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Larval history influences post-metamorphic condition in a coral-reef fish

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Abstract Upon settlement, many fishes undergo an energetically costly metamorphic period that requires substantial nutritional reserves. Larval growth and the accumulation of lipids prior to metamorphosis are likely to influence growth and survival following this critical period. On the Caribbean island of St. Croix, I investigated relationships between larval growth, early life-history characteristics, and post-metamorphic lipid content in the bluehead wrasse *Thalassoma bifasciatum*. Lipid reserves remaining after metamorphosis were positively related ($r^2 = 0.62$) to the width of the metamorphic band; thus, this otolith-derived trait may be used to estimate the condition at emergence of survivors collected at some later time. In contrast, pelagic larval duration, average larval growth, and otolith size at settlement were negatively related to post-metamorphic lipid content. Interestingly, the trend for slower growth among fish in good condition was not consistent over the entire pelagic larval duration. Analyses of daily larval growth histories indicated that fish with high lipid reserves grew rapidly in the last week prior to settlement, but relatively slowly during the early phases of larval life; those emerging with low lipid concentrations, however, displayed strikingly opposite patterns. These contrasting patterns of growth and energy storage were consistent at two sites and over three recruitment events. Otolith chemistry data suggested that differences in growth histories and body condition were consistent with the hypothesis of larval development in distinct oceanic environments (characterized by Pb concentration); but, within a water mass, differences reflected life-history trade-offs between growth and energy storage. The results have implications for understanding the processes driving juvenile survival, which may be condition dependent.

Keywords Condition at settlement · Early life-history traits · Growth-storage tradeoff · Larval–juvenile transition · Otolith chemistry

Introduction

For organisms with complex life histories (e.g., plants, insects, aquatic invertebrates, fishes, amphibians; Wilbur 1980), environmentally mediated performance in one habitat may carry over to affect individual quality at metamorphosis and ensuing performance in a second habitat following that life-history transition (Pechenik et al. 1998). The transition between developmental stages is often rapid and involves physiological, morphological, and behavioral changes that can occur as individuals adapt to a new environment (Wilbur 1980; McCormick et al. 2002). These modifications are energetically costly and initiate a new suite of challenges for developing organisms, which may affect fitness. For example, the size attained at the time of metamorphosis has been documented to influence fecundity and lifetime reproductive success in a stonefly (Taylor et al.

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1998). Many marine organisms provide an ideal system to examine life-history transitions because the habitats occupied by the two stages are quite distinct, accentuating the differences between them: a dispersive larval stage that develops in the pelagic zone and a fairly sedentary nearshore adult stage that follows settlement and metamorphosis.

For those larvae that do survive to the end of the larval period and reach suitable benthic habitat, most suffer high losses immediately following settlement (Caselle 1999; Almany and Webster 2006), and only a small fraction survive to sexual maturity (Jones 1990). Because mortality and selective forces are so intense during the larval phase and the first few days of post-settlement life, metamorphosis (which often occurs between these two stages) is a critical period during development and may represent a mortality bottleneck that shapes population dynamics. The importance of larval experiences in determining growth rates and the size and quality of individuals reaching metamorphosis has been demonstrated for terrestrial insects (Bradshaw and Johnson 1995) and amphibians (Berven 1990; Alvarez and Nicieza 2002), in addition to aquatic invertebrates (Phillips 2002; Wacker and von Elert 2002). Recently, for a number of tropical and temperate fishes, researchers have shown that specific events during the larval phase can have profound impact on the numbers of successful individuals reaching the juvenile stage (Campana 1996; Bergenius et al 2002; Jenkins and King 2006) and their performance in the adult environment (Searcy and Sponaugle 2001; Vigliola and Meekan 2002).

For marine species, mortality is extremely high during the larval period and most larvae are thought to starve or be killed by predators (Leggett and DeBlois 1994). Planktonic losses are not entirely unpredictable: favorable environmental conditions appear to influence resource availability, which has been linked to higher larval growth rates and improved year-class strength for some fish populations (Campana 1996). Because the pelagic environment is highly variable in space and through time, and it is the rare larva that survives in this unpredictable environment, different strategies and traits may be favorable for survival in different situations. Oceanographic circulation features (Sponaugle and Pinkard 2004) and flow disturbances (Suthers 1996; Munk 2007) may create spatial differences in prey abundance, which predictably influence growth rates and energy reserves. The consumption of available resources determines growth and developmental rates, so larvae that develop in different places (e.g., nearshore versus offshore) may settle with different environmentally determined traits and performance histories. When prey are limited or patchy in nature, important tradeoffs may determine how those resources are utilized for growth, development, maintenance, and storage.

An important tradeoff occurs between growth and storage. With a fixed amount of energy, individuals can either allocate that energy immediately toward skeletal growth or store it for potential harsh future conditions when resources are scarce (Metcalfe et al. 2002). Although a rapid growth rate and attainment of a large size may be beneficial for reducing predation, in a patchy food environment allocating ingested energy purely for growth may leave individuals more vulnerable to mortality in times of food shortage. A strategy of rapid growth may not necessarily be adaptive and beneficial to survival in all instances (Munch and Conover 2003; Gagliano et al. 2007). Survival, then, is likely a balance between utilizing energy to grow rapidly out of vulnerable sizes, while allocating sufficient energy for other demands.

Recent feeding success or starvation may affect an individual's susceptibility to mortality at a given point in time regardless of its past growth history. In both natural field settings and under experimental manipulations of food, researchers have detected positive relationships between recent growth and biochemical measures of condition (the ratio of RNA:DNA, Suthers 1996; lipid content, Molony and Sheaves 1998). Differences in physiological condition have been found to influence selective mortality at important transitional stages throughout the life cycle, especially at energetically costly transitions (Phillips 2002; Hoey and McCormick 2004). The requirement of nutritional reserves to undergo metamorphosis has been confirmed in a variety of marine invertebrates (Pechenik 1990) and some species of fish have been shown to deplete up to 50% of their lipid stores during this transition (Pfeiler and Luna 1984; Youson 1988; Hossain et al. 2003). As a consequence, individuals in substandard condition, or those that exhibit rapid growth with little storage, may be more vulnerable to predation immediately following the metamorphic period.

For the bluehead wrasse, *Thalassoma bifasciatum*, a common tropical reef fish in the Caribbean, Searcy and Sponaugle (2000) suggested that the width of the metamorphic band (MB) on the otolith reflected information about condition and it has since been shown to correlate strongly with survival (Searcy and Sponaugle 2001; Sponaugle and Grorud-Colvert 2006; Hamilton et al. 2008). However, no direct links have been established between the width of the MB and any biochemical measure of condition; thus, this hypothesis remains untested. This study was initiated to examine relationships between early life-history traits (e.g., larval duration, size, growth rate) and post-metamorphic condition of bluehead wrasse. Because it is presumed that lipids integrate feeding history over approximately 1 week (Ferron and Leggett 1994) and previous evidence supports selection in favor of wide MBs (Searcy and Sponaugle 2001), I hypothesized that fish with extensive post-metamorphic lipid reserves would have wide MBs and relatively fast growth in the days or weeks prior to settlement. Finally, due to extensive phenotypic variation in early life-history traits, which appears to be environmentally mediated (Sponaugle and Pinkard 2004; Sponaugle et al. 2006) and influenced by dispersal history (Swearer et al. 1999; Hamilton et al. 2008), I asked whether relationships between growth histories and condition were consistent across space and through time and could be explained by differences in performance within distinct oceanic environments.

Methods

Study system and species background

St. Croix, US Virgin Islands (17°45′N, 64°45′W), is a sedimentary island in the northeast Caribbean Sea (Fig. S1), which is isolated by more than 40 km from the nearest populations of reef fish and circled by shallow pavement and barrier reefs. The bluehead wrasse, *Thalassoma bifasciatum*, is a sex-changing labrid common on shallow reefs in St. Croix and throughout the Caribbean. Individuals spawn daily throughout the year and settle after spending an average of 45 days in the plankton, although the larval duration is quite variable (range: 35–70 days, Victor 1986; Caselle and Warner 1996; Sponaugle and Cowen 1997). On St. Croix, settlement is broadly lunar cyclic, with peak intensity around the new moon (Caselle and Warner 1996). Following settlement, individuals undergo a 3- to 5-day metamorphic period while buried in the sand or sequestered in reef crevices prior to emerging (Victor 1982). New recruits prefer benthic, low-relief rubble or coral crevices, although juveniles and adults (>25 mm standard length, SL) are highly mobile and shoal in the water column. Mortality is intense during the first month of life on the reef (Victor 1986) and strongest and often density dependent during the first 48 h post-emergence (Caselle 1999).

Study sites and collections

Newly emerged bluehead wrasse were collected haphazardly using aquarium dipnets from shallow (7–10 m depth) pavement reefs at Butler Bay (17°46′17″N, 64°52′46″W) on the northwest corner of St. Croix and Jacks Bay (17°45′00″N, 64°35′05″W) on the southeast side of the island (Fig. S1), during the June, July, and August recruitment pulses of 2001. Butler Bay (BB) and Jacks Bay (JB) were chosen as study sites because they consistently receive abundant levels of recruitment and because these sites were the focus of a larger study. I targeted newly emerged fish by alternating collections every other day at each site over a 10-day period, beginning on the new moon (peak of settlement lagged by 5-day metamorphic period). Recruits were measured to the nearest 0.1 mm SL and immediately frozen in liquid nitrogen for later lipid analyses. Samples were later transferred to a −80°C freezer for storage.

Early life-history traits, larval growth, and condition measurements

I examined relationships among several early life-history traits recorded in fish otoliths including: pelagic larval duration (PLD, days); pre-settlement growth rate (average larval otolith growth, µm day^{-1}); larval growth history (trajectories of daily otolith increment formation, µm); otolith radius at settlement (a proxy for size at settlement, µm); and width of the MB (µm). A random subsample of 268 ‘likely’ recent settlers (based on size and pigmentation) were chosen from the new recruit collections to assess early life-history traits, and their otoliths were removed and cleaned of adhering tissue. Prior to enumerating ages and examining growth histories, I placed the right sagittal otoliths of each individual into medium-viscosity immersion oil for a minimum of 30 days to enhance ring clarity. Otolith measurements were made along the longest axis of the otolith in the sagittal plane, from the core to the outer-most complete ring, using a compound microscope at 400× with polarized transmitted light and attached to an image analysis system (ImagePro 4.5). Otolith increment width was used as a proxy for somatic growth. As in previous studies (Victor 1986; Sponaugle and Cowen 1997), I documented a positive linear relationship between otolith radius and standard length for *T. bifasciatum* in St. Croix (range: 9.9–33.5 mm SL, $n = 219$, $r^2 = 0.98$). Furthermore, the formation of daily otolith increments has been validated for this species (Victor 1982). A conspicuous settlement mark, formed during metamorphosis (Victor 1983), was used as a reference point for the division between larval and post-settlement increments (i.e., the MB).

Of the 268 recent settlers, I chose 58 random fish from BB and JB that settled during the June, July, and August cohorts to examine relationships between early life-history traits and post-metamorphic condition. The total lipid content of each fish was determined gravimetrically using chloroform–methanol extraction following modifications of the methods of Bligh and Dyer (1959) and Mann and Gallager (1985). Fish were freeze-dried and weighed to the nearest 0.1 mg, then homogenized in 0.5 ml of distilled water. Individuals were further homogenized by means of sonication for 90 s in an additional 1 ml of distilled water (1.5 ml total). I extracted lipids from duplicate 500-µl aliquots of each sample of homogenate. Aliquots of solvent extract (chloroform layer containing lipids) were dried to a constant weight at 60°C and weighed to the nearest 0.01 mg on a Cahn C-33 microbalance. The mean of the duplicates was expressed as total lipid in mg g^{-1} dry weight. The coefficient of variation between duplicates was 5.5% for all samples, but showed considerable variation (range: 134.8–405.4 mg g^{-1}, $n = 58$, CV = 30.7%) among samples.

Otolith elemental analyses to determine larval water mass residence

Larvae developing in chemically distinct water masses may be exposed to environmental conditions (recorded in the otolith) that differentially affect their performance. To analyze the chemical composition of the larval portion of the otolith, the left sagittae (stored dry) of each fish was polished to expose the inner growth layers. Following a series of cleaning steps, I used a Finnegan MAT Element 2 sector field ICP-MS and a VG-UV microprobe Nd:YAG 266 nm laser ablation system to analyze the chemical composition of *T. bifasciatum* otoliths (see Hamilton et al. 2008 for instrument and analytical details). Of the 268 recent settlers whose otoliths were measured for early life-history traits (see previous section), 221 individuals from the June, July, and August cohorts had otoliths suitable for microchemical analysis (the drop in sample size resulted from lost or cracked otoliths and occasional mistakes of polishing through the otolith core). Lipid analyses (see previous section) were performed on a subsample of 58 of these 221 fish.

To provide information on the chemical history of individuals throughout their larval phase, I ablated and analyzed the elemental composition of individual pits along a transect stretching from the core to the edge of the otolith (along the longest axis). For each fish, 6–9 pits were ablated and each pit was categorized into one of five developmental periods based on the fraction of PLD elapsed (for details see Hamilton et al. 2008; Table S1). In each sample pit, I collected counts for the isotopes ^{24}Mg, ^{48}Ca, ^{55}Mn, ^{88}Sr, ^{138}Ba, and ^{208}Pb. Molar ratios of analyte to Ca were calculated using the ratio of each isotope to ^{48}Ca and an elemental mass bias correction calculated from calibration standards (repeated after every 3–5 otoliths) with known analyte-to-Ca ratios.

To group fish into different dispersal histories based on otolith elemental profiles, I used a Markov chain Monte Carlo simulation (Hamilton et al. 2008). Previous results indicated that elemental profiles of Pb could serve as reliable environmental markers of nearshore (elevated Pb concentration) or offshore (depleted Pb concentration) larval residence in this system (Swearer 2000; Hamilton et al. 2008). Fish with elevated Pb concentrations throughout development were assigned to the 'nearshore' group while those with relatively depleted Pb were assigned to the 'offshore' group. I randomly assigned all fish ($n = 221$) to a dispersal history and then employed iterative algorithms to assign the most likely dispersal history to each fish. The classification reliability was high, with over 80% of fish conforming to a particular dispersal history in at least 90% of the simulations (Hamilton et al. 2008).

Data analysis

Total lipids (mg g^{-1}) were log transformed to improve normality and meet assumptions of parametric tests. Mean log-transformed lipid levels decreased with post-emergence age ($y = -0.497x + 5.42$, $r^2 = 0.84$, $P < 0.001$; Fig. S2). To ensure that juvenile experiences did not have an effect on post-metamorphic condition, I excluded from further analyses all fish that were aged as more than 2 days post-emergence. Accordingly, sample sizes were reduced from 58 to 36 individuals for the remaining analyses. I used correlation analysis and linear regression to examine the relationship between condition (total lipids) and early life-history traits, with both a pooled analysis (all samples) and separate analyses for each group that developed in different water masses. Because of the broad range in larval duration for this species, I analyzed daily growth histories both forecast (post-hatch) and hindcast (backwards from settlement) following Searcy and Sponaugle (2000). Forecast larval growth trajectories reveal whether growth patterns diverge at a specific age. In contrast, hindcast growth trajectories enable an examination of recent growth in relation to the day of settlement. I examined this period for each individual, despite differences in larval duration, because the past 1 or 2 weeks of growth may significantly influence condition, independent of growth at a particular age. I used correlation analysis to test relationships between growth history and condition. Growth was summed into 3-day bins to account for potential aging errors, and probability values for detecting statistical significance of Pearson correlation coefficients were adjusted for multiple comparisons using sequential Bonferroni corrections (Rice 1989).

I used repeated-measures analysis of variance (JMP 6.0, SAS Institute, Cary NC) to examine relationships between hindcast growth and otolith size at age for recent settlers as a function of post-metamorphic lipid content. Because sample sizes were too low for a fully factorial spatiotemporal analysis of larval growth versus lipids ($n = 36$), which increased the chance of type-II error, I used the large data set ($n = 268$) of growth histories and MB widths (i.e., a proxy for condition; Fig. 1) to examine spatiotemporal variation in growth histories as a function of condition. Hindcast growth histories examined the last 30 days of growth prior to settlement while forecast growth histories and otolith size at age trajectories used only the first 30 days of growth post-hatch, in order to include all fish in the analysis regardless of PLD and maintain sufficient degrees of

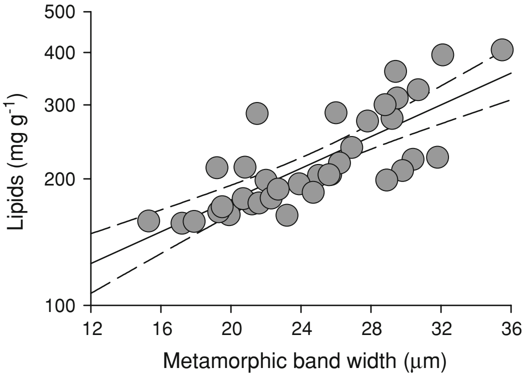

Fig. 1 Relationship between condition (lipid content; mg g^{-1}) and width of the metamorphic band (MB; µm) recorded in otoliths of recently emerged (i.e., early post-settlement) *Thalassoma bifasciatum*. *Dashed lines* represent 95% confidence intervals around the best-fit regression line (Ln lipids = 4.31 + 0.043 × MB; $r^2 = 0.62$, $P < 0.0001$)

freedom to perform statistical tests. I determined whether growth trajectories diverged through time by examining the daily growth × group (i.e., condition, site, month, etc.) interaction terms. Categories of site, month, and condition were treated as fixed factors in the analysis. In cases where the assumption of within-class sphericity was not met, I used the Greenhouse-Geisser (G-G) adjustments of degrees of freedom according to the recommendations of Von Ende (2001).

Relationships between daily growth histories (both hindcast and forecast) and post-metamorphic lipid content were visualized using 3-D response surfaces, and data were smoothed using Loess interpolation techniques (SigmaPlot 10.0). To aid interpretation of patterns (i.e., summarizing 3-D plots in 2-D), I separated recruits into two classes of response: high ($n = 13$) and low ($n = 23$) condition at a break point of lipids >220 mg g^{-1} and those <220 mg g^{-1}. This threshold was identified because the response surface of growth rates as a function of lipid content decreased during the last 10 days for fish with low lipid values (<220 mg g^{-1}) but continued to increase for fish with high lipid values (>220 mg g^{-1}) (Fig. 2a). Modifying the threshold did not affect the qualitative patterns that follow and was chosen simply to aid visualization. In analyses that substituted the MB width as a proxy for condition, I estimated the threshold MB width that corresponded to the threshold lipid content using the equation in Fig. 1.

Results

Early life-history trait correlations

Post-metamorphic condition correlated negatively with the following early life-history traits: pelagic larval duration, average larval otolith growth, and otolith size at settlement (Table 1). Fish in better physiological condition after metamorphosis had shorter PLDs, grew slower on average during larval development, and were smaller in size upon settlement. In contrast, there was a significant positive relationship between post-metamorphic condition and the width of the MB (Fig. 1), which explained the largest

Table 1 Correlations among early life-history (ELH) traits measured in the otoliths of recently emerged *Thalassoma bifasciatum* and early post-metamorphic lipid content (log transformed). *ns* non-significant, *MBW* metamorphic band width, *PLD* pelagic larval duration

ELH trait	PLD	Size at settlement	Average larval growth	MBW	Lipid content
(a) Pooled analysis ($n = 36$)					
PLD	–	0.81^{***}	−0.0014 ns	-0.61^{***}	-0.44^{*}
Size at settlement		–	0.57^{**}	-0.71^{***}	-0.66^{***}
Average larval growth			–	−0.37 ns	-0.52^{**}
MBW				–	0.78^{***}
Lipid content					–
(b) Low Pb (offshore) group ($n = 20$)					
PLD	–	0.88^{***}	−0.08 ns	-0.59^{*}	−0.54 ns
Size at settlement		–	0.54 ns	-0.72^{**}	-0.69^{**}
Average larval growth			–	-0.47^{ns}	0.53 ns
MBW				–	0.76^{***}
Lipid content					–
(c) High Pb (nearshore) group ($n = 16$)					
PLD	–	0.65^{**}	−0.12 ns	-0.66^{**}	−0.30 ns
Size at settlement		–	0.67^{**}	-0.72^{**}	-0.65^{**}
Average larval growth			–	−0.29 ns	−0.56 ns
MBW				–	0.81^{***}
Lipid content					–

(a) Pooled analyses were conducted on all samples combined, while (b) correlations were also calculated separately for the low Pb (offshore) group, and (c) the high Pb (nearshore) group. *P* values were corrected for multiple comparisons using sequential Bonferroni corrections

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

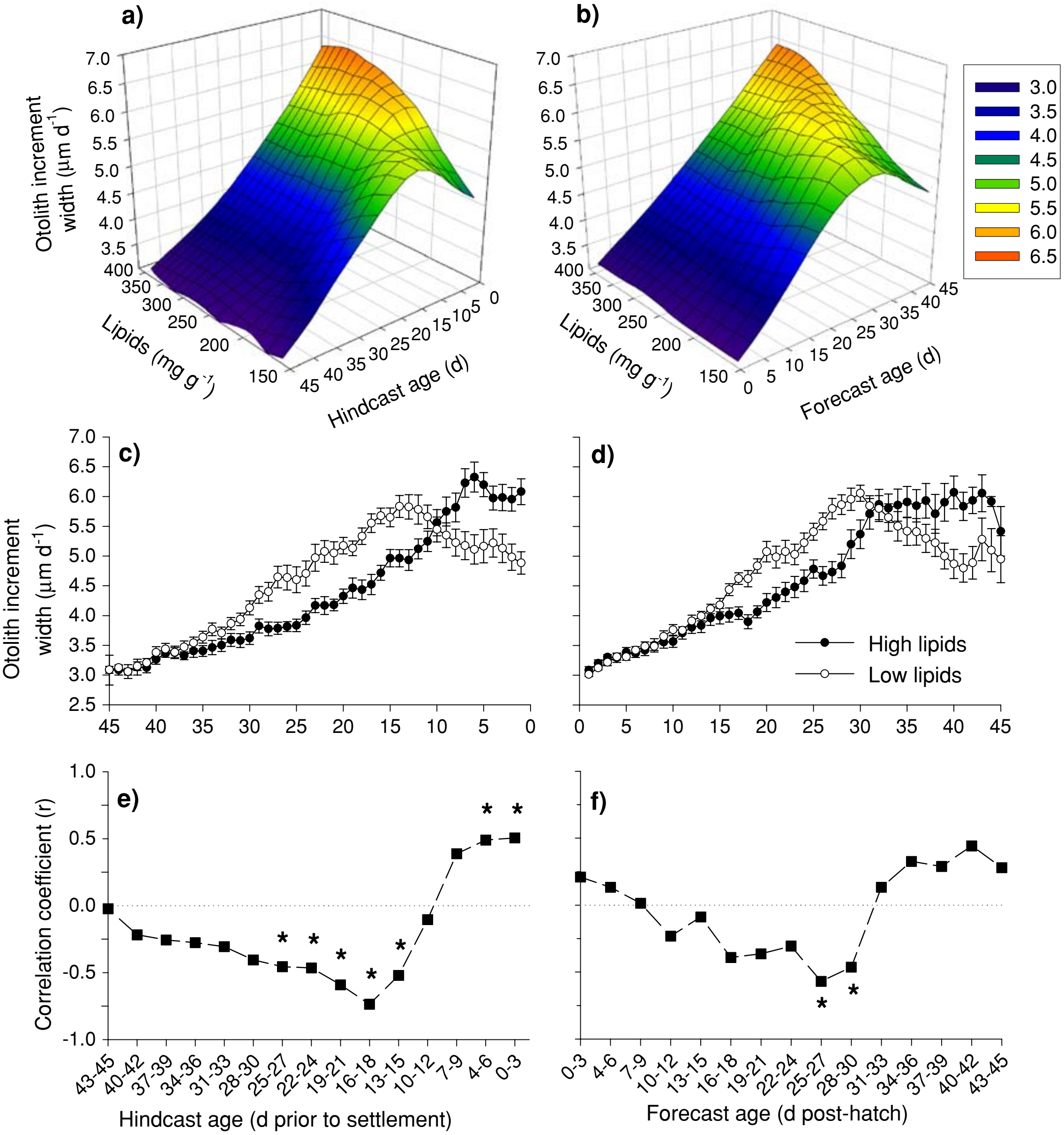

Fig. 2 Otolith growth trajectories for *Thalassoma bifasciatum* and correlations between growth histories and condition for hindcast and forecast growth. Surfaces of larval otolith growth (a function of daily otolith increment width at age) for fish that varied in lipid content at emergence. **a** Hindcast growth depicts daily otolith increment widths (µm day^{-1}) backwards from the time of settlement until hatching (settlement = age 0). **b** Forecast growth depicts daily otolith increment widths (µm day^{-1}) from the time of hatching until settlement (hatch = age 0). Hindcast (**c**) and forecast (**d**) otolith growth trajectories (mean ± SE) for fish separated into high (>200 mg g^{-1}; $n = 13$; *filled circle*) and low (<200 mg g^{-1}; $n = 23$; *open circle*) lipid groups are provided for comparisons with correlation plots (**e**, **f**). Correlations between larval otolith growth and condition (*filled square*) are presented in 3-day age bins (i.e., correlations of average otolith µm day^{-1} for each 3-day period versus lipid content) for hindcast (**e**) and forecast (**f**) growth histories. Statistically significant ($\alpha = 0.05$) pairwise correlations are labeled (*asterisk*) after sequential Bonferroni corrections of *P* values for multiple comparisons. The *gray dotted line* (panels *e*, *f*) represents the point at which there is no correlation ($r = 0$) between growth over each 3-day period and lipid content at emergence

percentage of variation in lipid content (Table 1). Fish in good condition had relatively wide MBs. Many of the early life-history traits recorded in otoliths correlated with one another (Table 1), and those fish that settled at a large size tended to have long PLDs but faster growth on average. There was no significant relationship between the length of the larval phase and average growth. Using otolith microchemistry to separate new recruits into those that developed in water masses characterized by high and low Pb content (i.e., onshore and offshore waters, respectively) showed that correlations between lipid content and various life-history traits were consistent in direction and magnitude, regardless of where individuals developed (Table 1).

Growth histories and condition

Response surfaces depicting the relationship between larval growth history and lipid concentration showed strikingly divergent patterns of growth between fish that emerged with high and low levels of lipids (Fig. 2a, b). Fish in good condition upon emergence had grown slower as larvae than fish in poor condition upon emergence, both on average (Table 1) and during the 3–4 weeks prior to settlement (Fig. 2a, c), but then grew significantly faster than poor-condition fish in the last 10 days prior to settlement (RM-ANOVA: age × lipid content, G-G $\varepsilon = 0.14$, $F_{3.9,134.2} = 9.79$, $P < 0.0001$; Fig. 2a). Correlations between hindcast growth and condition confirmed this crossing pattern; growth was significantly positively correlated with lipid content in the week before settlement, but was significantly negatively correlated with condition in the 3–4 weeks prior to settlement (Fig. 2e). Similar qualitative patterns were detected for forecast growth histories; however, I found few significant correlations between lipid content and forecast growth throughout the larval period (Fig. 2f). Therefore, I elected to focus on patterns in hindcast growth for the remainder of the study.

Otolith size at age trajectories differed among individuals as a function of post-metamorphic lipid content (RM-ANOVA: size × lipid content, G-G $\varepsilon = 0.047$, $F_{1.4,\ 46.6} = 7.58$, $P = 0.0042$); fish with low concentrations of lipids were larger at a given larval age (Fig. 3). Although fish with high lipid content grew faster than those with low lipid content during the last 7–10 days prior to settlement (Fig. 2), this brief period of accelerated growth was not sufficient to compensate for previous deficiencies in size at age. High-lipid fish did not catch up in size to low-lipid fish and, consequently, they settled at a smaller size.

Total lipid content was only directly assessed in 36 individuals. To test for spatial and temporal consistency of hindcast growth patterns as a function of post-metamorphic condition, I examined the larger data set ($n = 268$) of growth histories and used MB width as a proxy for condition. The distinct growth patterns exhibited by good and poor condition fish were consistent in space and through time (Fig. 4). At two sites on separate ends of St. Croix, larval growth histories diverged significantly as a function of MB width (RM-ANOVA, age × condition; $F_{5.7,\ 1195.7} = 9.21$, $P < 0.0001$; Table S2), and the qualitative pattern of slow-early larval growth followed by rapid late larval growth occurred in each monthly cohort to each site (Fig. 4), despite significant site and month differences in growth histories (RM-ANOVA; age × site, $F_{5.7,\ 1195.7} = 6.67$, $P < 0.0001$; age × month, $F_{11.4,\ 1195.7} = 10.15$, $P < 0.0001$; post-hoc comparisons with Tukey's HSD: JB > BB and Aug = July > June; Table S2). The crossing pattern of hindcast growth as a function of condition was also evident when just considering site (Fig. S3) and monthly (Fig. S4) differences for those fish whose lipid content I directly evaluated ($n = 36$). However, the low sample sizes for certain site-month combinations precluded statistical tests.

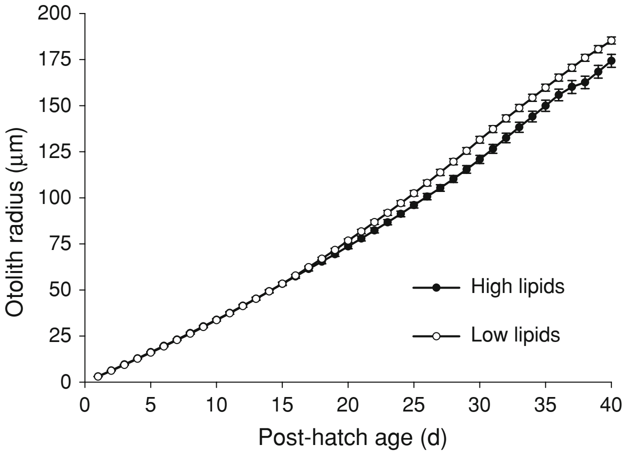

Fig. 3 Otolith radius at age (mean ± SE) for *Thalassoma bifasciatum* in good and poor condition at the time of emergence (i.e., early post-settlement), corresponding to high (>200 mg g^{-1}; $n = 13$; *filled circle*) and low (<200 mg g^{-1}; $n = 23$; *open circle*) lipids, respectively

Between and within water mass responses of growth and condition

The larvae of bluehead wrasse that recruited successfully to St. Croix generally developed in two different water masses—high Pb (nearshore) and low Pb (offshore)—and individuals assigned to each had distinct Pb/Ca elemental profiles (Hamilton et al. 2008). The profiles of fish assigned to the low Pb group reflected cross-shore dispersal in that Pb/Ca concentrations decreased significantly from the beginning of the larval period and then increased significantly at the end of the larval phase, likely signifying a switch in water mass and movement back into nearshore waters (Hamilton et al. 2008; Table S1). For those fish that I used to directly assess lipids ($n = 36$), their hindcast growth histories were significantly different as a function of larval water mass residence (RM-ANOVA: age × dispersal history, G-G $\varepsilon = 0.11$, $F_{3.2,110.4} = 3.41$, $P = 0.0175$; Fig. 5). On average, growth histories of fish that developed nearshore resembled those in poor condition upon emergence, while those that developed offshore reflected the growth histories of fish that emerged in good condition. However, of the 13 fish from the high-lipid group, 69% ($n = 9$) developed in offshore waters and 31% ($n = 4$) in nearshore

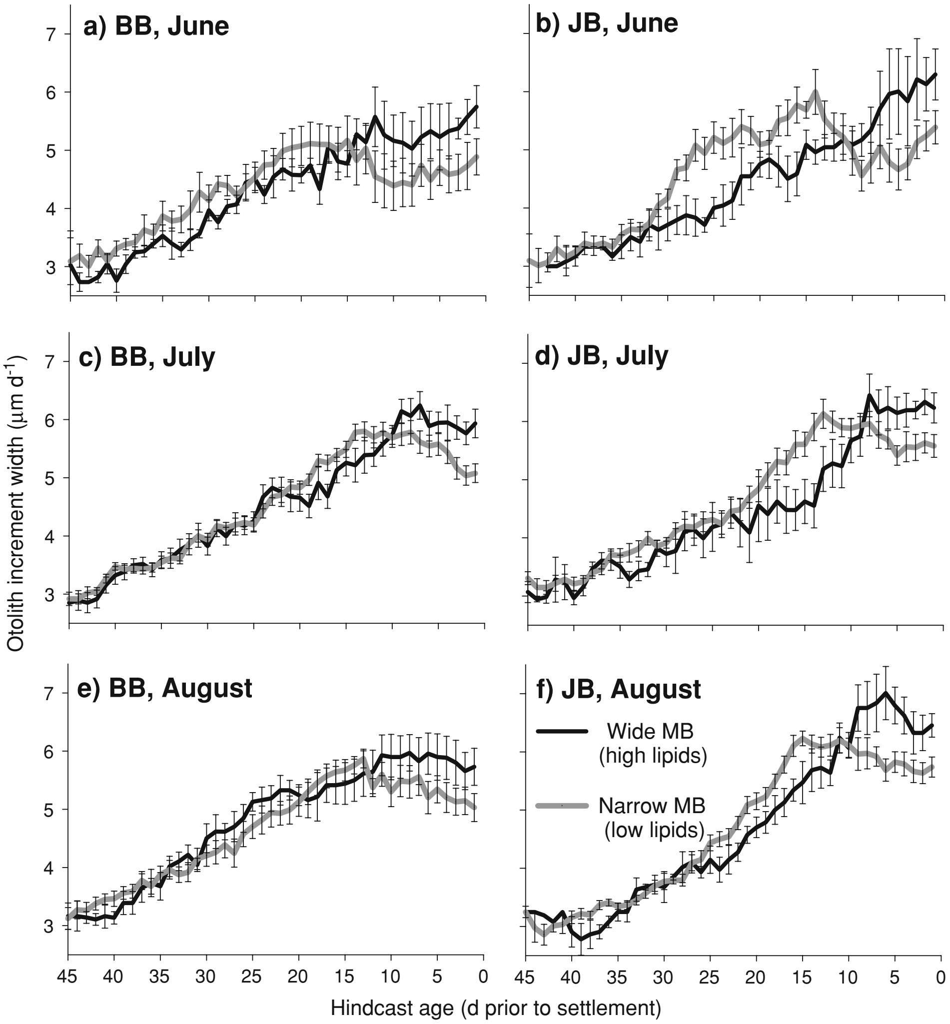

Fig. 4 Hindcast otolith growth trajectories (mean ± SE) as a function of metamorphic band width (i.e., proxy for condition; MB) for each cohort sampled in 2001 that recruited to Butler Bay (BB) and Jacks Bay (JB). Hindcast growth depicts the daily increase in otolith size (i.e., increment width, µm day^{-1}) with hindcast age (days prior to settlement). For visualization purposes, the fish were separated into wide MB (high lipid *black line*) and narrow MB (low lipid *gray line*) or the fish were separated into wide MB (high lipid *filled line*) and narrow MB (low lipid *shaded line*) groups by estimating the MB width that corresponded to the threshold lipid content (lipids = 220 mg g^{-1}) using the equation presented in Fig. 1. The qualitative growth history patterns were similar for each cohort. **a** BB in June (wide MB, $n = 9$; narrow MB, $n = 18$); **b** JB in June (wide MB, $n = 6$; narrow MB, $n = 17$); **c** BB in July (wide MB, $n = 22$; narrow MB, $n = 41$); **d** JB in July (wide MB, $n = 19$; narrow MB, $n = 36$); **e** BB in August (wide MB, $n = 28$; narrow MB, $n = 22$); and **f** JB in August (wide MB, $n = 23$; narrow MB, $n = 27$)

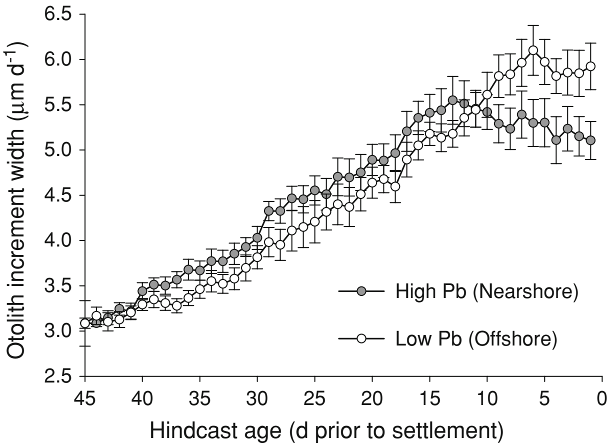

Fig. 5 Hindcast otolith growth trajectories (mean ± SE) as a function of the water mass that fish developed within. Newly emerged bluehead wrasse ($n = 36$) were assigned to have developed in either a high Pb (nearshore; $n = 16$; *shaded circle*) or low Pb (offshore; $n = 20$; *open circle*) water mass, based on elemental profiles of Pb and a Markov chain Monte Carlo assignment model (Hamilton et al. 2008)

waters. Of the 23 fish in the low-lipid group, 48% ($n = 11$) developed in offshore waters and 52% ($n = 12$) nearshore waters.

Given the extensive variation in condition of fish that developed within a water mass (Table 2), I examined relationships between growth and condition as a function of developing in nearshore or offshore waters ($n = 221$). For fish that developed in low Pb (offshore) waters, those that emerged from metamorphosis in good condition (i.e., wide MB) grew more slowly at the beginning and middle of the larval phase, but more rapidly at the end (RM-ANOVA: age × condition, G-G $\varepsilon = 0.149$, $F_{4.3,573.3} = 7.37$, $P < 0.001$; Fig. 6a). Correlations between growth and MB width confirm this pattern. Growth was negatively correlated with MB width at the beginning and middle of the larval phase, but was positively correlated with MB width at the end of the larval phase (Fig. 6c). In contrast, for fish that developed in a high Pb (nearshore) water mass, fish that emerged in good condition simply grew faster at the end

Table 2 Within water mass variation in measures of condition of recently settled *T. bifasciatum*. For newly settled fish, the otoliths of which were subjected to microchemical analysis of dispersal history, lipid content was directly measured in 36 fish, while metamorphic bands were measured in 221

Trait	*n*	Mean	Standard deviation	Range (min–max)	Coefficient of variation
Lipid content (mg g^{-1} dry wt.)					
Low Pb (offshore)	20	242.3	59.9	174.2–405.3	24.7
High Pb (nearshore)	16	210.9	73.2	156.7–394.5	34.7
Metamorphic band width (μm)					
Low Pb (offshore)	134	24.6	4.09	15.8–33.9	16.6
High Pb (nearshore)	87	22.7	4.37	11.5–32.1	19.2

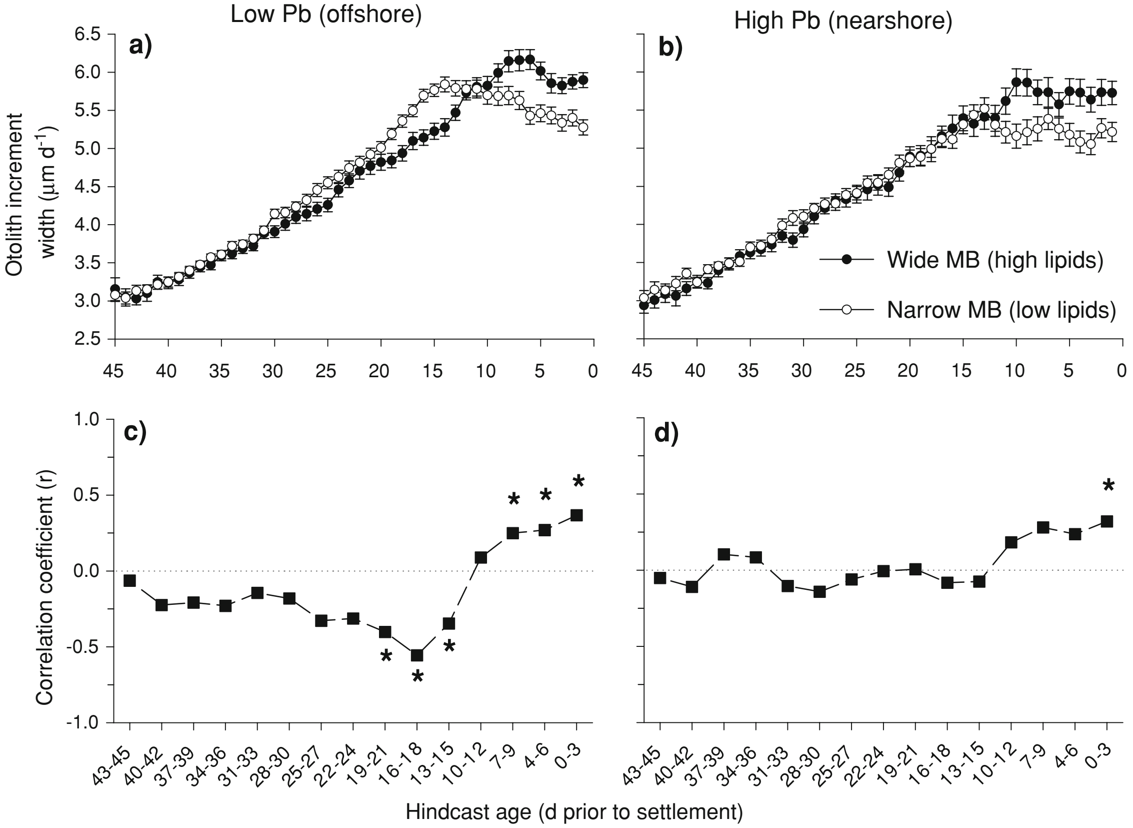

Fig. 6 Hindcast otolith growth trajectories (mean ± SE) as a function of lipid content (i.e., metamorphic band width; MB) for fish that developed in low Pb (**a**, offshore) or high Pb (**b**, nearshore) water masses. For visualization purposes, the fish were separated into wide MB (high lipid; *filled circle*) and narrow MB (low lipid; *open circle*) groups by estimating the MB width that corresponded to high and low lipid contents, respectively (threshold lipids = 220 mg g^{-1}; log lipids = 5.4), using the equation presented in Fig. 1. **a** Low Pb (offshore) water mass fish (wide MB, *n* = 61; narrow MB, *n* = 73); **b** High Pb (nearshore) water mass fish (wide MB, *n* = 26; narrow MB, *n* = 61). Correlations between larval otolith growth and metamorphic band width (*filled square*) are presented in 3-day age bins (i.e., correlations of average otolith μm day^{-1} for each 3-day period versus MB width upon emergence) for low Pb (**c**, offshore) and high Pb (**d**, nearshore) developing fish. Statistically significant ($\alpha = 0.05$) pairwise correlations are labeled (*asterisk*) after sequential Bonferroni corrections of *P* values for multiple comparisons. The *gray dotted line* (panels *c*, *d*) represents the point at which there is no correlation ($r = 0$) between growth over each 3-day period and MB width

of the larval phase than those that emerged in poor condition (RM-ANOVA: Age × Condition, G-G $\varepsilon = 0.167$, $F_{4.8,411.1} = 2.29$, $P = 0.047$; Fig. 6b, d). Of the 87 fish estimated to have settled with high lipid content, 70% (*n* = 61) developed in offshore waters and 30% (*n* = 26) nearshore. Of the 134 fish estimated to have settled in the low-lipid group, 54% (*n* = 73) developed in offshore waters and 46% (*n* = 61) in nearshore waters. These estimates of the proportion of good and poor condition that were fish assigned to each water mass are remarkably similar to that of the subsample used to assess lipid content directly.

Discussion

For organisms with complex life histories, performance in one phase of the life cycle may extend across life-history transitions to influence later stages. The results presented here for a common tropical reef fish, the bluehead wrasse, reveal a direct link between recent larval performance and physiological condition following metamorphosis. As expected, those settlers in good condition had grown faster in the days immediately before settlement. Numerous studies of fish have reported that faster growth is correlated with better condition (goatfish, McCormick and Molony 1992; cod, Suthers et al. 1992; lanternfish, Suthers 1996). Supplemental feeding has been found to enhance daily otolith growth in bluehead wrasse (Victor 1982), and for other fish species food deprivation and supplementation have been shown experimentally to modify otolith growth and lipid storage in predictable ways (reviewed by Ferron and Leggett 1994). Surprisingly, this contrasted with growth patterns in the earlier portion of planktonic life, when fish in poorer condition at settlement grew faster. Interestingly, these relationships between growth and condition were consistent both in space and through time. Growth and condition appeared to be influenced by the water mass that developing larvae encountered. Larvae that developed in offshore waters grew relatively slowly early-on, but completed the larval phase following a burst of rapid growth and emerged with relatively high stores of lipids. Fish developing in nearshore waters exhibited the opposite pattern of growth and emerged with relatively low lipid stores. Even within a water mass, however, past history determined the condition upon emergence, potentially reflecting trade-offs between growth and energy storage. To be in good condition following metamorphosis, individuals had to grow rapidly at the end of the larval phase, but it paid to grow slowly initially, especially if development occurred offshore.

Metamorphic band width and energy reserves

The presence of a MB on the otoliths of some labrids has been noted for decades (Victor 1982), and the importance of its width has been the subject of much speculation ever since. Previous studies have demonstrated extensive variation in the width of the MB (e.g., CVs of 20–30%, Sponaugle and Grorud-Colvert 2006) and documented intense selection associated with this trait at the beginning of the juvenile phase; survivors consistently have wider MBs (Searcy and Sponaugle 2001; Sponaugle and Grorud-Colvert 2006; Hamilton et al. 2008). The results of selective mortality and the observation that somatic growth is negligible during metamorphosis (Sponaugle and Cowen 1997) have led researchers (such as Searcy and Sponaugle 2001) to suggest that otolith accretion in the MB reflects conditions at settlement. Here, I confirm a direct link between a biochemical measure of condition and the width of the MB—post-settlement condition (i.e., lipid content) increased with the width of the MB, and this relationship explained over 60% of the variation in total lipid content remaining after metamorphosis. I measured nutritional reserves at the end of the metamorphic period, when lipid stores were presumably depleted to fuel that transition (Youson 1988). Relationships between condition just before settlement and ensuing otolith accretion during metamorphosis would presumably explain more variation, because bluehead wrasse do not feed during metamorphosis. In other fish species that experience a protracted metamorphic period encompassing a non-feeding stage (e.g., flatfish), lipids are rapidly depleted (Pfeiler and Luna 1984; Hossain et al. 2003) and growth significantly curtailed (Hossain et al. 2003), which can result in a precipitous decline in measures of nutritional status (e.g., RNA:DNA ratio) following metamorphosis (Gwak and Tanaka 2002).

The continued decline in total lipid content that I observed following metamorphosis (Fig. S2) may represent an energetic debt that must be repaid over a period of days to weeks to cover a costly non-feeding metamorphic period, which is analogous to recovery following a starvation event (McCormick and Molony 1992; Molony and Sheaves 1998). Alternatively, the continued decline in lipid content may signify a shift in the allocation of energy to growth versus storage. Mortality rates are extremely high in the first few days post-settlement for most reef fish (Almany and Webster 2006), including bluehead wrasse (Victor 1986; Caselle 1999), and a strategy to improve survivorship might include temporarily forgoing storage in favor of growth, in order to exit the most vulnerable size classes quickly (Gagliano et al. 2007). In support of this hypothesis, otolith growth is elevated during the early post-settlement phase relative to that in the larval phase for bluehead wrasse (Searcy and Sponaugle 2000, 2001; Sponaugle and Grorud-Colvert 2006), and survivors have been shown to exhibit faster growth immediately after emergence (Searcy and Sponaugle 2001).

Environmental heterogeneity, trade-offs, and compensatory growth

Differences among the oceanic environments encountered by larvae served as important drivers of patterns of larval growth and condition. Food concentrations in the pelagic zone can vary over multiple spatial scales, from the scale of an individual to that of an entire cohort. Oceanographic features, such as fronts (Munk 2007) and eddies (Sponaugle and Pinkard 2004), have been shown previously to influence the performance of larvae entrained within them. For bluehead wrasse, Sponaugle and Pinkard (2004) demonstrated that encountering a low-salinity eddy during the early larval phase had negative impacts on growth and MB width. On many oceanic islands, onshore–offshore gradients in food availability are often attributed to a process called the 'island mass effect' (Hamner and Hauri 1981). This enrichment of nutrients in nearshore waters results from the retention of local runoff and vertical mixing. Swearer (2000) detected a decrease in Chl *a* concentrations up to 2.5 km offshore and enriched zooplankton biomass in the island wake region of St. Croix (i.e., in the vicinity of BB) and found that fish recruitment levels and larval growth rates were elevated when zooplankton were abundant during early larval life. Therefore, divergent growth histories and levels of condition may be explained to some extent by development in distinct water masses that varied in food availability. Consistent with this interpretation, fish that developed in offshore waters (i.e., relatively low Pb concentrations) initially grew slowly and then accelerated in growth during the last week prior to settlement, likely upon encountering prey-rich nearshore waters (Hamilton et al. 2008). On average, those fish completed metamorphosis with relatively large lipid stores. In contrast, fish that grew rapidly in the early stages of larval development likely resided in nearshore waters (i.e., relatively enriched Pb content) throughout their larval life, but on average they emerged in relatively poor condition. The patterns of larval growth as a function of lipid content (Fig. 2) resemble the growth patterns as a function of the water mass larvae encountered (Fig. 5; Hamilton et al. 2008); however, settling in good condition depended directly on larval performance within that water mass. Therefore, successful settlement after an offshore development period did not guarantee good condition following metamorphosis.

To complete metamorphosis in good condition, fish that developed in nearshore waters simply had to grow rapidly at the end of the larval phase. Fast growers were likely those individuals that were fortunate enough to encounter a rich food patch in last two weeks before settlement, providing ample nutrition for growth and storage. In contrast, fish that developed in offshore waters only exited metamorphosis with high energy reserves if they had initially grown slowly, followed by rapid late larval growth. In tropical oceans, offshore waters are often characterized by depleted nutrients and prey concentrations (Hamner and Hauri 1981; Rissik et al. 1997). Therefore, a growth-storage trade-off in oligotrophic oceanic waters may be beneficial for surviving the larval phase when resources are patchy or scarce. Overall, fish in good condition were smaller in size than fish in poor condition at settlement. Similar negative relationships between size at settlement and condition have been reported for bluehead wrasse (size versus MB; Searcy and Sponaugle 2000, 2001) and other reef fishes (size versus lipid content; Hoey and McCormick 2004). Fish in good condition upon emergence also settled after a relatively short larval duration and size was strongly correlated with PLD. These fishes may have reached the minimum level of condition required to survive metamorphosis more rapidly (Searcy and Sponaugle 2000), thereby allowing them to exit the pelagic stage earlier. Growth-storage tradeoffs and growth-mortality tradeoffs may occur if size- and condition-dependent processes both act at some point during the life cycle to influence probabilities of survival. Gagliano et al. (2007) demonstrated for a coral reef damselfish that selective pressures favored growth-storage allocation strategies that changed throughout ontogeny. Early juvenile survival was enhanced by hatching at a large size, conserving stored energy while growing relatively slowly during a fixed larval phase, then growing rapidly immediately after settlement, and finally by growing relatively slowly once again to potentially minimize foraging risks. By growing slowly and conserving limited resources, the offshore developers in this study may have been better equipped to rapidly compensate upon entering nearshore waters at the end of the larval phase. For bluehead wrasse, the probability of surviving for the first month on the reef was related to the water mass larvae encountered and their larval growth rates and level of condition upon emergence (Hamilton et al. 2008). In general, survivors had wide MBs and rapid late larval growth.

Compensatory or catch-up growth is a common response to periods of food shortage in many animal groups (Arendt 1997) and is consistent with the accelerated growth response of initial slow-growing fish at the end of the larval period. Increasing intake rates in the week prior to settlement, potentially after entering nearshore waters, is a plausible mechanism that would account for both accelerated growth and increased energy reserves in the initially slow-growing fish after emergence. Both juvenile salmon (Nicieza and Metcalfe 1997) and walleye pollock (Sogard and Olla 2002) increase their intake rates and time spent foraging while exhibiting growth compensation during the recovery period following experimental food deprivation. Additional food resources may also be assimilated more effectively by the digestive physiology of smaller and slower-growing individuals that are adapted to restricted rations (i.e., offshore conditions). Increases in digestive efficiency have been attributed previously to restricted food consumption (Boyce et al. 2000) and can lead to compensatory responses in growth and storage once access to food is improved. The growth patterns presented in Fig. 2c indicated that compensatory growth occurred for initial slow-growers at the end of the larval period; however, it only occurred over a short time period. Because fish in good condition with wide MBs had relatively short larval durations (Table 1), previously established size discrepancies remained at settlement (Fig. 3).

Demographic implications and conclusions

Much attention had been given recently to the effects of larval performance on recruitment and mortality dynamics in marine fishes (Bergenius et al 2002; Vigliola and Meekan 2002; Jenkins and King 2006). Many studies have illustrated the role that large size, rapid growth, and short larval durations have on probabilities of avoiding the intense selective mortality commonly experienced early in the juvenile stage (Hare and Cowen 1997). In addition, evidence is accumulating that body condition appears to influence performance and survival following metamorphosis (Phillips 2002; Hoey and McCormick 2004). Using experimental manipulations of body condition in newly recruited bluehead wrasse, Grorud-Colvert and Sponaugle (2006) showed that individuals in better condition swam faster, were better able to evade a simulated predation event, and exhibited less-risky behavior by sheltering more in the presence of a predator. Those with faster larval growth, shorter larval durations, and that were smaller at settlement also exhibited faster critical swimming speeds in experimental trials. Thus, environmental features that improve growth rates and energy reserves prior to settlement will likely enhance recruitment success, and may extend to influence population growth rates and, ultimately, production.

For organisms with complex life cycles, experiences throughout the larval phase or at a particular critical period before metamorphosis undoubtedly influence fitness at later life stages. Here, I have shown that growth during the final week of larval life directly affected condition following the larval–juvenile transition in a common coral reef fish. The strong positive relationship between lipid reserves at emergence and MB width validates the use of the MB width as a proxy for condition. Furthermore, the distinct larval growth trajectories that culminated in a heightened state of nutritional condition were consistent at two sites at opposite ends of St. Croix and over three recruitment pulses, and were consistent both with evidence of larval development in distinct oceanic environments and differential performance and energy allocation within those environments. Researchers should use caution in equating average growth with survival potential, because the results indicate that average larval growth and size at settlement may not accurately reflect recent performance or physiological condition. Understanding the mechanisms that influence spatial and temporal variation in the strength of selective mortality on early life-history characteristics will provide valuable insight into the costs and benefits of different growth and allocation histories.

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