

Variable larval growth in a coral reef fish

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ABSTRACT: Understanding the functional linkages between the pelagic and demersal stages of marine organisms is a central goal in ecology. To better understand events that occurred during the larval period as well as their initial influence on juvenile traits, we examined individual level variation in early life-history traits (larval and early juvenile otolith growth rates, size-at-age, and larval duration) of 3 seasonal cohorts of the common coral reef fish *Thalassoma bifasciatum* (Bloch) (Labridae). Juveniles were collected at regular intervals (every second day) for 2 wk following their first appearance on the nearshore reefs of Barbados, West Indies. Otolith analysis indicated that each cohort exhibited a broad range of larval traits. Individuals with shorter larval durations had faster otolith growth and settled at relatively smaller sizes (based on otolith length and standard length) than larvae with longer larval durations, which exhibited slower otolith growth rates. Despite the range in larval durations for *T. bifasciatum*, otolith growth records revealed no evidence for delay of metamorphosis. Instead, the range in larval durations is likely to be the result of a variable pelagic environment influencing growth rates. Because metamorphosis in this species is an energetically costly non-feeding (3 to 5 d) period, we propose that successful metamorphosis requires a minimum energy reserve. Slower growers may need to remain in the plankton longer (consequently attaining larger sizes) to obtain this minimum condition. Variability in early life-history traits also occurred among the seasonal cohorts. Despite differences in patterns of larval otolith growth, mean larval duration was similar for the 2 fall cohorts (57 and 55 d), but much shorter for the spring cohort (42 d). Such inter-cohort variability in early life-history traits suggests a variable pelagic environment. In contrast to the larval period, juvenile growth rates were much less variable within and among cohorts, reflecting a more constant physical and biological environment on the reef.

KEY WORDS: Coral reef fish · Early life-history traits · Juvenile growth · Larval growth · Growth plasticity · Otolith · Pelagic larval duration · Condition at settlement · *Thalassoma bifasciatum*

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INTRODUCTION

In many benthic marine organisms, settlement to the juvenile/adult habitat divides the life history into a pelagic larval phase and demersal adult phase. Studies of temperate fishes recently have placed an emphasis on the role of larval traits (e.g. age-at-settlement,

growth rates, length-at-age) in the subsequent dynamics of juvenile growth and survival (Chambers & Leggett 1992, Bertram et al. 1993), however, similar issues have received little attention in studies of tropical (coral reef) fishes. Due to high predation on the youngest recruits (e.g. Hixon 1991), larval traits at settlement may influence initial survival on the reef. If such traits are propagated to older juveniles, they may also impact later competitive abilities and susceptibility to predators (reviewed in Sogard 1997). Analysis of the natural variability of larval traits at settlement should contribute to our understanding of events occurring in the pelagic larval phase, and how these events or processes impact subsequent juvenile traits and, ultimately, population dynamics.

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Fishes are ideal subjects in which to examine variability in early life-history traits as the otoliths (ear bones) of many fishes contain a daily record of previous events. Relative otolith growth and length-at-age may be reflected in somatic traits (e.g. Secor & Dean 1989, Hare & Cowen 1995). The use of otolith records in field studies has enabled the description of seasonal (Bell et al. 1995, Fowler & Short 1996), annual (Sponaugle & Cowen 1994, 1997, Meekan & Fortier 1996) and geographic differences in early life-history traits such as growth rates and larval duration (Thresher & Brothers 1989, Wellington & Victor 1992). These differences may be the result of maternal influence (egg quality: Chambers 1997) and genotype (Chambers & Leggett 1992), as well as environmental factors such as food availability (Mosegaard et al. 1988, McCormick & Molony 1992) and temperature (Hovenkamp 1990, Fitzhugh et al. 1997). However, a precursor to understanding such comparisons is the need to document the range of natural variation within a single cohort (McCormick 1994, Fowler & Short 1996).

Pelagic larval durations (PLD) are variable among recruiting fishes (Fowler 1989, Wellington & Victor 1992, Sponaugle & Cowen 1997) as well as invertebrates (Pechenik 1990, Stoner et al. 1996). The lower limit of time spent in the plankton may indicate when larvae are competent to settle, whereas the upper limit may be the result of delayed metamorphosis where larvae are capable of metamorphosis but await the proper settlement cue (e.g. Cowen 1991, Cowen & Sponaugle 1997, McCormick 1999). Alternatively, larvae may settle upon reaching competency, but as a result of variable precompetent growth, slower growers settle at older ages than relatively faster growers (e.g. Chambers & Leggett 1987, Bertram et al. 1993). Ultimately, the causes of variation in PLD may be the result of a range of precompetent growth rates, delayed metamorphosis, or both (Cowen 1991, Cowen & Sponaugle 1997).

Very little is known about how larval traits are translated into juvenile traits once a larva reaches the juvenile/adult habitat. As mortality is often highest for the youngest recruits (e.g. Hixon 1991), size and condition at settlement may be of immediate importance in avoiding selective predation. Although there is little empirical evidence for selective predation on very newly recruited fishes (Bertram & Leggett 1994, McCormick & Kerrigan 1996, but see Searcy & Sponaugle in press), size-selective predation has been detected among older juveniles (reviewed in Sogard 1997). In addition, size differences at settlement may be perpetuated into the juvenile period (Forrester 1990, Bertram 1996). This is potentially important for fishes with size-dominated social hierarchies, as size may determine competitive abilities in obtaining food,

space, and ultimately, reproductive success (e.g. Tupper & Boutilier 1995). Thus, either through selective mortality or influence on competitive abilities, traits at settlement may have a substantial impact on both newly recruited and older juveniles.

Variability in size, age, and growth rates of fish during the larval and juvenile periods may play an important role in population dynamics. Studies examining the range of natural variation in early life-history traits within and among cohorts should help identify traits upon which selection may act, as well as identify how such traits may be influenced by environmental factors. As part of a larger project, this study was designed to examine variation in a number of early life-history traits within and among seasonal cohorts of a common coral reef fish, the bluehead wrasse *Thalassoma bifasciatum*.

MATERIALS AND METHODS

Study site. Barbados is the easternmost island in the Lesser Antilles and is geographically isolated (140 km to the east of its nearest neighbor; see Fig. 1 of Sponaugle & Cowen 1996). The predominate current flows northwest at 0.35 to 0.55 m s⁻¹, and large-scale circulation appears to be topographically steered along the coasts before being recirculated and continuing downstream (Cowen & Castro 1994). As Barbados is upstream from other larval sources, it is generally believed that pelagic larvae spawned by island populations are retained in the vicinity of the island and recruit back to the local reefs (Cowen & Castro 1994, Sponaugle & Cowen 1996, Cowen et al. 2000).

Study species. *Thalassoma bifasciatum* the bluehead wrasse, is a common coral-reef fish found throughout the Caribbean. It is a sequential hermaphrodite (protogynous) and spawns daily (Warner & Robertson 1978, Robertson et al. 1999). The pelagic larval duration is variable (Victor 1986, Sponaugle & Cowen 1997) and settlement to the reef is pulsed (Sponaugle & Cowen 1997, Robertson et al. 1999). Larvae settle into the sand and undergo metamorphosis for 3 to 5 d (Victor 1982). After metamorphosis, recruits emerge from the sand and are found as solitary individuals swimming low in coral crevices (Sponaugle & Cowen 1997). As they age, individuals school in progressively larger groups higher in the water column (Sponaugle & Cowen 1997).

Collection methods. We collected juvenile fish in shallow water (1 to 6 m depth) on reef spurs along the western coast of Barbados. We collected cohorts of *Thalassoma bifasciatum* during May (Spring cohort), August/September (Fall 1 cohort), and September/October (Fall 2 cohort), evenly, offshore of Green-

sleeves, North Bellairs, the Bellairs Research Institute, and Batts Rock (equivalent to Site Nos. 2–3, 4, 6, 8 in Sponaugle & Cowen 1997). We collected juvenile fish as soon as they emerged from the sand and every other day over 2 wk using SCUBA, hand nets, and the anesthetic Quinaldine. We sampled on different areas of the reef (minimum of 25 m apart) so that previous collections would not bias later collections. After each sampling excursion, we brought the fish back to the laboratory, where they were immediately preserved in 95% ethanol.

Otolith analysis. Previous work has validated the daily nature of otolith increment deposition in *Thalassoma bifasciatum* (Victor 1982). Otoliths of *T. bifasciatum* have a clear mark corresponding to settlement of the larva onto the reef (validated for another common coral-reef wrasse, *Halichoeres bivittatus*: Victor 1983). This mark is followed by a wide, unreadable band (representing the period of time during which settlers are buried in the sand undergoing metamorphosis) that ends with an emergence mark, after which daily increment deposition is once again established (Victor 1983). The relationship between fish length and otolith length in *T. bifasciatum* is strongly correlated (Victor 1986, Masterson et al. 1997, Sponaugle & Cowen 1997, Searcy & Sponaugle in press). Despite this positive relationship, to avoid potential sources of error in back-calculating traits (Thorrold & Milicich 1990, Fowler & Short 1996), all comparisons of size and growth use otolith rather than derived somatic characteristics.

Prior to dissection, we recorded the standard length of each fish to the nearest 0.1 mm. Following otolith extraction, we placed fish in a drying oven at 60°C for 24 h. Upon removal, the dried fish were allowed to cool for 5 min and were weighed to the nearest 0.1 mg in a sealed Mettler balance. We dissected out 2 pairs of otoliths, the sagittae and lapilli, from each fish and placed them on microscope slides in medium-viscosity immersion oil for 30 d to allow clearing and to facilitate reading (Sponaugle & Cowen 1997). We read the sagittae using a Zeiss transmitted light microscope at 250 \times , with a rotating polarized filter placed between the light source and the first stage. The microscope image was captured with a frame-grabber and measurements were taken on a computer screen using the OPTIMAS image-analysis system (Version 6.1: OPTIMAS 1996). We analyzed all otoliths along their longest radius from the core to the outer edge, and for each increment in larval and juvenile period we recorded otolith length (radius). From this information we determined larval duration, width of the metamorphic band, juvenile age (post-emergence age), and increment width (proxy for daily growth) during the larval and juvenile periods. For larval duration measurements, we added 2 d to the total number of pre-settlement increments (reflecting a

standard time to hatching: Victor 1982, Sponaugle & Cowen 1997, Robertson et al. 1999).

Only 1 person read all otoliths. Before measurements were made, all abnormally shaped otoliths, pairs of unequally sized sagittae, and unclear (large portions with no discernable increments) otoliths were discarded (~15%). We made 2 independent measures of each otolith. If counts differed by <5%, then we randomly selected 1 of the readings. If increment counts differed by >5%, the otolith was read again. If the third count was within 5% of 1 of the former readings, then we randomly chose 1 of the 2 closest measurements for analysis. Alternatively, if the difference was still >5% of the previous readings, we discarded the otolith (~15%). To insure that individuals were from the same cohort while allowing a sufficiently high sample size, only fish that emerged during an 8 d window of recruitment were used in the analysis (total used in analysis, $n = 385$).

Data analysis. We divided each cohort into nearly equally sized groups based on pelagic larval duration (PLD) to determine the relationship between larval duration, growth trajectories, and size-at-age. Otolith length-at-age data were not normally distributed, so a natural log-transformation was applied to improve normality and homogeneity of variance (Sokal & Rohlf 1995). Because of the broad range in larval duration, we analyzed growth both progressively (post-hatch) and hindcast (back from settlement). Progressive larval growth trajectories revealed whether growth patterns diverged from an early age. Hindcast growth trajectories enabled the examination of temporal events that might have influenced the entire cohort.

We used a repeated-measures MANOVA (SYSTAT Version 5.1: Wilkinson 1992) for all comparisons of otolith growth and size-at-age among groups with different PLDs. We compared progressive larval growth and length-at-age among PLD groups using 5 d intervals. For example, to compare PLD groups of 35 versus 40 d, we compared otolith length on Days 5, 10, 15, 20, 25, 30, 35 and daily otolith growth averaged over the same 5 d intervals (Days 1–5, 6–10, 11–15, 16–20, 21–25, 26–30, and 31–35). All hindcast growth comparisons compared the 25 d prior to settlement using 5 d intervals, 0–5, 6–10, 11–15, 16–20, and 21–25 d prior to settlement. MANOVA techniques allow comparisons to be made at the resolution of an individual fish (Chambers & Miller 1995, Meekan & Fortier 1996). Comparisons were made between groups with the null hypothesis of no difference. The statistic used was Wilks' λ for the interaction term, which is based on sample size, number of groups in the comparison, and number of intervals being analyzed. When group differences were significant, canonical loadings revealed the relative importance of group differences at each interval by increasing in magnitude.

Thus, the interval with the highest canonical loading contributes the most to the rejection of the null hypothesis (Chambers & Miller 1995).

Finally, to determine whether post-settlement juvenile growth and length-at-age were similar within PLD subsets and among cohorts, we made comparisons among juveniles that had been on the reef for a minimum of 5 d (repeated-measures MANOVA). Similarly, we examined otolith length-at-settlement, width of the metamorphic band, and standard length and weight of <1 d old (post-emergence) fish to determine the influence of larval duration. Because all groups had unequal sizes, the T' method for unplanned comparisons among means was used (Sokal & Rohlf 1995: Biostat 3.1). We used a standard ANOVA where only 2 groups were compared.

RESULTS

Within-cohort comparisons

Larval traits

Each seasonal cohort exhibited a range of larval durations (Fig. 1). When larval duration was used to separate groups within each cohort, distinct patterns in otolith growth trajectories became evident. In all cohorts, otolith growth was faster in groups with shorter PLDs than those with longer PLDs (Fig. 2). This trend was significant for all groups in the 2 fall cohorts, but not significant among any groups in the spring cohort (repeated-measures MANOVA: Table 1). In both the Fall 2 and Spring cohorts,

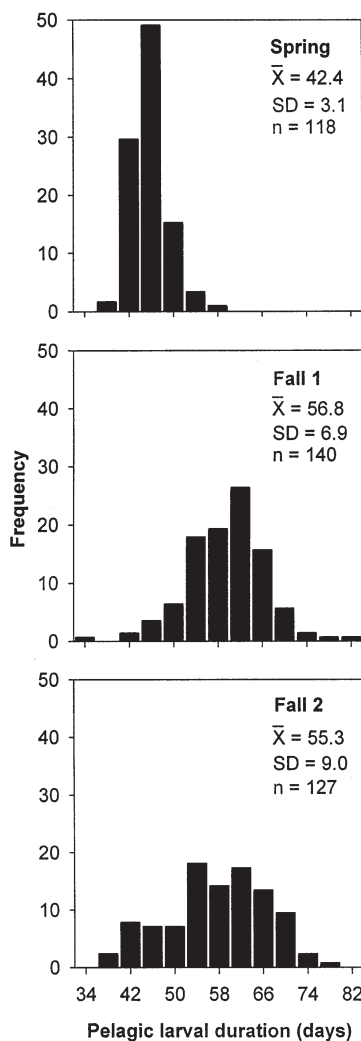


Fig. 1. *Thalassoma bifasciatum*. Frequency of pelagic larval duration (d) for 3 seasonal cohorts \bar{X} = mean, SD = standard deviation, n = sample size for each cohort

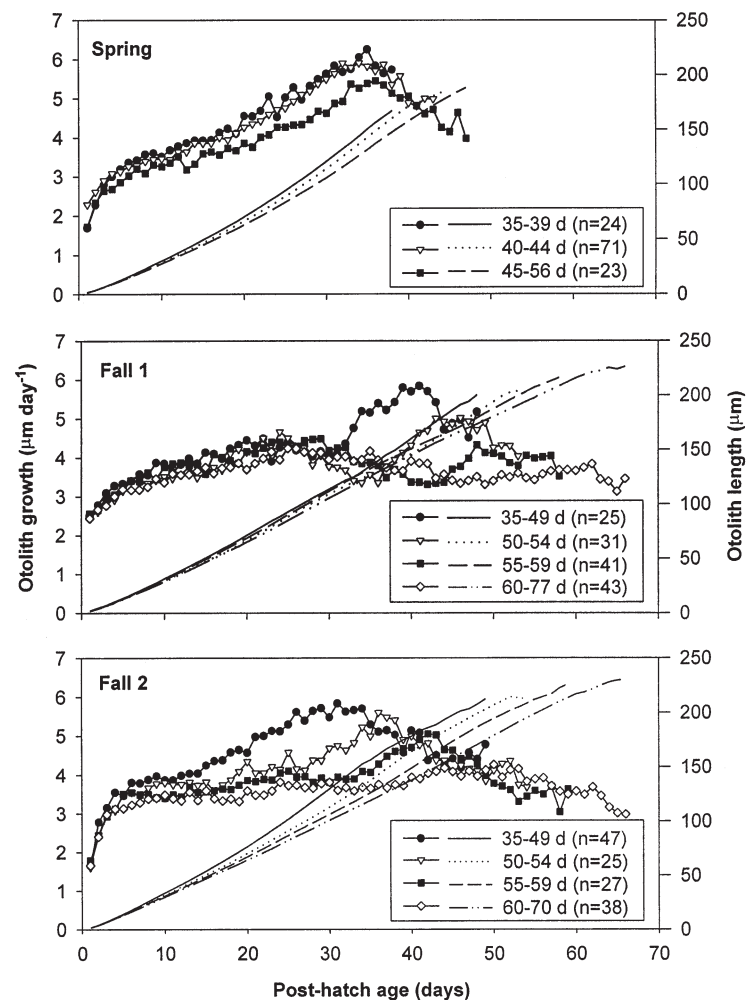


Fig. 2. *Thalassoma bifasciatum*. Mean progressive larval otolith growth rate (lines with symbols) and otolith length-at-age (continuous, dashed, and dotted lines) trajectories for 3 seasonal cohorts. Within each cohort, fish were divided into groups based on pelagic larval duration (PLD)

Table 1. *Thalassoma bifasciatum*. Within-cohort comparisons of early life-history traits between shorter (S) and longer (L) pelagic larval duration (PLD) groups using repeated-measures MANOVA and ANOVA (T' method: Sokal & Rohlf 1995). Where comparisons were significantly different, trend is indicated: $S > L$ = group with shorter PLD had larger value; $S < L$ = group with shorter PLD had smaller value; *, **, *** significant at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively; ns = non-significant at $p > 0.05$

Cohort	Comparisons		Repeated measures MANOVA			ANOVA (T' method)	
	Short PLD	Long PLD	Progressive larval otolith growth	Hindcast larval otolith growth	Larval otolith length-at-age	Otolith length-at-settlement	Otolith metamorphic band width
Spring	35–39 d	40–44 d	ns	$S > L^*$	ns	$S < L^{***}$	ns
		45–56 d	ns	$S > L^{***}$	ns	$S < L^{***}$	ns
	40–44 d	45–56 d	ns	$S > L^{***}$	ns	$S < L^{***}$	ns
Fall 1	35–49 d	50–54 d	$S > L^{***}$	ns	$S > L^*$	$S < L^{***}$	ns
		55–59 d	$S > L^{***}$	$S > L^{***}$	$S > L^{***}$	$S < L^{***}$	ns
		60–70 d	$S > L^{***}$	$S > L^{***}$	$S > L^{***}$	$S < L^{***}$	ns
	50–54 d	55–59 d	$S > L^{***}$	$S > L^*$	$S > L^{***}$	$S < L^{***}$	ns
		60–70 d	$S > L^{***}$	$S > L^{***}$	$S > L^{***}$	$S < L^{***}$	ns
		60–70 d	$S > L^{**}$	ns	$S > L^{**}$	$S < L^{***}$	ns
Fall 2	35–49 d	50–54 d	$S > L^{**}$	$S > L^{**}$	$S > L^*$	$S < L^{***}$	ns
		55–59 d	$S > L^{***}$	$S > L^{**}$	$S > L^{***}$	$S < L^{***}$	$S > L^*$
		60–70 d	$S > L^{***}$	$S > L^*$	$S > L^{***}$	$S < L^{***}$	$S > L^{**}$
	50–54 d	55–59 d	$S > L^{**}$	ns	$S > L^{***}$	$S < L^*$	$S > L^{**}$
		60–70 d	$S > L^{***}$	$S > L^*$	$S > L^{***}$	$S < L^{***}$	$S > L^{***}$
		60–70 d	$S > L^{**}$	$S > L^*$	$S > L^{***}$	$S < L^{***}$	ns

otolith growth trajectories were domed, and in general groups with shorter PLDs had faster otolith growth rates, starting at 5 to 10 d post-hatch and continuing throughout the remainder of the larval period (Fig. 2). Otolith growth trajectories of the Fall 1 cohort were more complex. Beginning around Days 5 to 15, otolith growth rates were faster for groups with shorter PLDs than those with longer PLDs, but this pattern then reversed during the middle 15 d of the period. Between Days 35 and 45, the initial pattern of higher growth for short PLD groups re-emerged (Fig. 2). All Fall 1 group comparisons exhibited this pattern, except for Groups 50 to 54 d versus 55 to 59 d, in which the shorter PLD group had initially slower otolith growth until ~25 d prior to settlement, when it exhibited faster otolith growth (canonical loadings).

Hindcast otolith growth rates among groups with differing PLDs exhibited a clear, consistent trend (Fig. 3). In general, groups with shorter PLDs grew significantly faster prior to settlement than groups with longer PLDs, and this difference was significant for all but 3 comparisons (repeated-measures MANOVA: Table 1). The dip in growth rates evident in the progressive trajectories in the Fall 1 cohort (Fig. 2) occurred at the same time for all fish in the cohort (~14 to 18 d pre-settlement: Fig. 3). In addition, this period of reduced otolith growth had the same duration (~15 d), and was of the same magnitude (lowest

otolith growth was ~3.5 mm d⁻¹) for all PLD groups. Furthermore, although progressive larval trajectories were not significantly different among PLD groups in the Spring cohort, hindcast trajectories were (Table 1). Fish with shorter PLDs were growing faster at the time of settlement.

We examined otolith length-at-age plots to see how differences in otolith growth related to length differences throughout the larval period. Similar to results for progressive larval growth, fish with shorter PLDs exhibited larger length-at-age. These trends were significant for all comparisons in both fall cohorts, but were not significant for any group comparisons in the spring cohort (repeated-measures MANOVA: Fig. 2; Table 1).

Settlement and metamorphosis

In all cohorts, average otolith length at settlement was smaller for groups with shorter larval durations (T' method: Tables 1 & 2). These otolith measurements were supported by somatic length measurements of fishes from both fall cohorts. Fish settling after shorter larval durations were smaller (smaller standard length and dry weight) at emergence (Table 3). In the metamorphic period, there was a consistent trend toward a narrower otolith metamorphic band in groups with longer PLDs (Table 2); however, this trend was signifi-

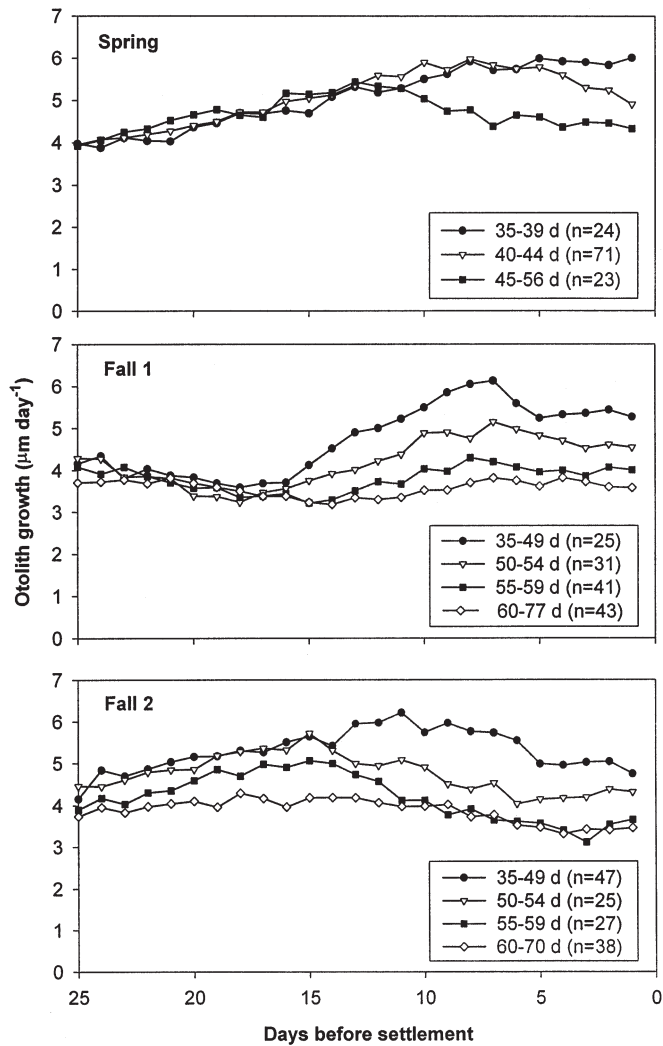


Fig. 3. *Thalassoma bifasciatum*. Mean hindcast larval otolith growth-rate trajectories for 3 seasonal cohorts. Within each cohort, fish were divided into groups based on PLD. Note that days are plotted prior to settlement (i.e. 5 = 5 d prior to settlement)

cant in only 4 PLD comparisons in the Fall 2 cohort (*T'* method: Table 1).

Juveniles

In all 3 cohorts there was no significant difference in juvenile otolith growth rates between groups with short and long larval durations (Fig. 4; repeated-measures MANOVA, $p > 0.05$). Despite this, the trend in juvenile otolith length-at-age was that fish with longer larval durations had larger otoliths at age in the early juvenile period (significant for both fall cohorts but not the spring cohort; repeated-measures MANOVA; Fig. 4).

Table 2. *Thalassoma bifasciatum*. Otolith length-at-settlement and width of otolith metamorphic band for 3 cohorts with different pelagic larval duration

Cohort, PLD group (d)	(n)	Otolith length-at-settlement (µm)			Otolith metamorphic band width (µm)		
		Mean	SD	Range	Mean	SD	Range
Spring							
35–39	(24)	169.0	8.7	150–186	29.5	3.4	23–36
40–44	(71)	181.0	7.8	163–197	28.8	4.8	15–42
45–56	(23)	188.5	11.9	163–214	27.9	4.0	21–37
Fall 1							
35–49	(25)	192.0	17.2	157–228	24.7	4.9	15–34
50–54	(31)	202.7	12.1	175–228	24.6	4.9	15–36
55–59	(41)	216.1	10.4	189–239	23.4	5.5	12–35
60–70	(43)	228.9	14.3	211–275	23.4	4.7	13–35
Fall 2							
35–44	(22)	185.2	11.7	167–204	22.0	3.3	16–30
45–54	(40)	212.5	10.5	186–236	22.7	4.2	13–32
55–59	(27)	219.4	11.6	196–244	19.7	4.2	13–30
60–70	(38)	230.9	13.0	209–268	18.7	4.2	9–27

Table 3. Mean standard length (SL) and dry weight (DW) for <1 d old recruits of *Thalassoma bifasciatum*. Comparisons were made between groups of short and long pelagic larval duration. ANOVA results: *,** significant at $p < 0.001$ and $p < 0.01$, respectively

Cohort, PLD group (d)	(n)	SL (mm)		DW (mg)	
		Mean	ANOVA	Mean	ANOVA
Fall 1					
34–59	(13)	11.5	**	4.7	*
60–69	(7)	12.2		5.5	
Fall 2					
34–55	(9)	11.21	*	4.7	*
58–69	(12)	11.7		5.5	

Among-cohort comparisons

Mean PLD for each cohort did not vary significantly between the 2 fall cohorts; however, the spring cohort spent a significantly shorter period in the plankton than either fall cohort (*T'* method, $p < 0.05$; Fig. 1). There is no consistent pattern (shape) in the mean progressive growth trajectories. The Fall 1 cohort had a sinusoidal growth trajectory, while the Fall 2 and Spring cohorts had a more sigmoidal (domed) shape (Fig. 5). Progressive larval growth trajectories for all 3 cohorts were significantly different from each other (repeated-measures MANOVA, $p < 0.001$). Canonical loadings indicated that the main difference in progressive otolith growth occurred between Days 25 and 40, with the Spring cohort exhibiting the highest growth and the Fall 1 cohort exhibiting the slowest growth during this period. Larval otolith length-at-age, following

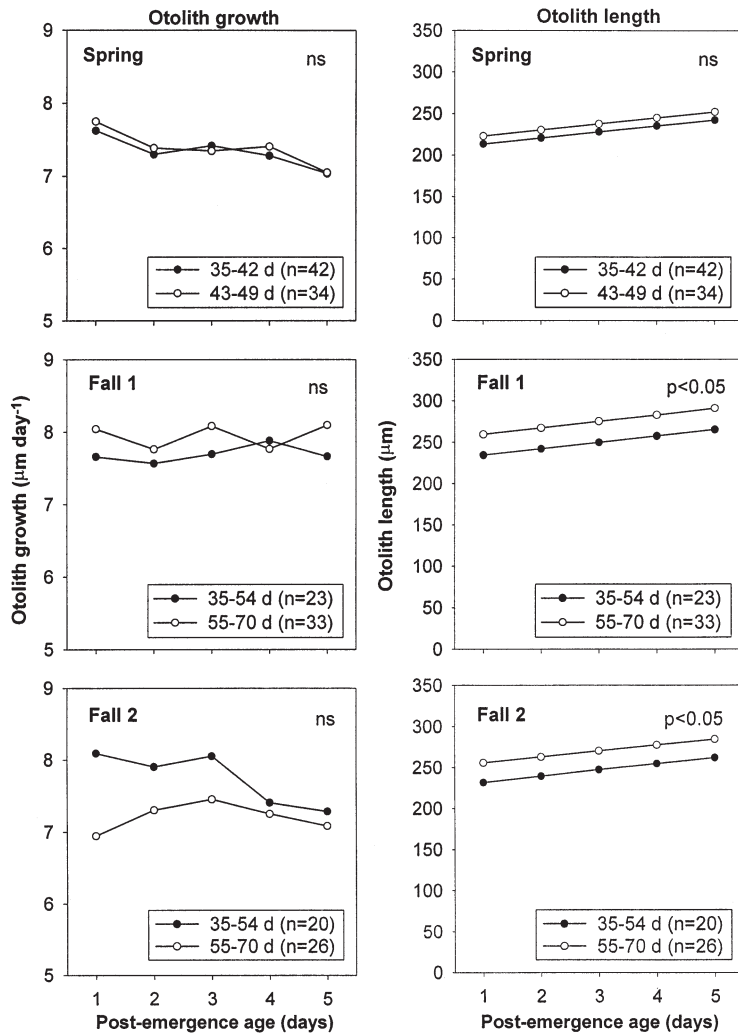


Fig. 4. *Thalassoma bifasciatum*. Mean juvenile otolith growth rate (left panels), and juvenile otolith length-at-age (right panels) for 3 seasonal cohorts. Each plot is based on 2 groups of shorter and longer PLD within each cohort. Results are repeated-measures MANOVA. ns = non-significant at $p > 0.05$

trends in growth, was also significantly different among all cohorts (repeated measures MANOVA, $p < 0.001$; Fig. 5). Similar to progressive trajectories, hindcast larval growth trajectories differed significantly among cohorts (repeated-measures MANOVA, $p < 0.001$; Fig. 5). The Spring cohort exhibited the fastest growth for 15 d prior to settlement and the Fall 1 cohort had the slowest growth as is evident in the a dip in growth between 10 and 25 d before settlement (canonical loadings; Fig. 5).

Daily juvenile otolith growth for the initial 7 d after emergence did not differ significantly among the 3 seasonal cohorts (repeated-measures MANOVA, $p > 0.05$; Fig. 6). Juvenile otolith length-at-age, however, was smaller for the spring cohort as a result of smaller otolith sizes at settlement (repeated-measures MANOVA, $p < 0.01$; Fig. 6).

DISCUSSION

Larval growth

The variability of early life-history traits (e.g. pelagic larval duration, growth rates, and size-at-age) for *Thalassoma bifasciatum* within the larval phase reveal that this is a dynamic period. Within each cohort, *T. bifasciatum* with shorter larval durations had faster otolith growth than individuals with relatively longer larval durations. While laboratory experiments may be necessary to disentangle endogenous and exogenous controls of growth (Conover & Schultz 1997), analysis of available factors can shed light on the most likely proximate causes. Among potential exogenous factors, temperature is unlikely to have contributed significantly to the observed differences in growth rates, as water temperatures were relatively similar during the larval period of each cohort: Spring, 27.0 to 27.4°C; Fall 1, 27.3 to 28.1°C; Fall 2, 27.4 to 28.4°C (data from moored CT sensors at 10 m depth, 2 km offshore of the west coast of Barbados; P. S. Kelly & K. M. M. Lwiza unpubl. data). Furthermore, contrary to what might be expected in colder temperatures, the spring cohort exhibited the fastest overall growth.

Of greater potential influence is variation in food availability. Previous studies have demonstrated increased otolith growth for larvae in areas of elevated food abundance (e.g. Hovenkamp & Witte 1991, Molony & Sheaves 1998). In addition, otolith growth of populations of juvenile *Thalassoma bifasciatum* was shown to increase when food levels were supplemented (Victor 1982). We suggest that the observed differences in otolith growth rates among individual *T. bifasciatum* larvae are due to variability in food abundance. Food concentrations may vary on the scale of individuals or patches of individuals as well as on the order of entire cohorts, and may result from 2 non-exclusive processes. A gradient of decreasing food concentrations may extend offshore of Barbados, whereby nearshore coastal waters are enriched relative to offshore waters (island mass effect: Sander 1981, Hernandez-Leon 1991). This onshore-offshore gradient would result in nearshore larvae with faster growth rates and offshore larvae with relatively depressed growth rates due to lower food concentrations. Alternatively, through hydrodynamic control, the distribution of food may be patchy throughout the

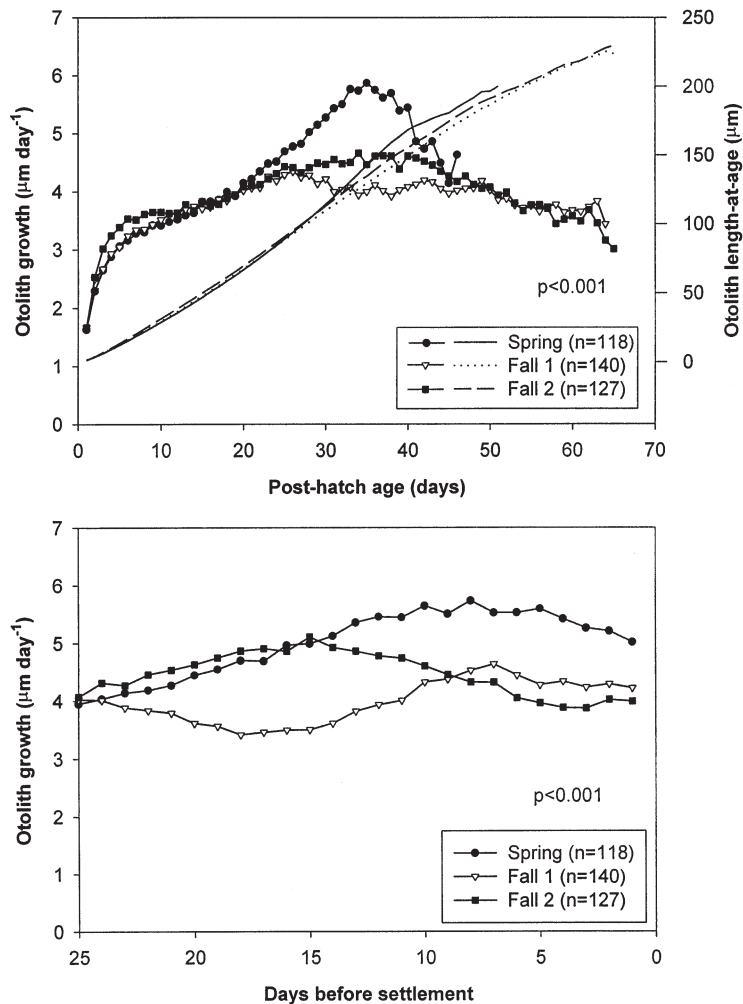


Fig. 5. *Thalassoma bifasciatum*. Upper panel is mean progressive larval otolith growth-rate trajectories (lines with symbols) and larval otolith length-at-age (continuous, dashed, and dotted lines) for 3 seasonal cohorts. Lower panel is mean hindcast larval otolith growth-rate trajectories. All among-cohort comparisons of trajectories were significantly different at $p < 0.001$; repeated-measures MANOVA

nearshore and offshore environment (e.g. concentrated at convergence zones: Kingsford 1990, Boehlert & Mundy 1993). As a result, relatively faster growth may occur in larvae that spend proportionally more time in food patches. The stability of these features, food concentration, as well as the proportion of time larvae are retained within them probably vary, producing a range of larval growth rates.

Variable growth rates versus delayed metamorphosis

The variability in larval durations observed for *Thalassoma bifasciatum* in this study is similar to that

reported in other studies (Table 4). Extreme differences in PLD may reflect the capacity of individuals to delay settlement and metamorphosis until certain criteria are met. In such cases, larvae typically grow at similar rates until they are competent to settle, at which time the majority settle and undergo metamorphosis. A minority that are unable to settle at that time experience reduced growth until settlement is possible (e.g. Victor 1986, Cowen 1991, Jenkins & May 1994). For example, Victor (1986) demonstrated that *T. bifasciatum* larvae with relatively long larval durations (~75 d) recruiting to Panama had a sharp decline in otolith growth rates prior to settlement. Recently, Robertson et al. (1999) observed that *T. bifasciatum* recruiting to Panama varied in PLD, depending on the period of the lunar cycle in which they were spawned, such that settlement is concentrated around the new moon. They suggested that variable larval duration provides greater flexibility in synchronizing settlement, as previously proposed for a tropical goby (*Gnatholepis thompsoni*: Sponaugle & Cowen 1994).

The results of the Spring of the current study suggest that the observed variation in PLD is not simply the result of delayed metamorphosis. Although the ranges of PLDs exhibited by *Thalassoma bifasciatum* in the current study are typical (see Table 4), none of the individuals examined exhibited a characteristic 'delayer' otolith growth trajectory (sensu Victor 1986). Larval duration appears to be the result of growth rates that vary from the time of hatching.

The relative importance of classic delayers to recruitment dynamics likely varies with geographic and hydrographic settings. The paucity of delayers recruiting to Barbados suggests that periodic physical mechanisms (e.g. tidally mediated flows and features: Kingsford 1990, Sponaugle & Cowen 1997, Leichter et al. 1998), retention mechanisms (e.g. Cowen & Castro 1994), or perhaps the swimming ability of late-stage larvae (Leis et al. 1996, Stobutzki & Bellwood 1997) insure successful return to the reef. Most workers who have found delayed metamorphosis to be common have collected fish far from their spawning grounds (Cowen 1991, Jenkins & May 1994, Fowler & Short 1996, but see Victor 1986). However, Barbados is upstream from other sources of larvae and thus recruits are likely to be spawned locally and retained within the vicinity of the island until set-

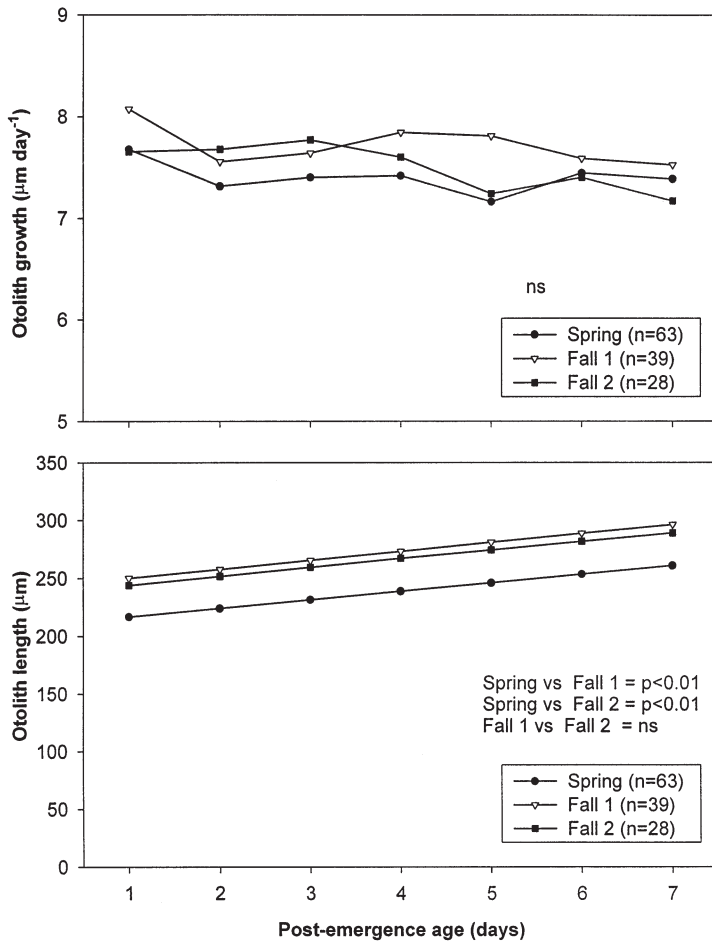


Fig. 6. *Thalassoma bifasciatum*. Mean juvenile otolith growth rate (upper panel) and juvenile otolith length-at-age (lower panel) for the 3 seasonal cohorts. Results are repeated-measures MANOVA for among-cohort comparisons. ns = non-significant at $p > 0.05$

tlement (Cowen & Castro 1994, Sponaugle & Cowen 1996, Cowen et al. 2000), or transported downstream and lost from the system.

Competency

The exact determination of when competency to settle is reached may be difficult to judge, as no 1 factor has been conclusively linked to its attainment. Invertebrates have been shown to reach competency according to behavior, size, morphological characteristics, or a minimum age (reviewed in Pechenik 1990). Similarly, competence in demersal fishes has also been defined based on median age, minimum weight, length, or according to a sharp reduction in otolith growth rates (reviewed in McCormick 1999). Implicit in these definitions is that competency is also related to developmental state. Recent physiological work has shown

that sensory development (eye, lateral line, nares) of *Thalassoma bifasciatum* at settlement is relatively invariant (Lara 1999). Thus, *T. bifasciatum* settles at a range of ages and sizes, yet at a similar developmental state. To account for this, development must be decoupled from growth rates (e.g. Gadomski & Caddell 1991, McCormick 1993), or arrested at a certain point. No doubt several criteria must be met for settlement to occur, but we suggest that final competency is linked not only to developmental level but also to condition.

Energy is lost, not gained, during metamorphosis (e.g. Balon 1985); therefore, only fishes with sufficiently high energy stores will successfully complete this energetically costly process. This is particularly critical for *Thalassoma bifasciatum*, which undergoes a protracted period of metamorphosis during which no feeding occurs (Searcy & Sponaugle in press). The need for nutritional reserves to undergo metamorphosis has been shown in a variety of marine invertebrates (e.g. Pechenik 1990, Pechenik et al. 1993). An increase in fat content just prior to metamorphosis and rapid depletion of lipids during metamorphosis has also been confirmed for multiple fish species (Potter et al. 1978, Pfeiler & Luna 1984, Nursall 1989). In addition, studies of temperate species have shown that critical developmental stages such as sexual maturation is suppressed until a minimum condition level is met (Rowe et al. 1990, Montgomery & Galzin 1993), and this may also be true of metamorphosis.

In the current study, a minimum condition level for settlement could explain the observed difference in length at settlement between slower and faster growers. Previous work on a variety of species has shown that larvae with faster otolith growth have a higher condition than larvae with slower otolith growth (reviewed by Suthers 1998). Therefore, slow-growing larvae may need to remain in the plankton longer (and thus attain larger sizes) to obtain sufficient energy stores for metamorphosis.

Although we have no direct measure of condition at settlement, we believe that condition is reflected in certain otolith characteristics. Molony & Sheaves (1998) suggested that the rate of the otolith growth-response to food deprivation may be influenced by lipid concentration, where decreased otolith growth is most likely to occur in fishes with low energy stores. Metamorphosis in *Thalassoma bifasciatum* is generally considered a period of food deprivation (starvation

Table 4. *Thalassoma bifasciatum*. Summary of published values of pelagic larval duration (PLD; in d). CV = coefficient of variation; ? = published value not given; values in parentheses are interpreted from authors' published data (Caselle 1997, Fig. 2; Robertson et al. 1999, Fig. 13); Masterson et al. (1997) report PLD range for all 3 cohorts collected and PLD estimate is obtained from lapilli rather than sagittae (sagittae used in other studies listed). Lapillae readings may (Victor 1982, Robertson et al. 1999) or may not (Schultz & Cowen 1991; 3 d difference) be similar to sagittae readings

Location, season	Year	(n)	PLD (d)		CV	Source
			Mean	Range		
Barbados						
Spring	1997	(140)	42.4	37–58	7.4	Current study
Fall	1997	(127)	56.8	34–79	12.2	Current study
Fall	1997	(118)	55.3	36–78	16.3	Current study
Spring	1992	(37)	49.2	41–66	10.4	Sponaugle & Cowen (1997)
Spring	1991	(26)	53.2	41–94	25.2	Sponaugle & Cowen (1997)
Spring	1990	(32)	49.0	38–64	12.7	Sponaugle & Cowen (1997)
St. Croix						
Summer	1993	(130)	37		16.2	Masterson et al. (1997)
Summer	1992	(157)	40	29–63	15	Masterson et al. (1997)
Summer	1991	(88)	41		12.2	Masterson et al. (1997)
Summer	1992	(286)	45.8	35–61	(9.9)	Caselle (1997)
Summer	1992	(20)	51.4	41–74	15.5	Sponaugle (1994)
Spring	1991	(22)	40.2	35–50	8.3	Sponaugle (1994)
St. Lucia						
Spring	1992	(31)	45.6	37–63	9.8	Sponaugle (1994)
Spring	1991	(28)	41	34–53	10.7	Sponaugle (1994)
Panama						
	1985–1987	(776)	(44.7)	29–67	(12.6)	Robertson et al. (1999)
	1981–1983	(1172)	49.3	38–78	11.2	Victor (1986)
Bermuda						
Fall	1991	(47)	55	?	18.9	Schultz & Cowen (1994)

event) during which somatic growth is negligible. We propose that otolith accretion in the metamorphic band is likely to reflect condition at settlement, such that individuals with wider metamorphic bands (more rapid accretion of material) have a higher condition at settlement (Searcy & Sponaugle in press). Furthermore, for both *T. bifasciatum* and another wrasse, *Halichoeres bivittatus*, individuals with wider metamorphic bands preferentially survived the early juvenile period (Searcy & Sponaugle in press), indicating that traits expressed during metamorphosis (i.e. condition) are critical in determining early juvenile mortality.

While a minimum condition level may be necessary for *Thalassoma bifasciatum* larvae to complete metamorphosis, a range in condition probably exists above this minimum that is independent of larval duration. The 3 cohorts examined exhibited an overall tendency for fish with shorter PLDs to have wider metamorphic bands; however, variation within each of these PLD groups encompassed the entire range observed for the cohort. Furthermore, Searcy & Sponaugle (in press) demonstrated that selective mortality on the width of the metamorphic band for *T. bifasciatum* was independent of larval duration. These results suggest that the width of the metamorphic band, or condition at settlement, is largely independent of age or size, as has been con-

cluded for different species in several previous studies (McCormick & Molony 1993, 1995, Kerrigan 1996).

Influence of larval traits on juveniles

Variability in early life-history traits at settlement did not appear to affect juvenile growth rates; consequently, size differences at settlement were propagated (and did not diverge or converge significantly) 5 d into the juvenile stage. Regardless of larval growth history, seasonal cohorts as well as all intra-cohort PLD groups exhibited similar juvenile growth rates. In a laboratory study of winter flounder *Pseudopleuronectes americanus*, Chambers et al. (1988) found that size advantages gained from the larval stage were perpetuated into the juvenile period. In contrast, Bertram et al. (1993, 1997) demonstrated that size differences at settlement for the same species were compensated for by juvenile growth rates. As adult *Thalassoma bifasciatum* exist in large conspecific groups, if size differences at settlement are maintained with age, then they may confer advantages in competing for resources such as food and mates (e.g. McCormick & Kerrigan 1996). Further, the fact that size differences from the larval phase were maintained during the first 5 d of the

juvenile period is interesting because post-settlement mortality rates (e.g. Victor 1986, Hixon 1991, Caselle 1999) and selective mortality are highest during the first few days on the reef (Searcy & Sponaugle in press). Relatively constant juvenile growth rates among individuals with different pelagic (larval) histories indicate that at least initially the reef environment (with regard to food availability for young fishes) is stable, or that selective pressures favor less variable growth regardless of what occurs in the pelagic environment.

Among-cohort variation in early life-history traits

The difference in the range of PLD between the fall and spring cohorts in the current study may have been due to cohort specific processes rather than seasonal features. Previous spring cohorts collected at Barbados in 1990, 1991, and 1992 (Table 4: Sponaugle & Cowen 1997 data) had mean PLDs that more nearly resembled the fall cohorts in the current study. The high larval growth rates exhibited by the spring cohort may have been caused by relatively high planktivorous food concentrations, or if slower growers are dispersed farther offshore, then perhaps the loss of these individuals from the recruiting cohort (breakdown in offshore-retention system).

The role of episodic events in influencing cohort characteristics is also suggested by contrasting larval growth trajectories. The large dip in growth rates midway through the larval period of the Fall 1 cohort occurred during the presence of a low-salinity eddy that passed Barbados just prior to the observed period of reduced growth (Kelly et al. 2000). We suggest that this eddy contained lower densities of prey organisms, which reduced the feeding success of larval fishes. Thus, on a small temporal scale, hydrodynamic features may significantly influence larval traits.

Oceanographic features may also help explain geographical differences in larval characteristics such as PLD (see Table 4). Although there is much spatial and temporal overlap in *Thalassoma bifasciatum* PLD, general trends between the longer time series from Barbados and St. Croix tentatively suggest that the 2 sites have distinctly different hydrodynamic regimes from each other (*T. bifasciatum* from St. Croix tend to have a shorter PLD). Physical transport processes (i.e. shorter period of a recirculating mechanism) as well as relatively constant local environmental conditions influencing growth (food or temperature) may be the basis for the observed shorter PLD in St. Croix. Overall, the fluctuations in PLD within each of the time series highlight the role of episodic events in influencing characteristics of individual cohorts, and caution against comparisons based on collections of only a few

cohorts. Clearly, conclusions as to a genetic basis for the observed differences cannot be made unless the pelagic environment is first taken into consideration.

The variable nature of growth rates and thus the PLD of fishes such as *Thalassoma bifasciatum* is probably a response to a range of planktonic food availability. For pelagic spawners with moderately long PLD (such as *T. bifasciatum*), larval growth plasticity would be advantageous since the odds of encountering low food conditions (by being transported offshore or encountering low food patches) are high. On the other hand, for certain species with relatively short, invariant larval durations (e.g. damselfish: Wellington & Victor 1989) fast growth may be coupled to a strategy of remaining in high food areas and/or maximizing retention near the adult habitat (e.g. Leis 1991, Cowen & Castro 1994). If these larvae are then transported out of nearshore or food-rich areas, or if productivity drops, their high physiological demands may be compromised, resulting in greatly reduced survival. In short, particular taxa (such as *T. bifasciatum*) appear to have the physiological ability to tolerate low growth rates while others do not. This dichotomy is evident in recent work that has shown that new recruits of another wrasse, *Halichoeres bivittatus*, with a relatively short and invariant larval duration (mean PLD 22 d \pm 1 SD) exhibit strong selection for faster larval growth, whereas *T. bifasciatum* does not (Searcy & Sponaugle in press). The fact that *T. bifasciatum* larvae are able to recruit successfully over a wide range of larval durations (within each cohort) as well as atypical growth patterns (i.e. Fall 1 cohort) stresses the potential ecological advantage and evolutionary importance of plastic growth and flexible larval durations.

A further implication of flexible larval growth schedules is the degree to which distant populations are ecologically connected. While physical diffusion and natural mortality combine to make long-distant transport unlikely (Cowen et al. 2000), the ability of larvae to survive long periods of low growth (i.e. in oligotrophic open-ocean waters) will clearly impact transport success. Significant population replenishment from distant locations would be more likely for species with larvae that are able to tolerate slow growth for extended periods of time.

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