoid copepods across the Straits of Florida (Fig. 4a,b), and only 1 larva had an empty gut. The weight of larval gut contents increased linearly with larval length ($y = 4.03x - 9.62$, $n = 93$, $r^2 = 0.39$, $p < 0.001$). Residuals from the gut weight–larval length relationship, used as a proxy for gut fullness, varied by month and spatially across the transect (Table 1). In September 2003, relative gut fullness was significantly higher in the western zone relative to the central and eastern zones (Table 1 & Fig. 4c). This trend was consistent, though non-significant, for larvae collected in October 2004. For larvae from the central and eastern zone stations, residual gut biomass in October 2004 was greater than September 2003.

Prey availability and selectivity

Mean relative gut fullness increased significantly with increasing environmental abundance of the 3 dominant prey of *Thalassoma bifasciatum* (*Farranula*, *Oncaea*, and harpacticoid copepods; Fig. 5). Prey selectivity analyses (Table 2) indicated that proportions of harpacticoid copepods consumed were 9 to 210 times greater than environmental proportions.

Table 1. *Thalassoma bifasciatum*. 2-way ANOVA comparing growth (otolith increment widths), size (otolith radius), and residual gut content biomass of larvae collected from western (W), central (C), and eastern (E) zone stations of a transect across the Straits of Florida in September 2003 (S) and October 2004 (O). Otolith traits were compared separately at each of 3 points: Day 10 (n = 106), Day 15 (n = 106), and Day 20 (n = 76) of larval life. Student-Newman-Keuls (SNK) tests were used for pairwise comparisons ($p < 0.05$) in all cases as a conservative approach, assuming all interactions were significant (Underwood 1997). –: not tested due to significant interactions; ns: not significant

Larval trait	Age (d)	Source p-value			SNK multiple comparisons				
		Month	Region	Interaction	Spatial		Temporal		
					Sep 03	Oct 04	Western	Central	Eastern
Increment width	10	–	–	0.04	ns	W,C>E	ns	ns	S>O
	15	0.75	0.15	0.09	ns	W>C,E	ns	ns	S>O
	20	0.69	0.001	0.40	W,C>E	ns	ns	ns	ns
Otolith radius	10	0.52	<0.001	0.28	W>E	W>C>E	ns	ns	ns
	15	0.67	0.13	0.07	W>C,E	W>C>E	ns	ns	S>O
	20	0.06	<0.001	0.71	W>E	W,C>E	ns	ns	ns
Residual gut content biomass (gut fullness)		0.001	<0.001	0.29	W>C,E	ns	ns	O>S	O>S

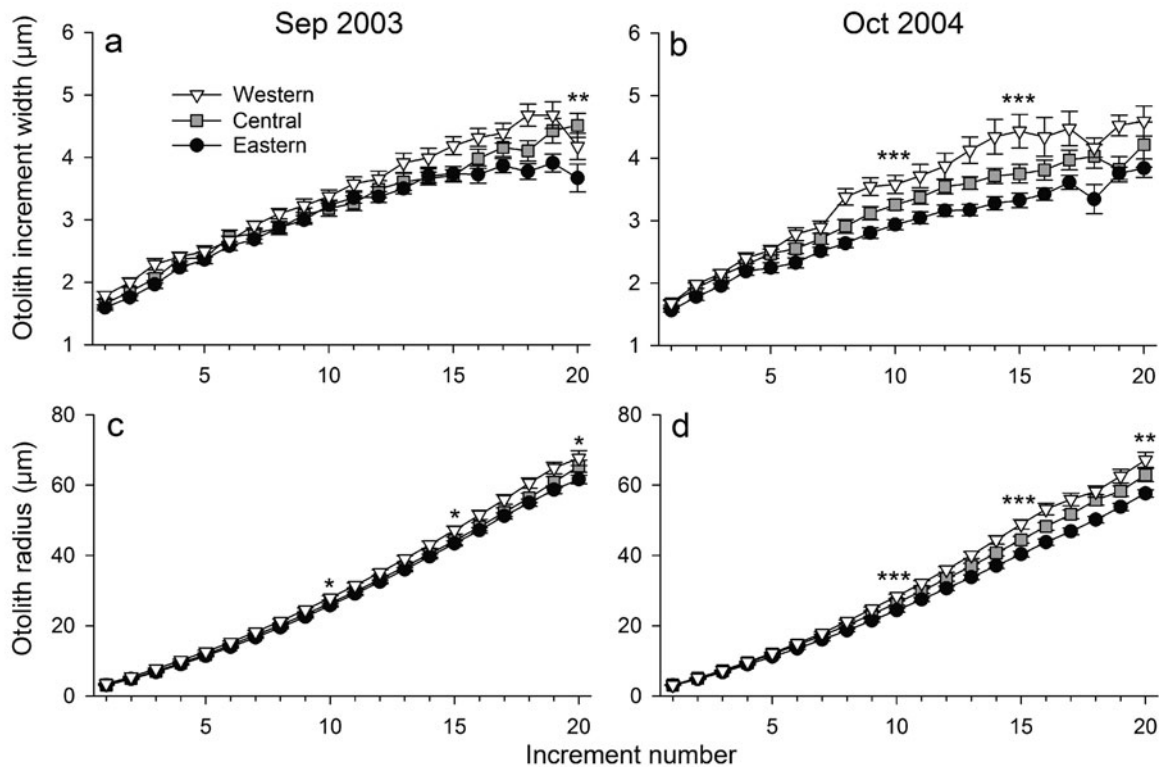


Fig. 3. *Thalassoma bifasciatum*. Mean (a,b) growth (\pm SE) and (c,d) otolith radius (\pm SE) during Days 1 to 20 of larval life for larvae ages 16 to 28 d collected at western, central, and eastern zone stations for (a,c) September 2003 and (b,d) October 2004. Mean growth (otolith increment width) and mean size (otolith radius) were compared at 3 points (Days 10, 15, and 20 of larval life). Significant difference between at least 2 regions is indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For details see Table 1

The more abundant *Farranula* and *Oncaea* copepods were also generally selected. Calanoid copepods were avoided and rarely consumed despite composing, of the 6 copepod taxa examined, ~60 to 80% of the copepods available in the environment.

Water temperature

Water temperatures measured at the surface during ichthyoplankton tows varied little across the transect in both months: September 2003 = 29.1 to 29.5°C; Octo-

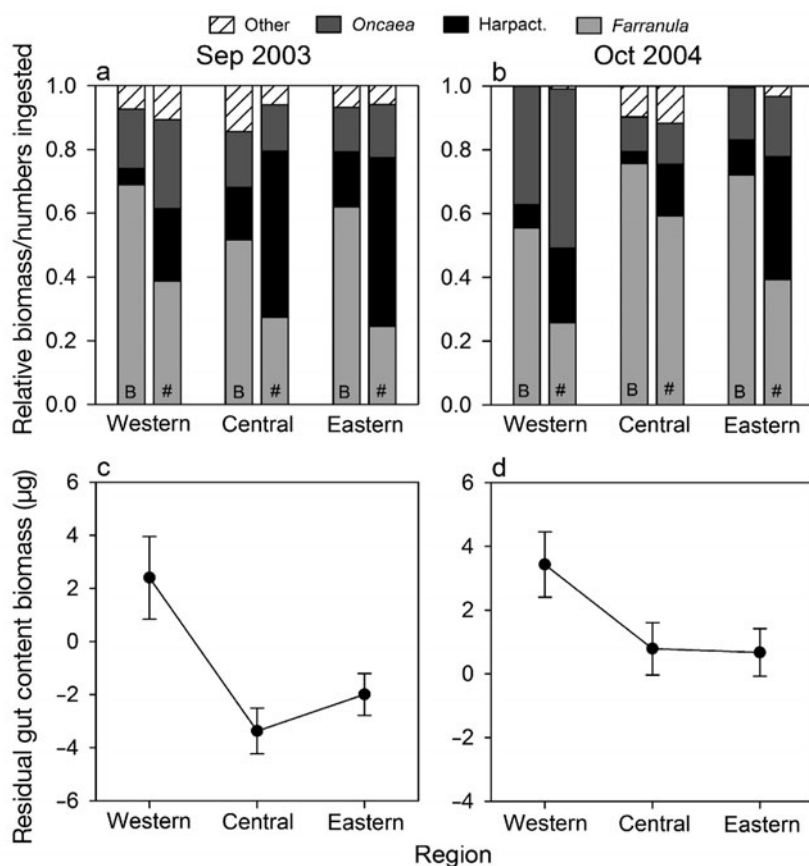


Fig. 4. *Thalassoma bifasciatum*. (a,b) Ingested biomass (B) and numerical proportions (#) of 3 major copepod prey types (*Farranula*, *Oncaea*, and harpacticoids), presented as proportion of all gut contents from each zone. (c,d) Mean (\pm SE) residuals from the linear relationship of gut content biomass and larval length (used as a standardized measure of gut fullness; see 'Materials and methods') for larvae collected from each of the 3 cross-straits zones in September 2003 and October 2004

ber 2004 = 28.1 to 28.5°C. Water temperatures at 25 to 50 m depth also varied little across the transect in October 2004, but shoaling of the thermocline at western nearshore stations was greater in September 2003, with temperatures of 23 to 29°C at 25 to 50 m at the westernmost station. These temperatures increased across the transect, remaining near 29°C in the 25 to 50 m depth range.

DISCUSSION

Larval *Thalassoma bifasciatum* exhibited significant spatial differences in growth across the Straits of Florida. During both September 2003 and October 2004, larval growth was generally faster at the western zone stations (closest to Miami) and de-

creased toward the east (closer to the Bahamas), resulting in larvae that were significantly larger-at-age at the western zone stations. While the among-region differences in growth rates at particular larval ages were not always significant, the trend of higher growth in the western zone stations (west > central \geq east) was maintained over the first 15 to 20 d of larval life. The dominant along-straits flow of the FC reduces the likelihood that larvae moved substantially among the 3 zones (i.e. cross-straits) prior to their collection. Further, larval movement among zones would tend to homogenize any growth differences; thus, our finding of distinct spatial patterns of larval growth is a conservative demonstration of this pattern.

Cross-transect variation in larval growth was not likely due to differences in water temperature because there was relatively little variation in surface temperature along the transect (0.4°C) during both months, with similar low variability (0.5°C) at 25 to 50 m in October 2004. Although water temperatures at 25 to 50 m in September 2003 varied more across the transect (4.4°C), temperatures were cooler towards the west, opposite to what would be expected to produce the observed spatial patterns in larval growth.

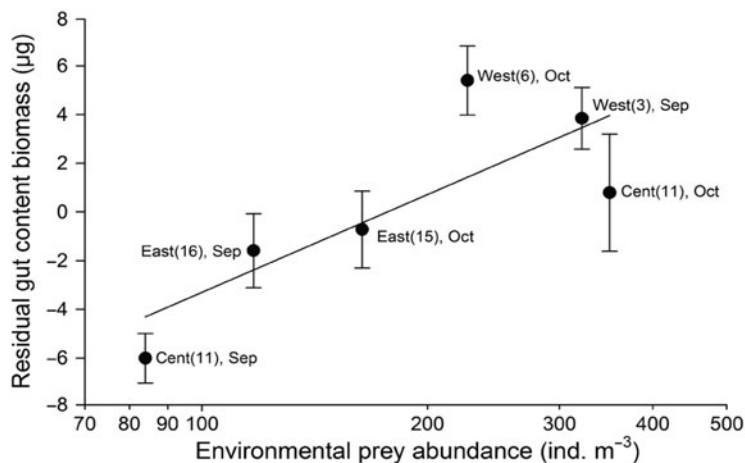


Fig. 5. *Thalassoma bifasciatum*. Linear regression between mean residual gut content biomass of larvae and total environmental abundance of *Farranula*, *Oncaea*, and harpacticoid copepods at 6 stations distributed among the 3 zones of the Straits of Florida during September 2003 (Sep) and October 2004 (Oct). Station number is indicated in parentheses. Relationship is $y = 5.80 \ln(x) - 29.99$, $r^2 = 0.65$

Table 2. *Thalassoma bifasciatum*. Prey selectivity of larvae collected at different distances (stations) along a transect across the Florida Straits. Proportions of zooplankton prey in the guts of larvae were compared to simultaneously sampled proportions of prey available in the environment (envir.) at 6 stations selected from the western, central, and eastern zones during each of 2 mo (September 2003 and October 2004). A selection ratio >1 indicates larvae selected for the prey type; a ratio of 0 to 1 indicates larvae selected against the prey type. Low sample sizes of prey consumed often precluded statistical significance, and selection ratios of 0 could not be statistically tested. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. n_p : number of prey consumed

	Sep 2003			Oct 2004		
	Stn 3 $n_p = 30$	Stn 11 $n_p = 37$	Stn 16 $n_p = 33$	Stn 6 $n_p = 51$	Stn 11 $n_p = 10$	Stn 15 $n_p = 24$
<Selection ratio						
Harpacticoids	32.6***	168.8***	210.2***	17.2***	9.0	36.8***
<i>Farranula</i>	2.9	3.2	1.2	4.6***	1.3	3.3
<i>Oncaea</i>	2.0	4.3	2.3	2.4*	0.8	1.0
<i>Corycaeus</i>	1.1	0	3.8	0	0	0
Calanoids	0.2***	0	0	0	0.5	0
<i>Oithona</i>	0	0	0	0	5.2	0.7
Consumed prey proportions						
Harpacticoids	0.33	0.65	0.67	0.31	0.10	0.46
<i>Farranula</i>	0.27	0.19	0.12	0.41	0.30	0.33
<i>Oncaea</i>	0.27	0.16	0.15	0.28	0.10	0.13
<i>Corycaeus</i>	0.03	0	0.06	0	0	0.04
Calanoids	0.10	0	0	0	0.30	0
<i>Oithona</i>	0	0	0	0	0.20	0.04
Environmental proportional abundance						
Harpacticoids	0.01	0.004	0.003	0.02	0.01	0.01
<i>Farranula</i>	0.09	0.06	0.10	0.09	0.23	0.10
<i>Oncaea</i>	0.13	0.04	0.07	0.12	0.13	0.12
<i>Corycaeus</i>	0.03	0.01	0.02	0.03	0.02	0.01
Calanoids	0.60	0.78	0.68	0.71	0.58	0.70
<i>Oithona</i>	0.14	0.12	0.13	0.04	0.04	0.06
Total prey envir. abundance (m^{-3})	1372	841	697	1004	959	694

Mean gut fullness of larval *Thalassoma bifasciatum* also varied across the Straits of Florida, with larvae collected from the western zone having fuller guts than larvae collected from the central and eastern zones. Thus, larvae from the western stations had fuller guts and exhibited faster growth rates relative to larvae collected from the central and eastern zone stations. Further, gut fullness of larvae was directly related to environmental prey availability, illustrating the role of ambient prey abundances. The dominant prey of *T. bifasciatum* were more abundant at western zone stations relative to the central and eastern zone stations, as has been indicated previously (Llopiz 2008; P. Lane & S. L. Smith, Rosental School of Marine and Atmospheric Science [RSMAS], unpubl. data). This pattern is consistent with the higher primary productivity and nutrients within and on the western edge of the FC due to physical processes such as upwelling and the passage of mesoscale cyclonic eddies (Hitchcock et al. 2005).

Spatial patterns of larval growth and size were generally similar between the 2 mo, with variability evi-

dent in only the eastern larvae, where growth and size-at-age were higher in September 2003 half of the time. Patterns of gut fullness in eastern larvae were the reverse; larvae in October had higher gut biomass than eastern larvae. Although gut fullness appears to have the most direct overall relationship to larval growth, at lower levels of gut fullness where prey availability is more variable (i.e. at eastern stations), diet composition may play a larger role.

Composed primarily of 3 prey types, the diet of larval *Thalassoma bifasciatum* is similarly narrow yet compositionally different to the diets of some other coral reef fish taxa (Llopiz & Cowen 2009). Such a diet is a clear result of a highly selective feeding behavior, either from active larval choice or relative catchability of the prey. Selectivity analyses indicated that harpacticoid copepods (mostly *Microsetella* spp.) were the most consistently preferred prey taxon despite calanoid copepods being up to 215 times more abundant in the environment. Harpacticoids may be easier for *T. bifasciatum* larvae to detect or catch than calanoids. Although higher numbers of harpacticoids in larval guts was not always consistent with higher larval growth, for eastern larvae where

gut fullness was low, larger and faster growing individuals in September 2003 consumed a higher number and biomass of harpacticoids than eastern larvae in October 2004. Thus, while overall environmental prey availability and larval gut fullness yields the most significant spatial pattern of larval growth, there is some suggestion that specific prey composition may also influence larval growth.

In western zone stations closest to the Florida shelf, copepod prey are more abundant, presumably leading to fuller guts and faster growth of their larval *Thalassoma bifasciatum* predators. A previous study of *T. bifasciatum* based on hindcast otolith analysis of settled juveniles hypothesized that variation in larval growth was due to their position onshore versus offshore (Searcy & Sponaugle 2000). Using trace elemental analysis of otoliths to estimate the pelagic larval position of settled recruits to St. Croix, Swearer et al. (1999) and Hamilton et al. (2008) found high larval *T. bifasciatum* growth rates to be associated with high Pb otolith signatures, suggesting that larvae in

nearshore waters grow faster. The present study is the first effort to directly measure the growth of reef fish larvae collected from known positions offshore. While we have no experimental data demonstrating cause and effect, the consistent spatial patterns of environmental prey availability and larval fish gut fullness and growth are highly indicative of such cause and effect relationships.

Among temperate fish species, spatial differences in larval growth usually have been ascribed to exposure to different water temperatures, and less frequently to prey availability. Growth of Arcto-Norwegian cod larvae varied between 2 water masses due to characteristic water temperature differences (Suthers & Sundby 1993). Cod larvae generally grew more rapidly at a hydrographic front where prey were more abundant; however, there was no significant relationship between prey availability and larval growth (Munk 2007). Similarly, differences in growth of radiated shanny larvae among 3 bays in Newfoundland reflected among-bay differences in temperature but not prey availability (Dower et al. 2002). Within a single bay, however, larger and faster-growing radiated shanny larvae had a larger volume of food in their gut (Dower et al. 2009). Several studies document an onshore-offshore pattern of larval growth, but the underlying causes are unclear (Takahashi et al. 2001, Chen & Chiu 2003). More frequently, studies have compared larvae collected during multiple seasons or years, with temporal differences in growth reflecting water temperature (Baumann et al. 2006), prey availability or consumption (Wexler et al. 2007), or neither (Lee et al. 2006).

Despite consistent spatial patterns in larval growth, more than 3 times the number of *Thalassoma bifasciatum* larvae were collected in the eastern and central zone stations relative to the western zone. One explanation for this apparently conflicting observation is that larvae may be transported to eastern stations from more extensive upstream adult spawning habitat than larvae from western zone stations. *Thalassoma bifasciatum* is a common constituent of most Caribbean reefs, thus numerous upstream sources are possible. The central and eastern zones may receive reef fish larvae spawned at and transported from a number of upstream locations, including Cay Sal Bank, the northern coast of Cuba, and the extensive Great Bahama Bank. Cross-straits larval abundances may simply reflect larval transport processes and spatially varying adult densities and spawning output more than differential growth and survival. As an aside, genetically homogenous populations of *T. bifasciatum* in the Caribbean (Shulman & Bermingham 1995, Purcell et al. 2006) reduce the likelihood that larvae from different zones might exhibit variable growth rates unrelated to

food availability (i.e. due to a genetic basis). Although we cannot exclude this possibility, the fact that faster growing larvae had fuller guts in a region with higher prey availability suggests that a direct predator-prey relationship is a more parsimonious explanation. It is also unlikely that larvae exhibit density-dependent growth rates (i.e. that larvae in the eastern zone stations exhibit reduced growth due to higher densities). The very diffuse concentrations of reef fish larvae are probably insufficient to deplete prey to any substantial degree even in the tropical oligotrophic ocean (J. K. Llopiz & R. K. Cowen, RSMAS, unpubl. data).

An alternative explanation for higher larval abundances in the eastern Zone is that spatial variation in predation mortality on larvae may result in higher larval mortality in the western Zone. Most theory regarding the adaptive advantages of offshore larval dispersal revolves around the concept that predators are more numerous in nearshore reef waters (e.g. Johannes 1978). Whether this is the case in the Straits of Florida (i.e. piscivores more numerous at western stations) is unknown, although it is worth noting that the larvae of other reef fish taxa exhibit a range of onshore-offshore distributions, including higher western densities (R. K. Cowen, J. K. Llopiz, D. E. Richardson et al. RSMAS, unpubl. data) that do not reflect higher nearshore predation by a common predator.

Spatial variation in predation strength has the potential to obscure relative growth by imposing more selective mortality on a portion of the population. In this situation, if predation on larvae was higher at the western edge of the FC, stronger selective loss of slower growers (growth rate hypothesis; Anderson 1988) would result in overall lower abundances consisting of primarily fast growing larvae (i.e. survivors), consistent with our observations. Importantly, selective mortality and growth-related processes are not mutually exclusive. In the Straits of Florida, western *Thalassoma bifasciatum* larvae have more access to prey, resulting in fuller guts and faster growth, and spatial variation in selective loss may accentuate this pattern. On average, faster-growing *T. bifasciatum* are more likely to survive, to settle at higher condition, and contribute to the benthic population (Searcy & Sponaugle 2001, Sponaugle & Grorud-Colvert 2006, Hamilton et al. 2008). Interestingly, Hamilton et al. (2008) found that juvenile survival was greater for fish that spent their early larval period offshore growing more slowly and re-entered nearshore waters later in larval life prior to settlement. They hypothesized that these larvae were subjected to a more 'selectively intense' environment offshore, leading to their enhanced survival as settled juveniles relative to fish that spent more time growing in more favorable nearshore waters. The degree to which a particular area subjects larvae to

high and potentially selective mortality should be a function of both food availability and predator abundance, however, relatively little is known about the extent of these pressures exerted on larvae in the wild.

The fact that western *Thalassoma bifasciatum* larvae grew faster than larvae from eastern and central zone stations increases the likelihood that they will contribute disproportionately to juvenile recruitment to Florida reefs. Thus, offshore larvae potentially transported from more distant locations not only have a reduced chance of finding suitable settlement habitat, but their chances of surviving the journey may be compromised where prey are not sufficiently abundant, as in oligotrophic, offshore tropical waters. Understanding growth and survival during the larval phase is a critical component of quantifying dispersal kernels and estimating the degree to which marine populations are connected over time and space (Pineda et al. 2007, Cowen & Sponaugle 2009). A deeper understanding of the linkages between larval and juvenile populations also will help us better define the constraints experienced by different life history stages.

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