# Environmental variability, early life-history traits, and survival of new coral reef fish recruits

Su Sponaugle[1] and Kirsten Grorud-Colvert

Marine Biology and Fisheries Division, Rosenstiel School of Marine and Atmospheric Science,
University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA

**Synopsis** For benthic marine organisms with complex life cycles, conditions experienced by pelagic larvae can influence juvenile survival. Trait-specific selective mortality has been documented in the laboratory and field, yet our knowledge of the factors contributing to the existence, strength, and consistency of natural selective mortality is limited. We compiled previously published and unpublished data on the common Caribbean coral reef fish, *Thalassoma bifasciatum*, recruiting to Barbados, West Indies, and the upper Florida Keys to examine how environmental variability during pelagic larval life influences the distribution of early life-history traits exhibited by new recruits. We explored how the scope of variability in otolith-derived traits such as larval growth, pelagic larval duration (PLD), size and condition at settlement, and early juvenile growth influences the degree to which mortality of juveniles is selective. At both locations, contrasting oceanographic conditions (periodic passage of large low-salinity North Brazil Current [NBC] rings near Barbados and seasonal variation in water temperature at Florida) led to significant differences in the early life-history traits of recruits. Mortality was most frequently selective for the two most variable traits, condition at settlement and early juvenile growth. Environmental variability (including variation in predation pressure and stress-inducing conditions) also likely influences juvenile mortality and consequently the degree to which selective loss of particular traits occurs. As we begin to better understand the spatial, temporal, and species-specific circumstances in which events occurring during larval life influence juvenile performance, studies must also be extended to examine how these processes are translated into adult fitness.

## Introduction

For organisms with complex life histories, where one life stage occupies an environment entirely different from that inhabited by other stages, events occurring during one stage can have important implications for the performance and survival of individuals in subsequent stages. This is particularly evident in benthic marine organisms, whose adults release pelagic larvae that spend from hours to months in the plankton before settling back to the demersal juvenile/adult habitat. Selective mortality of individuals with particular life-history traits has been shown to occur separately within larval and juvenile stages (reviewed in Anderson 1988; Sogard 1997), with important linkages between stages. Recent evidence points to the influence of larval growth, size, and condition on juvenile survival in molluscs (Pechenik and others 1996, 2002; Moran and Emlet 2001; Phillips 2002, 2004), barnacles (Pechenik and others 1993; Jarrett 2003; Thiyagarajan and others 2003), bryozoans (Marshall, Bolton, and others 2003), ascidians (Marshall, Pechenik, and others 2003), and fish (McCormick 1998; Searcy and Sponaugle 2001; Bergenius and others 2002, 2005; Shima and Findlay 2002; Vigliola and Meekan 2002; Wilson and Meekan 2002; Brunton and Booth 2003; Hoey and McCormick 2004; McCormick and Hoey 2004).

As longer time series are collected for species under natural field conditions, it is becoming more apparent, however, that mortality is not always selective (or consistently selective) with regard to particular traits (Meekan and Fortier 1996; Jarrett 2003; Grorud-Colvert 2006). Thus, as more evidence of trait-specific selective mortality accumulates, we can refine our focus from one of simply identifying whether mortality is selective in a particular species to one seeking to define the circumstances under which mortality might be more or less selective. Under what conditions are events occurring during larval life important for juvenile survival? The degree to which mortality might be more or less selective with regard to particular traits will depend on the scope of variability in the trait(s), as

---

From the symposium "Integrating Function over Marine Life Cycles" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2006, at Orlando, Florida.

[1] E-mail: ssponaugle@rsmas.miami.edu

*Integrative and Comparative Biology,* volume 46, number 5, pp. 623–633
doi:10.1093/icb/icl014
Advance Access publication July 11, 2006

well as the intensity of mortality rates, both of which are influenced in part by environmental variability. A sufficiently wide range in a given life-history trait is a prerequisite for mortality to be selective with regard to that trait (Sogard 1997). Such trait variation will be defined by a species' plasticity and life history together with the range of environmental conditions experienced by an individual. Water temperature, for example, has been shown to explain 30% of the variability in larval growth of a goatfish (McCormick and Molony 1995) and damselfish (Meekan and others 2003) and 78% in a wrasse (Sponaugle and others 2006). Larvae settling to locations or during seasons with greater environmental variability may tend to exhibit greater variation in early life-history traits. Is mortality more selective under these circumstances? Mortality experienced by juveniles can also affect the carryover of traits since mortality rates (and potentially degree of selective loss) will be influenced by levels of predation, competition, and physical environmental conditions affecting stress and survival, all of which are frequently difficult to quantify.

Our goal was to compile previously published and unpublished data from our laboratory for a single model species, the common Caribbean bluehead wrasse, *Thalassoma bifasciatum*, to explore the relationship between environmental variability, the suite of early life-history traits exhibited by new settlers, and early selective mortality. We examined environmental variability in 2 systems—the geographically isolated Caribbean island of Barbados and the continental subtropical reef system along the upper Florida Keys. Fish settling in these 2 areas experience variable pelagic conditions from 2 major sources: in Barbados, large-scale low-salinity North Brazil Current (NBC) rings periodically impinge upon the local, otherwise oceanic island environment, and in Florida, water temperatures vary seasonally. Here we examine the role of environmental variability in creating variation in early life-history traits and explore how these may influence the existence and strength of selective mortality.

## Materials and methods

### Data sources

We compiled data on early life-history traits of *T. bifasciatum* from previously published sources as well as from recruits that were not used in any other study. Data for fish from Barbados were obtained from Searcy and Sponaugle (2000, 2001) and Sponaugle and Pinkard (2004a), with additional recruitment data from Sponaugle and Cowen (1997). Data for fish from the Florida Keys were obtained from Sponaugle and colleagues (2006) and Grorud-Colvert (2006), as well as from ongoing monthly recruitment surveys.

### Environmental setting of study sites

***Barbados***—Barbados is the easternmost island in the Lesser Antilles and is isolated from the mainland and other islands in the Caribbean (nearest neighbor is 140 km to the west). Embedded within the northwest flowing Guyana Current, large-scale flow is topographically steered around Barbados (Cowen and Castro 1994) and is thought to help retain locally spawned larvae within the vicinity of the island (Cowen and others 2000; Paris and Cowen 2004). Evidence suggests that Barbados fish populations are largely self-recruited (Cowen and others 2000, 2006).

As would be expected for the island's low latitude, waters surrounding Barbados show little seasonal temperature fluctuation, for example, maximum fluctuation of 2°C over the year (Sponaugle and Pinkard 2004a). However, periodic passage of mesoscale low-salinity current rings by the island generate substantial variability in characteristics of the surrounding water mass (Kelly and others 2000; Goni and Johns 2001; Cowen and others 2003). These large anticyclonic rings are shed at the retroflexion of the North Equatorial Counter Current and the NBC. They entrain low-salinity water from the Amazon River and propagate northwestward to encounter the Lesser Antilles, frequently passing by or near Barbados (5–7 rings per year; Fratantoni and others 1995; Kelly and others 2000; Goni and Johns 2001).

Fish examined by Sponaugle and Pinkard (2004a) experienced pelagic conditions that were periodically influenced by a passing NBC ring. The timing of ring passage was determined from hydrographic data collected at 10–13 m depth by a CT sensor moored 2 km off the west coast of the island at 290 m depth (Kelly and others 2000; Sponaugle and Pinkard 2004a).

***Florida Keys***—The Florida Keys (FK) comprise a chain of islands curving southwesterly off the southern tip of mainland Florida, separating the shallow Florida Bay from the Atlantic Ocean. Approximately 10 km seaward of the Keys, spur-and-groove bank reefs fringe the nearshore lagoon and the western edge of the Florida Current, a major western boundary current. Typically, the Florida Current enters the Straits of Florida from the Gulf of Mexico Loop Current and rapidly (mean speeds = 160 cm $s^{-1}$; Richardson and others 1969) passes by the Keys, turning northward and eventually becoming the Gulf Stream farther north (see map by Lee and colleagues [1994]).

The western boundary of the Florida Current is characterized by frontal meanders and mesoscale and submesoscale eddies (Lee and Williams 1999), which have been hypothesized (Lee and others 1994) and recently shown to play a role in the population replenishment of benthic marine organisms (submesoscale: Limouzy-Paris and colleagues [1997]; mesoscale: Yeung and colleagues [2001]; Yeung and Lee [2002]; Criales and colleagues [2003]; Sponaugle and colleagues [2005]).

Coral reefs of the Florida Keys support a typical suite of tropical fish species; however, water temperatures are more seasonally variable than in tropical locations. Newly settled fish (recruits) studied by Sponaugle and colleagues (2006) and Grorud-Colvert (2006) experienced mean water temperatures varying by 6°C. Daily water-temperature data were obtained previously from the National Underwater Research Center, where temperatures were continuously recorded at 21 m on Conch Reef (24°59′N, 80°25′W).

## Study species

The bluehead wrasse, *T. bifasciatum,* is a common coral reef fish found throughout the Caribbean. It spawns daily (Warner and Robertson 1978), and pelagic larvae spend ~50 days in the plankton before settling back to the reef (Victor 1986a; Sponaugle and Cowen 1997). Settlement generally occurs in pulses associated with the third quarter moon (Sponaugle and Cowen 1997; Sponaugle and Pinkard 2004b) or new moon (Victor 1986b; Robertson and others 1999). Transparent larvae settle to the sand and rubble at the periphery of coral reefs and remain buried for 3–5 days until metamorphosis is complete and fully pigmented juveniles emerge onto the reef (Victor 1982). A record of these phases and transitions can be obtained by examining the otoliths (see Fig. 1), or ear stones, as increments are deposited daily (Victor 1982), and there is a strong relationship between body length and otolith length (Victor 1986a; Masterson and others 1997; Sponaugle and Cowen 1997; Searcy and Sponaugle 2001). The width between successive increments provides a relative measure of somatic growth (Searcy and Sponaugle 2000, 2001), and the width of the broad band deposited during the non-feeding metamorphic period between settlement and emergence is thought to reflect relative condition (since higher condition fish likely deposit more material as they undergo metamorphosis; Searcy and Sponaugle 2000; Fig 1). Thus, the otoliths of individuals provide an estimate of timing of spawning, timing of settlement, larval growth, pelagic larval duration (PLD), size-at-age, condition at settlement, and juvenile growth.

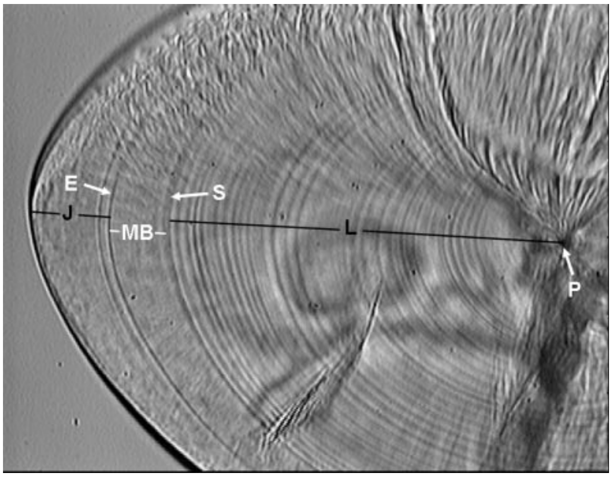

**Fig. 1** Image of sagittal otolith from *Thalassoma bifasciatum* recruit with life-history transitions marked. P = otolith primordium or core; L = larval increments, S = settlement; E = emergence; MB = metamorphic band; J = juvenile, post-emergence increments. Otolith radius (size) at settlement was measured as the distance between P and S.

## Sampling

Sampling (described in detail in primary sources) was similar between locations and studies. Cohorts (fish settling within a single lunar cycle) of *T. bifasciatum* recruits (≤20 mm, standard length) were censused and collected biweekly or monthly from replicate sites along the nearshore fringing reefs of Barbados and the offshore bank reefs of the upper Florida Keys. At each site, 6–30 (depending on the study) replicate 5 × 1 m haphazardly placed quadrats were sampled to obtain estimates of density. A team of 2 divers counted and collected recruits using hand nets and the anesthetic quinaldine. When necessary, additional recruits were collected at the end of each census to provide sufficient sample sizes for otolith analysis. To examine selective mortality over time, particular cohorts were repeatedly sampled every 3 days for the first 2 weeks of life on the reef. Collected recruits were preserved in 95% ethanol.

## Otolith analysis

All otoliths were extracted and processed using standard techniques (for example, Sponaugle and others 2006). After clearing in immersion oil for 15–30 days, sagittal otoliths were examined at 400× oil immersion magnification through a Leica microscope equipped with a polarizing filter between the light source and the first stage. The microscope image was transferred through a video camera and frame grabber to either OPTIMUS (Searcy and Sponaugle 2000) or Image Pro 4.5 software (Sponaugle and Pinkard 2004a;

Grorud-Colvert 2006; Sponaugle and others 2006) where it was sharpened and analyzed.

The longest sagittal radius was selected to enumerate each larval and juvenile increment as well as the transitional marks indicating settlement and emergence (see Sponaugle and Pinkard 2004a). For the purposes of the study, we compiled only the following early life-history traits: mean larval growth (otolith increment widths over the entire PLD), PLD, size (otolith radius) at settlement, relative condition at settlement (otolith metamorphic bandwidth), and juvenile growth (mean otolith increment width during days 0–4 post-emergence, following metamorphosis).

### Data analysis

We examined the distribution of early life-history traits in *T. bifasciatum* cohorts that experienced different pelagic conditions using otolith data obtained during previous studies (see Data sources) as well as from additional fish. Fish were divided into cohorts that, in Barbados, experienced an NBC ring (RING) versus those that did not (NO RING), and, in Florida, experienced cooler (22.8–24.8°C) versus warmer (26.4–29.3°C) water. We calculated frequency distributions for each ELH trait and for illustration purposes fit a curve to the resulting histograms using the spline function of SIGMAPLOT (Version 8.0). Fewer otolith growth trajectories were available for examining larval and juvenile growth, so sample sizes differed by analysis (Table 1).

We also compared coefficients of variation (CVs) for each trait exhibited by the different environmental subgroups (RING/NO RING; cooler/warmer water) at the 2 locations to determine the magnitude of variability in early life-history traits. For this analysis, we compared the CVs for recruits of all ages as well as only for those $\leq$4 days old; the latter fish represented the youngest settlers with a record of early juvenile growth.

To illustrate differences in selective mortality among cohorts, we similarly plotted the frequency histograms of ELH traits for 2 representative cohorts from the Florida Keys, one that experienced average, intermediate water temperatures and one that experienced the coldest and likely most stressful water temperatures. For each cohort, traits of the initial group of settlers (juvenile ages 0–4 days post-emergence) were compared with the trait distributions of the survivors (juvenile ages $\geq$10 days post-emergence).

## Results

Early life-history traits are generally quite variable for *T. bifasciatum*, whether they recruit to Barbados or the Florida Keys. CVs were highest for 2 traits: condition (otolith metamorphic bandwidth) and juvenile growth (Table 2). Larval growth and settlement size had the lowest CVs, and PLD had intermediate CVs. This pattern of differential trait variation was evident for all recruits considered together as well as for those only 0–4 days old post-emergence and did not change appreciably with the environmental conditions experienced by larvae (that is, CVs for RING versus NO RING and cool versus warm water were roughly similar). Trait CVs at Barbados were generally similar to or exceeded corresponding CVs for Florida fish (that is, when comparing paired values, all fish; NO RING versus warm; RING versus cool) (Table 2).

The frequency distributions of early life-history traits differed between groups of fish experiencing different pelagic oceanographic conditions. Relative to fish that did not experience an NBC ring in Barbados, larvae experiencing a ring had slower larval growth, longer PLDs, larger settlement sizes, and were of lower condition at settlement, although early juvenile growth was similar for both groups (Fig. 2).

**Table 1** Sample sizes of new recruits of *Thalassoma bifasciatum* from Barbados and the upper Florida Keys used in compilation of otolith-derived early life-history traits, and sources for previously published data

| | PLD, SS, BW | LG, JG | Source |
|---|---|---|---|
| Barbados | | | Searcy and Sponaugle 2000; Sponaugle and Pinkard 2004a |
| Total | 597 (256) | 268 (147) | |
| NO RING | 269 (102) | 60 (29) | |
| RING | 282 (128) | 162 (89) | |
| Florida Keys | | | Sponaugle and others 2006; Grorud-Colvert 2006; Additional (unpublished data) fish |
| Total | 1596 (388) | 1472 (357) | |
| Cooler | 265 (83) | 265 (147) | |
| Warmer | 729 (117) | 729 (114) | |

Samples sizes in parentheses are those used for fish 0–4 days post-emergence, the initial populations for examination of selective mortality. Early life-history traits examined were pelagic larval duration (PLD), settlement size (SS), metamorphic bandwidth (BW, a proxy for condition), larval growth (LG, mean increment width over the entire PLD), and juvenile growth (JG, mean increment width over the first 4 days of juvenile life). Fewer otolith growth trajectories were available for examining LG and JG. Cohorts of recruits at Barbados were divided by whether they encountered a North Brazil Current ring (RING) or not (NO RING) as larvae. Florida fish were divided by whether they experienced cooler (22.8–24.8°C) versus warmer (26.4–29.3°C) water during larval life.

**Table 2** Coefficient of variation (CV) of 5 early life-history traits exhibited by new recruits of *T. bifasciatum* from Barbados (BR) and the upper Florida Keys (FK)

| ELH Trait | BR ALL | BR NO RING | BR RING | FK ALL | FK COOL | FK WARM |
|---|---|---|---|---|---|---|
| All recruits | | | | | | |
| LG | 10.8 | 10.4 | 9.9 | 10.3 | 9.4 | 8.3 |
| PLD | 19.1 | 18.5 | 17.4 | 15.9 | 14.5 | 14.4 |
| SS | 11.8 | 11.7 | 11.0 | 10.3 | 10.5 | 9.9 |
| BW | 26.2 | 22.1 | 28.4 | 20.6 | 20.3 | 20.9 |
| JG | 25.2 | 27.4 | 24.7 | 17.4 | 21.7 | 12.6 |
| Recruits 0–4 days | | | | | | |
| LG | 11.4 | 12.3 | 9.5 | 10.9 | 9.5 | 8.3 |
| PLD | 19.1 | 18.1 | 18.3 | 16.1 | 14.2 | 13.7 |
| SS | 11.8 | 11.9 | 11.5 | 10.4 | 10.8 | 9.8 |
| BW | 27.0 | 22.5 | 28.6 | 24.0 | 23.5 | 25.8 |
| JG | 30.4 | 34.0 | 29.7 | 20.1 | 24.3 | 16.4 |

CVs were calculated for all fish corresponding to the frequency distributions in Figure 2, as well as for fish between 0–4 days post-emergence, the initial population for examination of selective mortality. Cohorts of recruits at BR were divided by whether they encountered a North Brazil Current ring (RING) or not (NO RING) as larvae. FK fish were divided by whether they experienced cooler (22.8–24.8°C) versus warmer (26.4–29.3°C) water during larval life. Early life-history traits examined were pelagic larval duration (PLD), settlement size (SS), metamorphic bandwidth (BW, a proxy for condition), larval growth (LG, mean increment width over the entire PLD), and juvenile growth (JG, mean increment width over the first 4 days of juvenile life).

Likewise, larvae in cooler waters off the Florida Keys had slower larval growth and longer PLDs, and the youngest settlers (initial fish) were of lower mean condition (Grorud-Colvert 2006). Note that condition at settlement is plotted for younger and older recruits together in Figure 2; therefore, age-specific differences in condition are not as evident. Settlement size was a non-linear function of water temperature; fish at intermediate water temperatures were larger at settlement than fish from either cooler or warmer water (Sponaugle and others 2006). Thus, division of all fish into only 2 simplistic categories (cooler and warmer water) obscures these differences. Water temperatures experienced by juveniles were related to larval water temperatures, so juvenile growth was reduced in cohorts from cooler water relative to those from warmer water (Fig. 2).

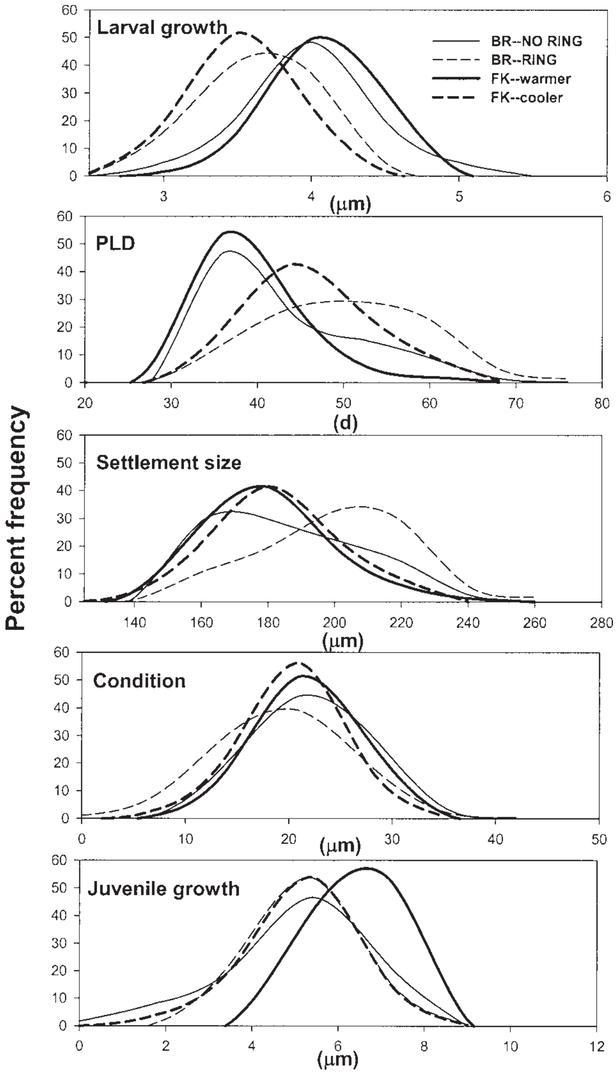

**Fig. 2** Frequency curves for 5 early life-history traits exhibited by *T. bifasciatum* recruits collected from Barbados and the upper Florida Keys. Larval growth, pelagic larval duration (PLD), settlement size, condition at settlement (metamorphic bandwidth), and early juvenile growth were obtained from otoliths of individual fish and lines were fit to frequency histograms of traits. Cohorts of recruits at Barbados (BR) were divided by whether they encountered a North Brazil Current ring (RING) or not (NO RING) as larvae. Florida Keys fish (FK) were divided by whether they experienced cooler (22.8–24.8°C) versus warmer (26.4–29.3°C) water during larval life.

Mortality was selective for condition at settlement and early juvenile growth in all 3 cohorts examined from Barbados (Searcy and Sponaugle 2001) as well as 5 (condition) and 4 (juvenile growth) cohorts out of 9 examined from the Florida Keys (Grorud-Colvert 2006). The distributions of ELH traits of 2 representative cohorts from the FK illustrate general findings (Fig. 3). Within each of the 2 cohorts that experienced different water temperatures as larvae (Cohort 3 in average, intermediate water temperatures and Cohort 10 in the coldest, potentially most stressful water temperatures), there was no apparent selective mortality based on larval growth, PLD, or size-at-settlement, regardless of the absolute values of traits (Fig. 3). For both cohorts, mortality was selective for condition at settlement (otolith metamorphic bandwidth), with

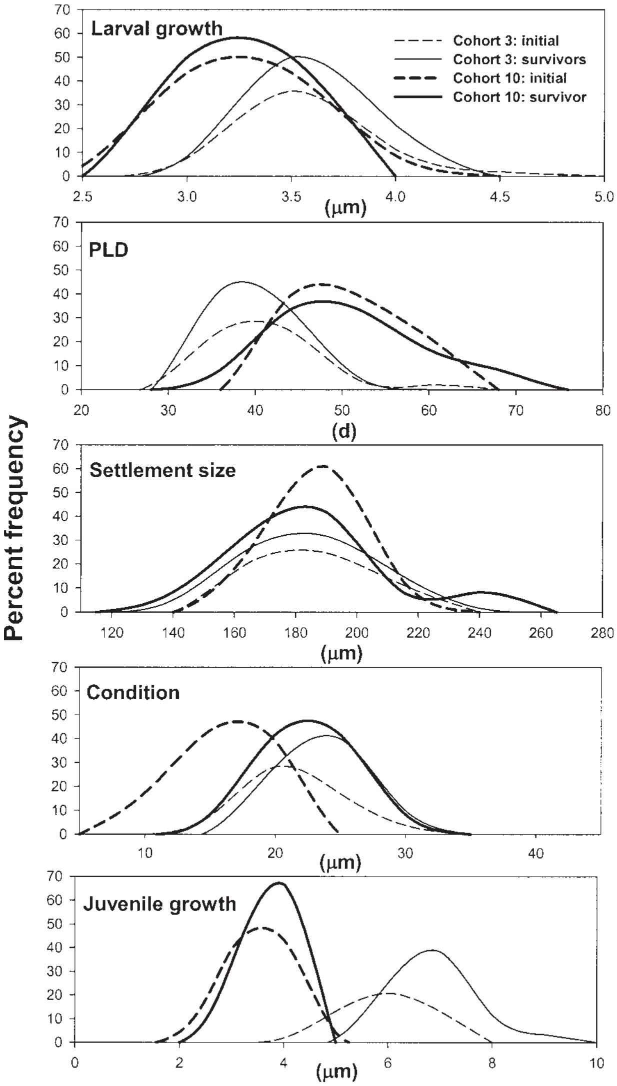

**Fig. 3** Frequency curves for 5 early life-history traits of initial (aged 0–4 days post-emergence) and surviving ($\geq$10 days post-emergence) *T. bifasciatum* recruits from the upper Florida Keys. Larval growth, PLD, settlement size, condition at settlement (metamorphic bandwidth), and early juvenile growth were obtained from otoliths of individual fish and lines were fit to frequency histograms of traits. Cohort 10 experienced cold water (mean of 22.82°C during larval life) and Cohort 3 experienced intermediate-temperature water (mean of 25.58°C during larval life) throughout larval and early juvenile life.

stronger selective loss in Cohort 10. For all 9 cohorts examined from the FK, mean metamorphic bandwidth of survivors converged to a similar absolute value (~25 μm; Grorud-Colvert 2006). In contrast, selective mortality based on juvenile growth occurred in both cohorts with different initial and final absolute values. In other words, there was greater loss of slower growing juveniles, regardless of absolute values (Fig. 3).

## Discussion

The degree to which events occurring during, or traits exhibited by, one stage carryover and influence performance in a subsequent stage should be determined by both the absolute values of, and variation in, traits of individuals as well as the nature and degree of mortality. Our model organism, *T. bifasciatum*, exhibits a suite of early life-history traits that vary within and among monthly cohorts of new recruits, depending on environmental conditions. While the total range of environmental conditions experienced by larvae is no doubt very large, we isolated 2 major sources of environmental variation to examine variation in larval traits and its effect on juvenile survival.

Two sources of environmental variation in 2 different geographic locations produced roughly similar trends in the early life-history traits exhibited by *T. bifasciatum*. Larvae that encountered either low-salinity NBC rings (at Barbados) or lower water temperatures (in the Florida Keys) had reduced larval growth, longer PLDs, and lower condition and larger sizes at settlement (Sponaugle and Pinkard 2004a; Sponaugle and others 2006) than those that either did not encounter an NBC ring or were in warmer water. Compromised quality of larvae in NBC rings is likely due to an indirect effect of changes in larval food sources in different water masses. While invertebrate studies have demonstrated reduced growth or biomass as a direct result of variation in salinity (Qiu and Qian 1998; Gimenez and Anger 2001; Torres and others 2002), salinity differences alone were likely not sufficient to reduce fish growth. Instead, disruption of the prey field due to mixing of water masses may have contributed to reduced food availability and slower larval growth rates (Sponaugle and Pinkard 2004a). Decreased food consumption reduces larval quality as well as lowers metamorphic and juvenile performance in various other organisms (Pechenik and others 1996, 2002; Qiu and Qian 1997; Phillips 2002; Thiyagarajan and others 2003). Adverse environmental conditions such as increased rainfall, solar radiation, and along-shore winds resulted in slower larval growth and longer PLDs of a newly settled surgeonfish, which negatively affected recruitment (Bergenius and others 2005). Similar to the temperature-mediated differences in the early life-history traits of Florida recruits, fluctuations in water temperatures also influenced the growth, PLD, metamorphic success, behavior, or survival of other fishes (for example, Rutherford and Houde 1995; Wilson and Meekan 2002; Meekan and others 2003; Green and Fisher 2004) and invertebrates (for example, Thiyagarajan and others 2002; Phillips 2005).

Variation in early life-history traits in response to environmental fluctuations was frequently linked among traits, likely through the effects of variable growth. Slower growth consistently led to longer PLDs, and although size-at-age during larval life was larger for fast growers, because slow growers were in the plankton longer, actual size-at-settlement was larger for slow growers (except for the very slowest growers, where additional days in the plankton could not compensate for very slow growth rates). Fast growers settling at smaller sizes were of higher condition at settlement and could more readily evade potential predators than could larger settlers (Grorud-Colvert and Sponaugle in press). Where size-selective mortality was evident (see below), *T. bifasciatum* survivors were smaller at settlement (Grorud-Colvert 2006), similar to results for a temperate labrid (Raventos and Macpherson 2005). Early juvenile growth was comparable in Barbados fish that did or did not encounter an NBC ring because these fish experienced similar conditions post-settlement. In contrast, Florida juveniles experienced a seasonal range of water temperatures on the reef, and those in cooler waters grew more slowly than did those in warmer waters. Interestingly, traits exhibited by fish experiencing different pelagic conditions at different geographic locations had consistent levels of variability. The least variable traits were larval growth and settlement size (CVs = 8.3–12.3), followed by PLD (13.7–19.1). In all cases, except for juvenile growth in warm Florida waters (CV = 12.6), condition at settlement and juvenile growth were substantially more variable (CVs = 16.4–34.0) than the other traits. Other studies have also identified high variability in measures of condition relative to size or age (McCormick and Molony 1993; Kerrigan 1996; Molony and Sheaves 1998).

This range in variation likely contributed to the fact that condition at settlement and early juvenile growth were the traits most frequently implicated in selective mortality. In Barbados all 3 cohorts examined had evidence of condition-based selective mortality (that is, survivors had wider otolith metamorphic bands; Searcy and Sponaugle 2001). Out of a total of 9 monthly cohorts examined in Florida, mortality was selective for settlement condition in 5 cohorts and for early juvenile growth in 4. In 3 cohorts, survivors were smaller at settlement (Grorud-Colvert 2006), but neither larval growth nor PLD was important to survivorship at either location. For mortality to be selective there must be sufficient variation in a specific trait within the population of new settlers. Where traits are highly variable, strong selective mortality should result in the largest shift in traits between initial settlers and survivors. When traits are less variable, selective mortality may not be apparent (Sogard 1997). Traits of fish from Barbados tended to be somewhat more variable (higher CVs) than those from Florida fish; therefore, all things being equal (that is, assuming that environmental and predation pressures are similar), selective mortality may be more apparent in Barbados. While the data collected from each site are not entirely comparable in that more cohorts were examined from Florida than from Barbados, condition at settlement was important to survival in 100% of the Barbados cohorts and 56% of the Florida cohorts. Condition-based mortality has also been identified in the field for recruits of other reef fishes (Booth and Hixon 1999; Booth and Beretta 2004; Hoey and McCormick 2004) and newly metamorphosed marine invertebrates (Phillips 2002, 2004; Thiyagarajan and others 2005) as a result of both laboratory-created and natural variation in condition. In all cases, individuals of higher condition preferentially survived.

The absolute value of traits may also contribute to the degree to which mortality is selective for a trait. In Florida, the mean condition at settlement converged to an intermediate value in survivors (that is, metamorphic bandwidth of ~25 μm) such that cohorts settling with a mean condition close to this value experienced no condition-based selection. Those settling at sharply lower conditions experienced the strongest selection for higher condition, and 1 cohort settling at a higher condition actually experienced reverse selective loss (that is, survivors had smaller metamorphic bandwidths; Grorud-Colvert 2006). On the other hand, for some traits, absolute value was unimportant: mean larval growth and PLD varied significantly among fish experiencing cooler versus warmer water in Florida, yet mortality was never selective for these traits. Juvenile growth followed yet an additional pattern; fish experiencing different water temperatures had significantly different juvenile growth rates (faster in warmer water), and survivors were those that grew faster, regardless of the absolute value of growth rates of initial settlers. Thus, for some life-history traits, absolute value may influence the degree of selective mortality experienced by recruits, while for other traits absolute value is of little consequence.

The other critical components of selective mortality are the nature and degree of mortality. For 9 cohorts recruiting to the upper Florida Keys, mortality was not consistently selective for any single trait, possibly due to fluctuating environmental conditions including predation pressure. Predator activity may change seasonally, and the availability of alternate prey (for example, recruitment pulses of other conspecifics) may affect

**Table 3** Fish densities on nearshore fringing reefs of Barbados and the bank reefs in the upper Florida Keys

| Fish density (no. $m^{-2}$) | Barbados | Florida Keys |
|---|---|---|
| Herbivores | 0.009 | 0.046 |
| Invertivores | 0.009 | 0.022 |
| Piscivores | 0.002 | 0.014 |
| *T. bifasciatum* recruits | 0.60–0.74 | 0.29 |

Densities for Barbados from Chapman and Kramer (1999) and for the Florida Keys from Bohnsack and colleagues (1999). Densities of new *T. bifasciatum* recruits at Barbados from Sponaugle and Cowen (1997) and at the Florida Keys from Sponaugle and colleagues (unpublished data).

rate of loss and the corresponding degree of selectivity. It is difficult to quantify these factors since little is known about predator behavior and its temporal or spatial variability, or about the interactions among prey. Does the degree of selective mortality increase with increasing mortality rates? Is there a point at which predation is so high that selectivity is obscured? Moran and Emlet (2001) found that mortality of a snail was selective under ambient water temperatures but became non-selective at stressfully high water temperatures. Mortality is difficult to quantify for *T. bifasciatum* recruits due to this species' mobility, ontogenetic changes in behavior, and broad temporal settlement patterns. Existing data for *T. bifasciatum* reveal no obvious trends in patterns of selective mortality with magnitude of recruitment events (unpubl. data), although there is some suggestion that condition-based selection is stronger in the coldest, potentially most stressful, months (that is, Cohort 10). There are likely basic differences in the ecological pressures encountered by new recruits among geographic locations. Reef-fish densities, including those of piscivores, are generally higher and recruitment pulses of *T. bifasciatum* are generally smaller in Florida than at Barbados (Table 3); thus, it is possible that intraspecific competition is lower but losses to predation higher in Florida. Regardless of direct predation-induced mortality, environmental variation at both locations in the form of NBC ring passage and seasonal temperature fluctuation is the norm rather than the exception.

Environmental variability and subsequent variation in early life-history traits of new recruits contribute to a range of phenotypes present in the juvenile population. As these individuals survive over time, it is possible that the adult population will reflect these initial differences. In Barbados, fish exposed to different water masses and selective pressures during their larval period will encounter roughly similar benthic conditions as juveniles, potentially leading to patterns of selective loss that may reduce the majority of variation at an early age. For Florida Keys fish, however, settlers during different seasons will have markedly different life histories, persisting for the duration of the season as juveniles experience nearshore waters over the reef that have an even stronger seasonal fluctuation than offshore waters. Patterns of selective mortality may also be more variable in Florida, where predators experience seasonal changes in water temperature as well. Such seasonally variable traits, coupled with potentially variable predation pressure, may result in the maintenance of a more variable suite of early life-history traits in Florida fish as they age. The influence of early life-history traits and their selective loss over longer periods of time is unknown. Studies of the long-term impacts of selective mortality on population dynamics are needed to address the importance of larval carryover effects for juvenile and adult survival.

## Acknowledgments

This was an outcome of a presentation at the Society of Integrative and Comparative Biology's Symposium on Integrating Function over Marine Life Cycles. The authors thank the organizers, A. Moran and R. Poldolsky, for the invitation to participate. The collection of the original data used in this compilation was supported in Barbados by NSF Grant No. OCE-9521104 to R. K. Cowen, K. Lwiza, and E. Schultz, and in Florida by NSF Grant No. OCE-9986359 to S. Sponaugle. The authors thank many individuals who participated in the fish census and collection at Barbados—S. Searcy, S. Dorsey, N. Reyns, C. Masterson, and M. Frey—and in the Florida Keys—J. Fortuna, D. Pinkard, M. Paddack, K. Denit, M. Sullivan, C. Paris, E. D'Alessandro, D. Richardson, C. Dickman, A. Mass, and R. Fortuna. Fish from the Florida Keys were collected under the permits #00S-524 and 02R-524 from the Florida Fish and Wildlife Conservation Commission and permits #2001-004, 2002-025A from the Florida Keys National Marine Sanctuary. All collection and fish handling procedures were approved under the UM Animal Care and Use Permit #01-056. We are also grateful for vessel support through Institute of Marine Science, Maytag Chair Endowment, and the EPA-funded National Caribbean Coral Reef Research Center. T. Rankin and L. Matragrano helped dissect fishes from some of the cohorts; J. Fortuna and D. Pinkard helped with image-analysis and otolith aging. The original water-temperature data were provided by S. Miller at the National Undersea Research Center. The manuscript benefited from the comments of R. K. Cowen, M. Paddack, and 2 anonymous reviewers.

*Conflict of interest*: None declared.

## References

Anderson JT. 1988. A review of size dependent survival during pre-recruitment stages of fishes in relation to recruitment. J Northwest Atl Fish Sci 8:55–66.

Bergenius MAJ, McCormick MI, Meekan MG, Robertson DR. 2005. Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. Mar Biol 147:291–300.

Bergenius MAJ, Meekan MG, Robertson DR, McCormick MI. 2002. Larval growth predicts the recruitment success of a coral reef fish. Oecologia 131:521–5.

Bohnsack JA, McClellan DB, Harper DE, Davenport GS, Konoval GJ, Eklund A, Contillo JP, Bolden SK, Fischel PC, Sandorf GS, and others. 1999. Baseline data for evaluating reef fish populations in the Florida Keys, 1979–1998, v. NMFS-SEFSC-427, NOAA Technical Memorandum.

Booth DJ, Beretta GA. 2004. Influence of recruit condition on food competition and predation risk in a coral reef fish. Oecologia 140:289–94.

Booth DJ, Hixon MA. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. Oecologia 121:364–8.

Brunton BJ, Booth DJ. 2003. Density- and size-dependent mortality of a settling coral-reef damselfish (*Pomacentrus moluccensis* Bleeker). Oecologia 137:377–84.

Chapman MR, Kramer DL. 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. Mar Ecol Prog Ser 181:81–96.

Cowen RK, Castro LR. 1994. Relation of coral-reef fish larval distributions to island scale circulation around Barbados, West Indies. Bull Mar Sci 54:228–44.

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB. 2000. Connectivity of marine populations: Open or closed? Science 287:857–9.

Cowen RK, Paris CB, Srinivasan A. 2006. Scaling of connectivity in marine populations. Science 311:522–7.

Cowen RK, Sponaugle S, Paris CB, Lwiza KMM, Fortuna JL, Dorsey S. 2003. Impact of North Brazil Current rings on local circulation and coral reef fish recruitment to Barbados, West Indies. In: Goni GJ, Rizzoli PM, editors. Interhemispheric water exchange in the Atlantic Ocean. Amsterdam: Elsevier. p 443–62.

Criales MM, Yeung C, Jones DL, Jackson TL, Richards WJ. 2003. Variation of oceanographic processes affecting the size of pink shrimp (*Farfantepenaeus duorarum*) postlarvae and their supply to Florida Bay. Est Coast Shelf Sci 57:457–68.

Fratantoni DM, Johns WE, Townsend TL. 1995. Rings of the North *Brazil* Current—their structure and behavior inferred from observations and a numerical simulation. J Geophys Res 100:10633–54.

Gimenez L, Anger K. 2001. Relationships among salinity, egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. J Exp Mar Biol Ecol 260:241–57.

Goni GJ, Johns WE. 2001. A census of North Brazil Current rings observed from TOPEX/POSEIDON altimetry: 1992–1998. Geophys Res Lett 28:1–4.

Green BS, Fisher R. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. J Exp Mar Biol Ecol 299:115–32.

Grorud-Colvert K. 2006. Predation in marine reserves and its impact on the survival and early life histories of newly-settled reef fishes [PhD thesis]. Coral Gables, FL: University of Miami.

Grorud-Colvert K, Sponaugle S. In press. Influence of condition on behavior and survival potential of a newly settled coral reef fish. Mar Ecol Prog Ser.

Hoey AS, McCormick MI. 2004. Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologia 139:23–9.

Jarrett JN. 2003. Seasonal variation in larval condition and postsettlement performance of the barnacle *Semibalanus balanoides*. Ecology 84:384–90.

Kelly PS, Lwiza KMM, Cowen RK, Goni GJ. 2000. Low-salinity pools at Barbados, West Indies: their origin, frequency, and variability. J Geophys Res 105:19699–708.

Kerrigan BA. 1996. Temporal patterns in size and condition at settlement in two tropical reef fishes (Pomacentridae: *Pomacentrus amboinensis* and *P. nagasakiensis*). Mar Ecol Prog Ser 135:27–41.

Lee TN, Clarke ME, Williams E, Szmant AF, Berger T. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull Mar Sci 54:621–46.

Lee TN, Williams E. 1999. Mean distribution and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. Bull Mar Sci 64:35–56.

Limouzy-Paris CB, Graber HC, Jones DL, Ropke AW, Richards WJ. 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida current. Bull Mar Sci 60:966–83.

Marshall DJ, Bolton TF, Keough MJ. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84:3131–7.

Marshall DJ, Pechenik JA, Keough MJ. 2003. Larval activity levels and delayed metamorphosis affect post-larval performance in the colonial, ascidian *Diplosoma listerianum*. Mar Ecol Prog Ser 246:153–62.

Masterson CF, Danilowicz BS, Sale PF. 1997. Yearly and inter-island variation in recruitment dynamics of the bluehead wrasse (*Thalassoma bifasciatum*, Bloch). J Exp Mar Biol Ecol 214:149–66.

McCormick MI. 1998. Condition and growth of reef fish at settlement: is it important? Aust J Ecol 23:258–64.

McCormick MI, Hoey AS. 2004. Larval growth history determines juvenile growth and survival in a tropical marine fish. Oikos 106:225–42.

McCormick MI, Molony BW. 1993. Quality of the reef fish *Upeneus tragula* (Mullidae) at settlement—is size a good indicator of condition? Mar Ecol Prog Ser 98:45–54.

McCormick MI, Molony BW. 1995. Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. Mar Ecol Prog Ser 118:59–68.

Meekan MG, Carleton JH, McKinnon AD, Flynn K, Furnas M. 2003. What determines the growth of tropical reef fish larvae in the plankton: food or temperature? Mar Ecol Prog Ser 256:193–204.

Meekan MG, Fortier L. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar Ecol Prog Ser 137:25–37.

Molony BW, Sheaves MJ. 1998. Otolith increment widths and lipid contents during starvation and recovery feeding in adult *Ambassis vachelli* (Richardson). J Exp Mar Biol Ecol 221:257–6.

Moran AL, Emlet RB. 2001. Offspring size and performance in variable environments: field studies on a marine snail. Ecology 82:1597–612.

Paris CB, Cowen RK. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol Oceanogr 49:1964–79.

Pechenik JA, Estrella MS, Hammer K. 1996. Food limitation stimulates metamorphosis of competent larvae and alters postmetamorphic growth rate in the marine prosobranch gastropod *Crepidula fornicata*. Mar Biol 127:267–75.

Pechenik JA, Jarrett JN, Rooney J. 2002. Relationships between larval nutritional experience, larval growth rates, juvenile growth rates, and juvenile feeding rates in the prosobranch gastropod *Crepidula fornicata*. J Exp Mar Biol Ecol 280:63–78.

Pechenik JA, Rittschof D, Schmidt AR. 1993. Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. Mar Biol 115:287–94.

Phillips NE. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83: 2562–74.

Phillips NE. 2004. Variable timing of larval food has consequences for early juvenile performance in a marine mussel. Ecology 85:2341–6.

Phillips NE. 2005. Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. Mar Ecol Prog Ser 259:79–89.

Qiu JW, Qian PY. 1997. Effects of food availability, larval source and culture method on larval development of *Balanus amphitrite* Darwin: implications for experimental design. J Exp Mar Biol Ecol 217:47–61.

Qiu JW, Qian PY. 1998. Combined effects of salinity and temperature on juvenile survival, growth and maturation in the polychaete *Hydroides elegans*. Mar Ecol Prog Ser 168:127–34.

Raventos N, Macpherson E. 2005. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Mar Ecol Prog Ser 285:205–11.

Richardson WS, Schmitz WJ Jr, Niiler PP. 1969. The velocity structure of the Florida Current from the Straits of Florida to Cape Fear. Deep Sea Res 16S:225–34.

Robertson DR, Swearer SE, Kaufmann K, Brothers EB. 1999. Settlement vs. environmental dynamics in a pelagic-spawning reef fish at Caribbean Panama. Ecol Monogr 69:195–218.

Rutherford ES, Houde ED. 1995. The Influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fish Bull 93:315–32.

Searcy SP, Sponaugle S. 2000. Variable larval growth in a coral reef fish. Mar Ecol Prog Ser 206:213–26.

Searcy SP, Sponaugle S. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecology 82:2452–70.

Shima JS, Findlay AM. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. Mar Ecol Prog Ser 235:303–9.

Sogard SM. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60:1129–57.

Sponaugle S, Cowen RK. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol Monogr 67:177–202.

Sponaugle S, Grorud-Colvert K, Pinkard D. 2006. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. Mar Ecol Prog Ser 308:1–15.

Sponaugle S, Lee T, Kourafalou V, Pinkard D. 2005. Florida current frontal eddies and settlement of coral reef fishes. Limnol Oceanogr 50:1033–48.

Sponaugle S, Pinkard DR. 2004a. Impact of variable pelagic environments on natural larval growth and recruitment of the reef fish *Thalassoma bifasciatum*. J Fish Biol 64: 34–54.

Sponaugle S, Pinkard D. 2004b. Lunar cyclic population replenishment of a coral reef fish: shifting patterns following oceanic events. Mar Ecol Prog Ser 267:267–80.

Thiyagarajan V, Harder T, Qian PY. 2002. Effect of the physiological condition of cyprids and laboratory-mimicked seasonal conditions on the metamorphic successes of *Balanus amphitrite* Darwin (Cirripedia; Thoracica). J Exp Mar Biol Ecol 274:65–74.

Thiyagarajan V, Harder T, Qiu JW, Qian PY. 2003. Energy content at metamorphosis and growth rate of the early juvenile barnacle *Balanus amphitrite*. Mar Biol 143: 543–54.

Thiyagarajan V, Hung OS, Chiu JMY, Wu RSS, Qian PY. 2005. Growth and survival of juvenile barnacle *Balanus amphitrite*: interactive effects of cyprid energy reserve and habitat. Mar Ecol Prog Ser 299:229–37.

Torres G, Gimenez L, Anger K. 2002. Effects of reduced salinity on the biochemical composition (lipid, protein) of zoea 1 decapod crustacean larvae. J Exp Mar Biol Ecol 277:43–60.

Victor BC. 1982. Daily otolith increments and recruitment in two coral reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar Biol 71:203–8.

Victor BC. 1986a. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can J Fish Aquat Sci 43:1208–13.

Victor BC. 1986b. Larval settlement and juvenile mortality in a recruitment-limited coral-reef fish population. Ecol Monogr 56:145–60.

Vigliola L, Meekan MG. 2002. Size at hatching and planktonic growth determine post-settlement survivorship of a coral reef fish. Oecologia 131:89–93.

Warner RR, Robertson DR. 1978. Sexual patterns in the labroid fishes of the western Caribbean. I. The wrasses (Labridae). Smithson Contrib Zool 254:1–27.

Wilson DT, Meekan MG. 2002. Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). Mar Ecol Prog Ser 231:247–60.

Yeung C, Jones DL, Criales MM, Jackson TL, Richards WJ. 2001. Influence of coastal eddies and counter-currents on the influx of spiny lobster, *Panulirus argus*, postlarvae into Florida Bay. Mar Freshw Res 52:1217–32.

Yeung C, Lee TN. 2002. Larval transport and retention of the spiny lobster, *Panulirus argus*, in the coastal zone of the Florida Keys, USA. Fish Oceanogr 11:286–309.