

Variability in water temperature affects trait-mediated survival of a newly settled coral reef fish

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Abstract As animals with complex life cycles metamorphose from one stage to the next, carry-over effects from earlier stages can affect future mortality. To examine the relationship between early life history traits and survival, seven monthly cohorts of newly-settled bluehead wrasse *Thalassoma bifasciatum* were collected immediately after settlement and over sequential 3-day periods. Otolith analysis was used to quantify mean larval and juvenile growth rates, pelagic larval duration (PLD), and settlement size and condition of different age classes to identify the traits most important for survival. Overall, survivors tended to have shorter PLDs, to settle at smaller sizes and higher condition levels, and to exhibit faster early juvenile growth. Water temperature contributed to among-cohort variability in traits as warmer water led to faster larval and juvenile growth and shorter PLDs. Trait-specific fitness functions demonstrated that temperature can influence fitness by changing the nature of selection on each trait. Estimates of selection intensity revealed that settlement condition contributed the most to variation in fitness across cohorts, followed by juvenile growth. Frequent loss of low settlement condition individuals and occasional loss of the very highest condition fish suggest that particularly

high settlement condition during the warmest temperatures may be detrimental. Not only does the quality of settlers vary over time, but selective loss of individuals with particular phenotypic traits is not pervasive and can vary with environmental conditions such as temperature.

Keywords Selective mortality · Fitness · Condition · Juvenile growth · Otoliths

Introduction

Although ecological theory states that individuals with certain traits will have a better chance of obtaining resources and surviving than conspecifics lacking these characteristics, benefits may vary due to different pressures associated with seasons, habitats, and life stages (e.g., Blums et al. 2005; Gagliano et al. 2007a). Many animals have complex life cycles (e.g., insects, amphibians, marine invertebrates, and fishes), and selective pressures can differ ontogenetically as larval forms are exposed to an environment different from that of the juvenile and adult. During the larval period, mortality is frequently high, driven primarily by predation, starvation, and larval transport away from suitable juvenile habitat (Thorson 1950; Houde 1989). In addition, metamorphosis from the larval to juvenile stage represents a “critical period” during which energy reserves are depleted and larvae of lower condition are unable to complete the transition (Searcy and Sponaugle 2001; Marshall et al. 2003b). For most marine organisms, transition to the juvenile stage takes place after a variable period of pelagic transport from the source population to the juvenile benthic habitat. When individuals settle to the benthos, high mortality occurs as predators prey on incoming settlers (Doherty and Sale 1986;

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Hunt and Scheibling 1997). Even relatively small differences in mortality during the larval stage can lead to large fluctuations in numbers of juvenile survivors (Houde 1989).

A growing body of work has shown for a number of organisms that larval experience can influence future growth, development, and survival as individuals enter the juvenile population (polychaetes: Qian and Pechenik 1998; sponges: Maldonado and Young 1999; gastropods: Moran and Emlet 2001; bivalves: Phillips 2002; crustaceans: Jarrett 2003; bryozoans: Marshall et al. 2003a; amphibians: Vonesh 2005; fish: Gagliano et al. 2007a). As selective mortality acts during the early life stages, individuals that grow faster as larvae (Bergenius et al. 2002; Shima and Findlay 2002; Takasuka et al. 2003), metamorphose more quickly out of vulnerable life stages (Qian and Pechenik 1998; Marshall et al. 2003b), are larger in size (Moran and Emlet 2001; Vigliola and Meekan 2002), or are of higher condition (Searcy and Sponaugle 2001; Phillips 2002; Hoey and McCormick 2004) are more likely to make a successful transition to the juvenile population.

Larval and juvenile exposure to a varying environment adds another level of complexity (Sponaugle and Grorud-Colvert 2006; Gagliano et al. 2007b; Durieux et al. 2009; Shima and Swearer 2009). Fluctuations in variables such as temperature and food supply can lead to differences in growth rate, size, stage duration, and condition (Qian and Pechenik 1998; Phillips 2002; Meekan et al. 2003; Gagliano et al. 2007b). Thus, inherent variability in seasonal environments can be a strong predictor of early life history during different parts of the year (Houde 1989; Thiagarajan et al. 2002). Highly variable across seasons and latitudes, water temperature has been shown to influence the magnitude of larval traits across a range of marine organisms (e.g., Moran and Emlet 2001; Gagliano et al. 2007b; O'Connor et al. 2007; Durieux et al. 2009). We previously identified significant relationships between water temperature and both larval growth and duration of the pelagic stage for the bluehead wrasse *Thalassoma bifasciatum* (Bloch), a common western Atlantic coral reef fish (Sponaugle et al. 2006).

The present study was designed to build upon this previous work and examine how such environmentally induced variation in early life history traits may affect selective loss of traits over time. Selective trait-based mortality can only occur when traits are sufficiently variable, creating a range across which predation may be selective (Sogard 1997). Although most studies of selective mortality establish an experimental range of life history traits using lab-based techniques (e.g., Phillips 2002; McCormick and Hoey 2004; Gagliano et al. 2007b), fewer studies have investigated natural variability in the field. Of these, most are short-term field studies tracking a few cohorts (Searcy and Sponaugle 2001; Marshall et al.

2003b; Hamilton et al. 2008). We chose to investigate selective mortality of *T. bifasciatum* in a variable environment subjected to seasonal fluctuations in water temperature over multiple years. To examine how environmental fluctuations and trait variability affect juvenile performance, early life history traits of field-caught juveniles from multiple cohorts were examined to identify selective loss over the first 2 weeks of benthic life. Our overall objectives were to determine whether selective mortality is pervasive for cohorts of a single species in a naturally variable environment and, if so, to identify which early life history traits are most important for survival.

Materials and methods

Field sampling

Thalassoma bifasciatum is distributed throughout the Caribbean and is one of the most abundant coral reef fish in the Florida Keys, making it an ideal species for repeated collections. After a variable pelagic duration of 38–94 days (Sponaugle and Cowen 1997), *T. bifasciatum* larvae settle and bury into the sand and rubble for a period of 3–5 days, during which they undergo metamorphosis. New recruits emerge as juveniles onto the reef (Victor 1982), where mortality is high during the first few days (10–70%; Victor 1986; Carr and Hixon 1995; Caselle 1999).

We censused and collected seven cohorts of newly recruited *T. bifasciatum* from three shallow (3–10 m depth) offshore reefs in the upper Florida Keys, FL, USA (Pickles Reef, 24°59.23'N, 80°24.88'W; Sand Island Reef, 25°01.09'N, 80°22.08'W; North of French Reef, 25°02.53'N, 80°20.64'W). Sampling of new recruits was timed to each monthly settlement event to census and collect *T. bifasciatum* immediately after metamorphosis and emergence onto the reef. Following a settlement event, a team of divers captured approximately 30 new recruits (individuals ≤ 20 mm standard length, SL) using hand nets and the anesthetic quinaldine. Subsequent collections were conducted every 3–5 days thereafter, resulting in three or four total collections for each cohort. Due to sampling and logistical constraints, not all reefs were sampled during each recruitment event. Sampling took place from 2000 to 2003 and targeted cohorts during the peak settlement season (July to September) as well as lower settlement months (e.g., February, March). After sampling, fish were immediately preserved in 95% ethanol and transported to the laboratory.

Water temperature measurements were recorded from 2 February 2000 to 30 May 2000 using two Sontek Argonaut acoustic current and temperature recorders deployed at 25°04'N, 80°19'W at 12 m depth (T. Lee, RSMAS). For

the remaining dates (31 May 2000 to 9 May 2003), temperatures were measured nearly continuously by a Ryan Tempmentor recorder operated by the National Undersea Research Center (S. Miller, NURC) and moored at Conch Reef (24°59'N, 80°25'W) at a depth of 21 m. Measurements from both instruments were converted to daily means.

Otolith analysis

Like many fishes, *T. bifasciatum* possesses a daily record of age and transitional events (i.e. settlement) in its otoliths, or ear stones (Victor 1982; Sponaugle and Cowen 1997), providing a valuable opportunity to examine early life history. Daily otolith growth increments enable age estimates, and a strong relationship between fish SL and otolith size allows measurement of relative size-at-age (Victor 1982; Searcy and Sponaugle 2001). Widths between successive otolith increments provide a relative measure of larval and juvenile growth, and width of the band deposited during metamorphosis (material deposited after settlement and before emergence) is a proxy for settlement condition. Hamilton et al. (2008) confirmed this proxy for *T. bifasciatum* by demonstrating that metamorphic band width is strongly correlated with total lipid content. More material is deposited on the otoliths by faster-growing fish with presumably higher energy reserves during the energetically costly non-feeding period that occurs at settlement (Searcy and Sponaugle 2000).

We followed a standard protocol for preparing otoliths (see Sponaugle et al. 2006 for details). Prior to otolith extraction, the SL of each *T. bifasciatum* specimen was measured to the nearest 0.01 mm. Both pairs of lapillar and sagittal otoliths were removed, although for the purposes of this study, only the sagittae were examined. Otolith increments were identified as larval, metamorphic, or juvenile and were enumerated along the longest axis from the primordium to the edge of the otolith. The position of each otolith increment was digitized to provide estimates of relative size-at-age (distance from core to each increment) and growth rates during particular periods (distances between selected increments). All otoliths were read blind and re-examined blind to confirm interpretations.

Data analysis

Each of the seven cohorts had a significant relationship between SL and otolith radius (and between residuals of each, unpublished data; see Thorrold and Hare 2002); thus, we avoided introducing error when back-calculating somatic growth from otoliths (Chambers and Miller 1995) by describing relative size and growth using only otolith measurements. Hereafter, size and growth refer to otolith

size and growth unless otherwise noted. Further, the SL–otolith radius relationship did not differ significantly among the seven cohorts (unpublished data), enabling inter-cohort comparisons. To ensure all fish from a monthly collection were from the same cohort, only fish that settled within a 10-day window were used in the analyses. Fish were assigned to one of three groups by juvenile age. Initial settlers were those with a juvenile post-emergence age from 0 to 4 days, intermediate fish were those with a juvenile age of 5–9 days, and survivors were fish with a juvenile age ≥ 10 days. These age windows were chosen to partition events during early juvenile life while also maximizing the sample size within each group. Individual records were examined for larval and juvenile increment widths (daily growth), pelagic larval duration (PLD), size at settlement, width of the metamorphic band (settlement condition), and cumulative size-at-age.

We used least-squares regression to compare the coefficient of variation (CV) of each trait by juvenile age to investigate whether variability of each trait changed over time, indicating selective loss (Zar 1999). We investigated larval growth during various periods of larval life (over the entire larval duration, days 1–10, 11–20, and 21–30 of larval life, and 2 and 1 weeks prior to settlement); however, partitioning the growth led to very little additional information. Therefore, we present only the mean larval growth throughout the entire PLD, as well as PLD, settlement size, settlement condition, and mean juvenile growth over the first 3 days post-emergence. Only fish ≥ 3 days post-emergence were used to investigate mean juvenile growth, resulting in slightly smaller samples sizes for these analyses (Table 1).

Sponaugle et al. (2006) demonstrated that the early life history traits of *T. bifasciatum* in the Florida Keys are significantly related to water temperature. To further investigate how selective mortality might be influenced by water temperature, we used least-squares regressions to examine patterns between phenotypic traits of the studied cohorts and water temperature. We calculated the mean water temperature larvae experienced during the period between the earliest hatch date and the latest settlement date of each cohort. For newly settled juveniles on the reef, we calculated water temperature during the period between the earliest settlement date and latest settlement date plus 3 days. We then compared larval traits of initial settlers to the mean temperature experienced by individuals during the larval phase and juvenile growth during the first 3 days on the reef to water temperatures experienced by juveniles during this period.

If mortality is selective during the early juvenile period, mean early life history traits of survivors across cohorts should significantly increase (e.g., loss of slow growers; survivors with faster mean growth rates) or decrease (e.g.,

Table 1 Seven cohorts of *Thalassoma bifasciatum* used for analysis of selective mortality

Cohort	Survey reef (s)	Earliest settle date	Latest settle date	Mean larval temp (°C) ± SE	Mean juvenile temp (°C) ± SE	Initial	Initial ≥3 days	Intermediate	Survivors
1	NF, PI	5/1/2000	5/10/2000	24.67 ± 0.04	25.95 ± 0.06	37	27	57	24
3	NF, PI	6/22/2000	6/29/2000	26.36 ± 0.10	28.05 ± 0.05	27	19	75	48
4	NF, PI	7/16/2000	7/25/2000	26.91 ± 0.11	28.32 ± 0.16	14	13	35	37
6	NF, PI	8/19/2000	8/28/2000	28.37 ± 0.04	28.78 ± 0.04	41	32	69	87
7	SI, PI	5/15/2001	5/24/2001	24.65 ± 0.06	25.66 ± 0.06	15	3	55	23
8	SI, PI	7/31/2001	8/9/2001	28.16 ± 0.03	28.83 ± 0.05	13	11	26	50
10	SI, PI	1/23/2003	2/3/2003	22.82 ± 0.09	20.63 ± 0.05	21	15	11	12

Initial number of individuals with juvenile age 0–4 days, *Initial* ≥3 days fish used in juvenile growth analyses, *Intermediate* number of individuals with juvenile age 5–9 days, *Survivors* number of individuals with juvenile age ≥10 days

loss of individuals with long PLDs; survivors spent fewer days in the plankton) relative to initial settlers. To identify whether selective loss occurred among age groups (initial settlers, intermediate fish, and survivors) for all fish pooled across cohorts for each early life history trait, we conducted logistic ANCOVAs (SAS 8.2) with age groups as the categorical factor and temperature as a covariate. Data were tested for assumptions of normality and homogeneous variance as well as for an interaction between temperature and age group. When there was no interaction, we ran a reduced model with the interaction term removed. Where there was a significant interaction between age group and temperature for a specific trait, we also examined patterns within each cohort.

To identify the presence of linear or nonlinear phenotypic selection on early life history traits, we used non-parametric cubic splines to visualize each trait's fitness functions and describe the form of selection acting on each trait (Sinclair et al. 2002). This method estimates the fitness surface without making any prior assumptions about its shape (except that it is smooth) and calculates the best spline fit by searching over a range of values of the smoothing parameter λ . Cubic splines were calculated using a binomial distribution with initial and survivor age groups to obtain relative survival over time (e.g., Gagliano et al. 2007a). Standardizing the data did not appreciably change the shape of the fitness functions for each early life history trait; thus, actual trait values were used to generate the functions. Because the logistic ANCOVAs revealed the importance of temperature to patterns of selection, we also estimated the effect of temperature on each trait's selection surface by generating cubic splines using residuals from linear regressions of each trait and mean temperature during either the larval phase or juvenile phase, as appropriate.

For one trait (settlement condition, see “Results”), a significant interaction between age group and temperature necessitated examining patterns of selective mortality for each cohort. To simplify the presentation, and for coherence with fitness functions and estimates of selection

intensity, we compared the traits of only the initial and surviving recruits using two-sample *t* tests with Bonferroni adjustments. For each cohort, we also investigated the magnitude of selective mortality for each trait. We quantified the intensity of linear (S_i) selection (Endler 1986) using the equation

$$S_i = (z_{\text{after}} - z_{\text{before}}) / SD_{\text{before}}$$

where z_{after} and z_{before} are the means of the early life history trait before and after selection, and SD_{before} is the standard deviation of the trait before selection.

Finally, to illustrate the changing shape of selection surfaces and fitness functions in cohorts exposed to different temperatures, we used cubic splines as above to generate relative fitness surfaces based on settlement condition for the two cohorts that were exposed as larvae and juveniles to the coolest and warmest water temperatures.

Results

After assignment of appropriate cohorts based on settlement windows, 777 out of a total of 1,102 aged fish were assigned to one of three age groups and used in the analysis (Table 1). Cohorts experienced water temperatures encompassing a range of 8°C, with Cohort 10 subjected to the coolest temperatures and Cohort 6 experiencing the warmest temperatures (Table 1).

Examination of trait CV by juvenile age indicated that settlement condition was the most variable trait with the highest coefficients of variation (Fig. 1). CV of PLD and settlement size did not vary significantly over time; however, CV of larval growth ($r^2 = 0.36$, $P = 0.007$) decreased slightly over time, and both settlement condition CV and juvenile growth CV decreased sharply ($r^2 = 0.57$, 0.77, respectively; $P < 0.001$).

Larval growth of initial settlers increased significantly with increasing water temperature during the pelagic larval phase ($r^2 = 0.87$, $P = 0.002$) as did juvenile growth

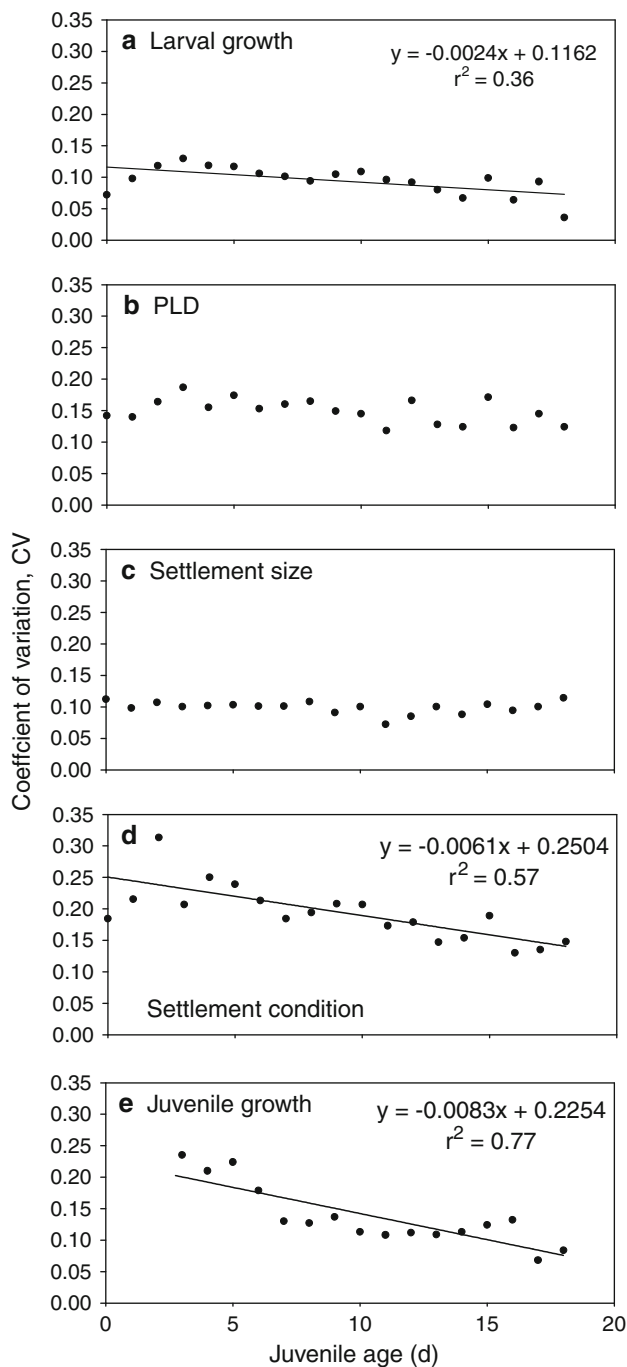


Fig. 1 Coefficient of variation (CV) of five early life history traits by juvenile age for recruits from seven *Thalassoma bifasciatum* cohorts: **a** larval growth, **b** PLD, **c** settlement size, **d** settlement condition, **e** juvenile growth. The equations and R^2 values from least-squares regressions are presented for significant relationships ($P < 0.05$)

during the first 3 days on the reef ($r^2 = 0.96$, $P < 0.001$). PLD decreased significantly with increasing water temperature during the larval phase ($r^2 = 0.82$, $P = 0.005$). Settlement condition increased with increasing water temperatures during the larval phase, although this relationship was not as strong ($r^2 = 0.64$, $P = 0.031$). There

was no significant relationship between settlement size and water temperature during the larval phase.

Analyses of covariance (ANCOVA) comparing early life history traits among the three age groups with temperature as a covariate revealed significant differences for three of four early life history traits (Fig. 2). Survivors generally had shorter PLDs ($F_2 = 5.66$, $P = 0.004$), were of smaller size ($F_2 = 3.74$, $P = 0.024$), and grew faster as juveniles ($F_2 = 13.01$, $P < 0.0001$). For settlement condition, a general linear model with categorical factors of temperature and age group indicated that survivors settled at higher condition levels ($F_2 = 8.96$, $P < 0.0001$) and were significantly influenced by temperature ($F_1 = 27.59$, $P < 0.0001$), but age group and temperature significantly interacted to influence selective mortality ($F_2 = 7.70$, $P < 0.0001$). Because the nature of selection changed with temperature, we also examined selective mortality between the initial and survivor age groups on a cohort by cohort basis (detailed below).

Cubic-spline generated fitness functions describing selection acting on the initial and survivor groups indicated positive directional selection for larval growth (Fig. 3a), negative directional selection for PLD (Fig. 3b), and to a lesser, almost negligible, extent, negative directional selection for settlement size (Fig. 3c). Fitness functions indicated stabilizing selection for settlement condition (Fig. 3d), and disruptive selection for juvenile growth (Fig. 3e) across all recruits. However, all fitness surfaces were dampened when accounting for temperature effects (Fig. 3f, g, h, i and j).

Analysis of linear selection intensity on a cohort-by-cohort basis demonstrated that settlement condition was the trait that most frequently influenced selective mortality, followed by early juvenile growth (Table 2). Selective mortality based on settlement condition was significant for five of the seven cohorts (Fig. 4; Table 2; Cohorts 3, 6, 7, 8, 10: $t_{33-126} = -5.278$ to 2.207 , $P = 0.045$ to $P < 0.0001$), whereas selection intensity of juvenile growth was significant in three of the seven cohorts (Table 2; Cohorts 1, 3, 8: $t_{49-65} = -3.977$ to -2.944 , $P = 0.005$ to $P < 0.0001$). Selection intensity for settlement size was typically negative (five of seven cohorts) but significant selection only occurred in two cohorts (Cohort 7: $t_{44} = 2.753$, $P = 0.009$; Cohort 8: $t_{61} = 2.309$, $P = 0.024$). For PLD, consistently negative selection intensity only corresponded to significant selection in one cohort (Cohort 8: $t_{61} = 2.497$, $P = 0.015$). No cohorts exhibited significant selection based on larval growth.

Fitness functions calculated for recruit settlement condition in the coolest and warmest cohorts illustrate opposite patterns of directional selection based on water temperature. In the cohort experiencing the coolest water temperatures (Cohort 10, Fig. 5a), individuals with low settlement

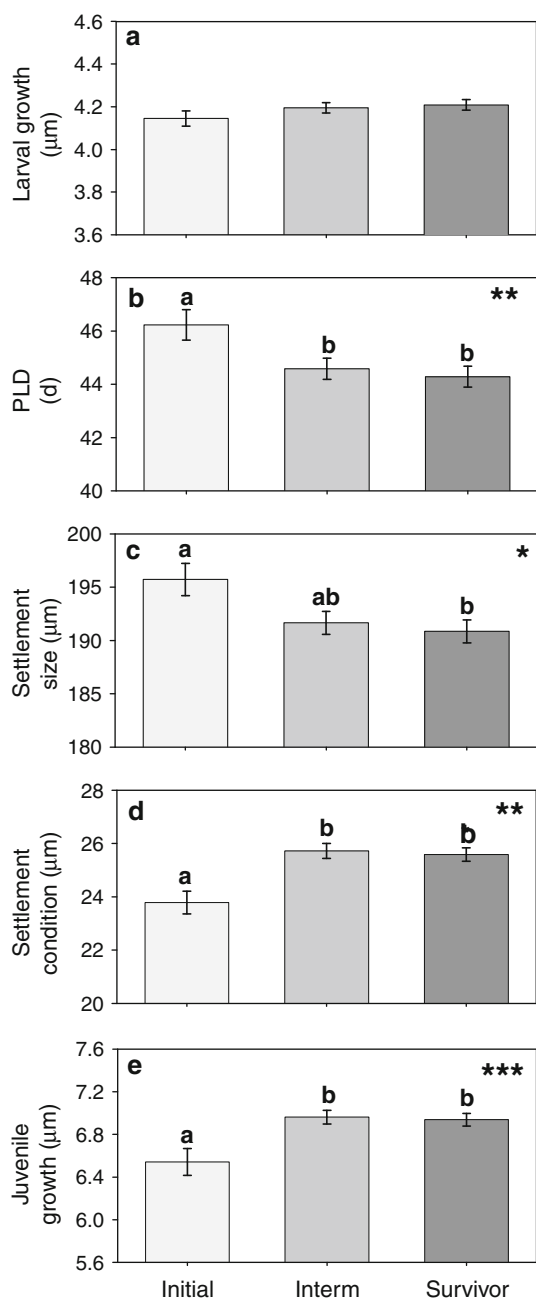


Fig. 2 Early life history traits of *Thalassoma bifasciatum* for three juvenile age groups across all cohorts (adjusted means \pm SE). ANCOVA was used to separate the effects of temperature on four traits: **a** larval growth, **b** PLD, **c** settlement size, **e** juvenile growth. Different letters indicate statistical differences among means based on Tukey tests at $P < 0.05$. **d** Settlement condition (otolith metamorphic band width) was tested using a general linear model due to a significant interaction between age group and temperature for this trait. Age groups were *initial* (juvenile age 0–4 days), *intermediate* (*Interm* juvenile age 5–9 days), and *survivor* (juvenile age ≥ 10 days). * $P = 0.024$, ** $P < 0.010$, *** $P < 0.0001$

condition were selectively lost, whereas in the cohort experiencing the warmest temperatures (Cohort 6, Fig. 5b), there was selective loss of individuals of high settlement

condition. This positive versus negative selection for settlement condition is also evident in the analysis of selection intensity, where only Cohort 6 demonstrated negative selective mortality (Table 2).

Discussion

Increasing evidence points to the importance not only of the numbers of individuals surviving and contributing to the population but also the quality of these newly settled individuals (McCormick 1998), creating a strong link between larval life and early juvenile survival for a number of different taxa (e.g., Searcy and Sponaugle 2001; Phillips 2002; McCormick and Hoey 2004; Gagliano et al. 2007a). We examined this carry-over effect between life stages for seven natural cohorts of a common reef fish and found differences in juvenile performance based on early life history traits, which varied in their relative importance for survival and were strongly influenced by temperature. Our results demonstrate that selective mortality is not always strong and consistent, and differences in water temperature can mediate the impact of certain traits on juvenile survival.

Four out of five early life history traits showed significant changes over the first few weeks of life on the reef as individuals with particular traits were selectively removed from the population. The trait most frequently associated with juvenile survival was settlement condition (significant selective mortality in five out of seven cohorts). Measured as otolith metamorphic band width, this trait also influenced *T. bifasciatum* survival in Barbados (Searcy and Sponaugle 2001) and St. Croix (Hamilton et al. 2008). Hoey and McCormick (2004) found that predation on a juvenile damselfish was selective for fish of lower condition, and survivors from high mortality reefs were of higher condition. Similarly, gastropods, bivalves, and barnacles of higher larval condition were also more likely to survive as juveniles (Moran and Emlet 2001; Phillips 2002; Thiagarajan et al. 2002; Jarrett 2003). Higher condition can lead to several behavioral advantages: higher condition juveniles may obtain more resources due to increased foraging rates (Puvanendran and Brown 1999) or evade predators more quickly due to faster evasion speeds (Gorud-Colvert and Sponaugle 2006). Individuals of higher condition are often larger (Booth and Hixon 1999; Moran and Emlet 2001; Phillips 2002); however, fast-growing, high condition individuals in our study frequently settled earlier (i.e. had shorter PLDs) and were smaller at settlement, although there was no consistent overall relationship between settlement condition and size.

Selection on three additional traits was consistent when considering all cohorts of *T. bifasciatum* together and

Fig. 3 Fitness functions generated using cubic splines for five early life history traits of *Thalassoma bifasciatum* both with (left column) and without (right column) the effect of temperature. Dashed lines indicate 95% confidence bands

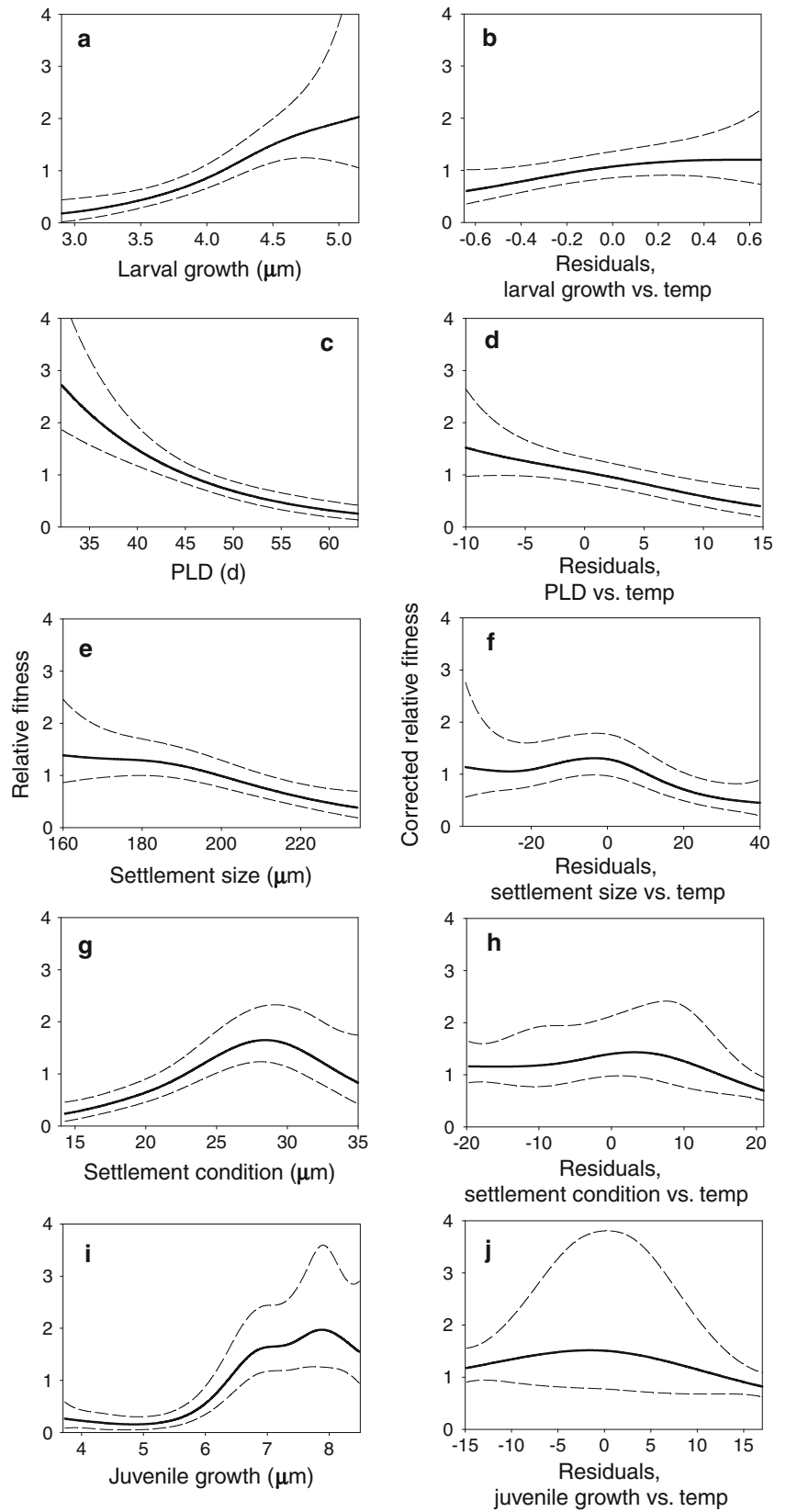


Table 2 The intensity of linear selection (S_i) measured for each of five early life history traits by cohort of *Thalassoma bifasciatum* (arranged by coolest to warmest temperatures during the larval phase)

Cohort	Larval growth (μm)	PLD (days)	Settlement size (μm)	Settlement condition (μm)	Juvenile growth (μm)
10	0.151	-0.102	0.058	2.074***	0.326
7	-0.194	-0.496	-0.710*	1.279***	-0.613
1	0.180	-0.035	0.082	0.113	1.0775***
3	0.171	-0.227	-0.124	0.597*	0.918***
4	-0.236	-0.268	-0.548	-0.143	0.272
8	0.298	-0.687*	-0.665*	1.143**	0.974*
6	0.127	-0.153	-0.082	-0.324*	-0.069

Bold indicates significant trait differences between initial fish and survivors based on two-sample t tests with Bonferroni adjustments: * $P < 0.050$, ** $P < 0.010$, *** $P < 0.0001$

accounting for variation in temperature: survivors had significantly shorter PLDs, were smaller at the time of settlement, and grew faster during the first 3 days of juvenile life. On a cohort-by-cohort basis, however, consistent directions of selection (PLD: all negative selection intensities; settlement size: negative selection intensities for five out of seven cohorts; juvenile growth: positive selection intensity for five out of seven cohorts) were not frequently significant (PLD: significant selective loss of traits in one cohort; settlement size: two cohorts; juvenile growth: three cohorts). Although these traits were not frequently related to significant selective loss on their own, they likely interacted with settlement condition (see below).

Collected fish exposed to seasonally variable water temperatures in their natural environment had variable early life history traits: settlement condition and juvenile growth were highly variable, with settlement condition exhibiting the highest overall CV. Other studies have found similar variability in measures of condition, specifically in lipids (Wendt 1998; Hoey and McCormick 2004). Differences in the occurrence and strength of selective mortality can be influenced by the degree of variability in early life history traits, because mortality can only be selective when traits are sufficiently variable (Sogard 1997). High variation likely contributes to the fact that mortality was most frequently selective with regard to settlement condition and, secondarily, juvenile growth. As low condition, slow-growing *T. bifasciatum* juveniles were typically removed from the cohort over time (i.e. with increasing juvenile age), variability in settlement condition and juvenile growth decreased. Larval growth was the least variable trait (i.e. CV remained stable over time). In fishes, larval growth is often tightly coupled to water temperature during the pelagic phase (Houde 1989; Meekan et al. 2003; Green and Fisher 2004), and seasonal fluctuations in temperature can lead to large differences in larval growth for cohorts settling during different times of the year. For 13

T. bifasciatum cohorts, including those used in the present study, water temperature explained almost 80% of the variation in cohort-specific larval growth (Sponaugle et al. 2006). However, the temperature range experienced by larvae of a single cohort was much less, and low variability in larval growth for different age groups within a cohort may reflect this.

Initial settlers had widely varying early life history traits over the seven cohorts we sampled. If an optimum value of a trait exists, significant relationships between early life history traits and temperature will likely change the direction of selective mortality as initial fish with high or low trait values experience positive or negative selection. On average, there was selective loss of initial fish with lower settlement condition; however, some loss of high condition individuals also occurred: selection intensity was negative for both Cohorts 4 and 6 (significant for 6). Considering all cohorts together, selective loss of recruits with both very high and very low condition levels at settlement points to an optimal settlement condition, evident in the fitness function as the mid-range of metamorphic band widths at $\sim 28 \mu\text{m}$ (Fig. 3d). Selective mortality can be stabilizing, minimizing variation by removing both the high and low extremes of a certain trait (Sogard 1997). Interestingly, mean settlement condition of the initial settlers in Cohorts 4 and 6 was the highest of all seven cohorts (Fig. 4). Selective loss of very high condition fish suggests a cost associated with higher condition levels. Either high condition itself becomes detrimental (as with very fast growth leading to decreased swimming capability; Billerbeck et al. 2001) or a negative effect associated with tightly coupled traits may overwhelm the benefits of high condition. For example, Cohort 4 settlers were also the largest at settlement (mean \pm SE 206.7 ± 5.8 mm, range: 184.4–206.7 mm). If condition is a reflection of accumulated energy storage, high condition can be attained through fast larval growth over short periods in the plankton (i.e. more energy available for rapid storage) or

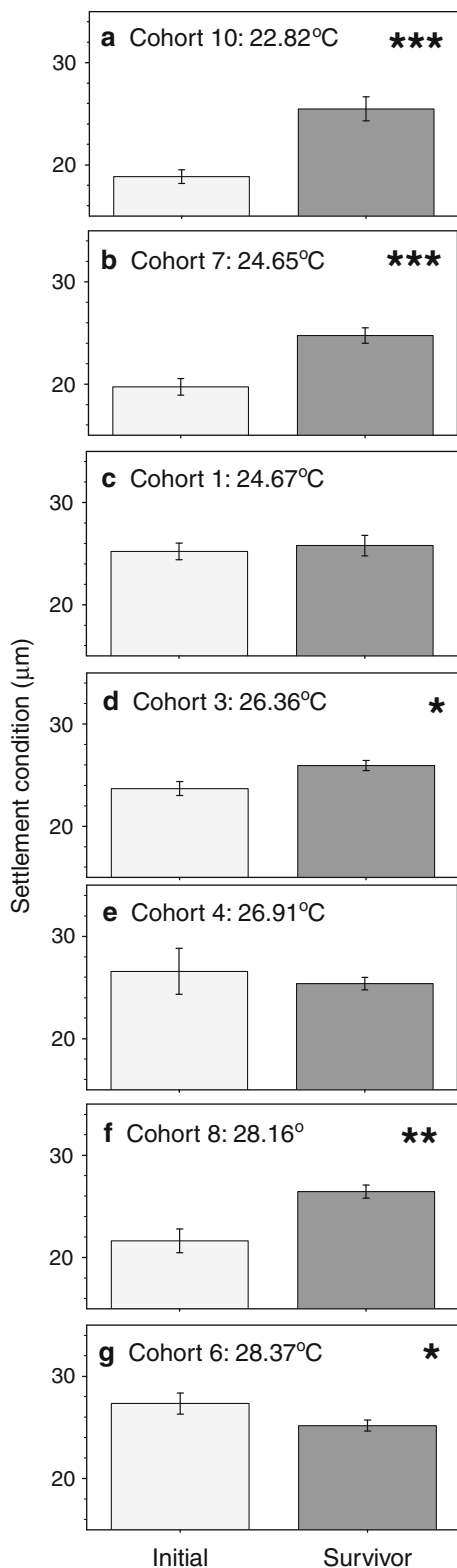


Fig. 4 Settlement condition (mean otolith metamorphic band width \pm SE) of *Thalassoma bifasciatum* by cohort for initial fish and survivors based on *t* test with Bonferroni adjustment. *Initial* (juvenile age 0–4 days), *survivor* (juvenile age \geq 10 days). * $P < 0.05$, ** $P < 0.010$, *** $P < 0.0001$

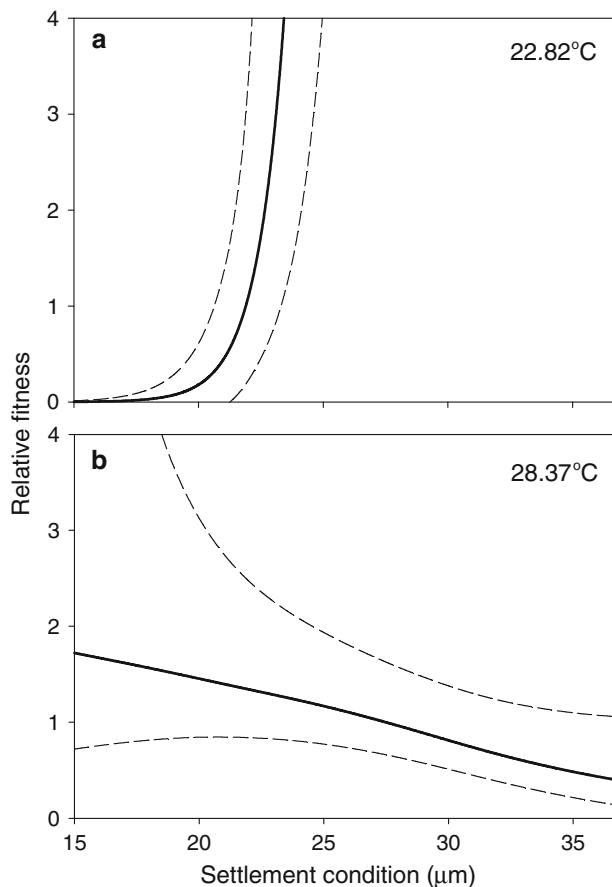


Fig. 5 Settlement condition fitness functions generated using cubic splines for the cohort of *Thalassoma bifasciatum* subjected to **a** the coolest water temperature (Cohort 10, 22.82°C), and **b** the warmest water temperature (Cohort 6, 28.37°C) during the larval phase. *Dashed lines* indicate 95% confidence bands

slightly slower growth (slower energy accumulation) over longer periods. Each scenario results in larvae of substantially different sizes at settlement. Thus, although condition is the trait most frequently selected against, tight linkages with other traits may make trait-specific mortality difficult to distinguish.

Although our results point to an intermediate settlement condition for *T. bifasciatum*, in other situations, optimal traits may shift with environmental variables. For example, if predator abundance shifts seasonally (e.g., piscivory of a snapper decreases in winter; Rooker 1995), it may be more advantageous for prey to settle at larger sizes and thus obtain a size refuge from predators during that time of the year. Thus, temperature may mediate the importance of selective advantages acquired during either the larval or juvenile phase in several ways. It is likely, therefore, that changes in selective mortality among cohorts of fish settling in highly variable environments with seasonal temperature shifts is common. Although an

argument could be made that such changes in selective mortality may be less apparent in environments with lower seasonal variability, such as those found in tropical settings, there are likely other factors that contribute to fluctuating patterns of selective survival. Where water temperatures are not as variable, *T. bifasciatum* recruits in St. Croix (Hamilton et al. 2008) and Barbados (Searcy and Sponaugle 2001), and a pomacentrid in the northern Great Barrier Reef (Hoey and McCormick 2004) also showed evidence of selective mortality based on settlement condition. In some environments, variation in other factors such as food availability (e.g., Phillips 2004) and seasonal water-mass differences (e.g., Sponaugle and Grorud-Colvert 2006) also influence early life history traits. Thus, there is potential for patterns of selective mortality to shift over time and space.

While overall trends indicated that survivors generally had shorter PLDs, were smaller at settlement, settled at higher condition levels, and exhibited faster juvenile growth, the strength and direction of within-cohort selective loss were variable on a cohort-by-cohort basis. Because the relative importance of specific survival characteristics can change due to differences in environmental factors, predation rates, distribution of traits, and prevalence of selective loss, it is important to study multiple natural cohorts across seasonal conditions. All *T. bifasciatum* cohorts revealed differences in juvenile performance with respect to early life history traits, but the trait most important for survival varied somewhat among cohorts. Jarrett (2003) observed similarly variable juvenile survival based on metamorphic success and subsequent growth of newly settled barnacles from multiple cohorts. For any given cohort of *T. bifasciatum*, selective mortality based on a single trait was highly variable, but consideration of all seven cohorts revealed significant patterns of selective mortality for four out of five traits. Selection for fast larval growth was weak for juvenile Atlantic cod *Gadus morhua* on the Scotian Shelf during one winter, but strong selection was detected the following winter, potentially due to poor environmental conditions during that year (Meekan and Fortier 1996). During times of the year with especially stressful conditions, very high mortality may obscure selective loss of traits for cohorts sampled during those times (Moran and Emler 2001).

In summary, simple seasonal variation in water temperature can lead to differences in the quality of individuals: fish settling during cooler water temperatures had longer PLDs, were larger and of lower settlement condition, and grew more slowly as juveniles. This variability in traits as well as differences in the occurrence and strength of selective mortality led to a diversity of early life histories exhibited by individuals within cohorts. Differences among cohorts, largely driven by

seasonal and other environmental factors, adds another level of complexity. Strong relationships among early life history traits led to predictable patterns, such as faster larval growth and shorter PLDs in warmer months. However, some relationships broke down as particular traits, such as settlement condition, were related to optimum survival at intermediate trait values. Condition-based selective mortality occurred most frequently, reflecting the importance of this trait to early survival, but the nature of selective mortality acting on the traits was influenced by water temperature. The effect of phenotypic traits on selective mortality can change with environmental conditions as the nature of selective loss depends on the temperature experienced during early life stages. For organisms with complex life cycles, the quality of survivors in one life history stage can affect later performance in subsequent stages. The degree to which these carry-over effects further influence fitness in adults that survive to reproduce could have important consequences for fish populations.

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