SELECTIVE MORTALITY DURING THE LARVAL–JUVENILE TRANSITION IN TWO CORAL REEF FISHES

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Abstract. For organisms with complex life histories, processes occurring during transitions between stages can strongly affect population dynamics. The major life history transition for many marine species is settlement from pelagic larvae to benthic or demersal juveniles. We examined differential mortality at settlement as a function of early life history traits (size–at–age, growth rates) in three cohorts of two common Caribbean coral reef fishes, Thalassoma bifasciatum and Halichoeres bivittatus (Labridae). We deployed light traps to collect late-stage larvae of each cohort. We also collected juveniles of each cohort at regular intervals (every second day) for two weeks following their first appearance on the nearshore reefs of Barbados, West Indies, during the spring (April–May) and fall (August–October) of 1997. Comparisons of otolith-derived traits exhibited by younger recruits (initial group) to those exhibited by older juveniles (survivor group) revealed that there was a difference in otolith growth during metamorphosis for both species: survivors had wider metamorphic bands. In addition, surviving H. bivittatus exhibited higher larval growth rates than settlers, while surviving T. bifasciatum had higher juvenile growth during the first day following emergence onto the reef. Differences in otolith growth rates in the absence of similar changes in somatic size indicate that mortality may have acted upon a growth-based characteristic of condition. We hypothesize that larvae settling in better physiological condition differentially survived the early juvenile period. Finally, selective mortality appeared to be greatest during a relatively brief window of time surrounding metamorphosis, indicating that this is a critical period. These results point to the demographic importance of transitional periods between stages for animals with complex life cycles. Furthermore, traits exhibited by earlier stages can significantly influence survival during these transitional periods.

Key words: coral reef fishes; critical period; early life history traits; growth–mortality hypothesis; Halichoeres bivittatus; juvenile growth; Labridae; larval growth; metamorphosis; otoliths; selective mortality; Thalassoma bifasciatum.

INTRODUCTION

Identifying processes driving population dynamics remains a central goal in ecology. For organisms with complex life cycles, such as fishes, amphibians, marine invertebrates, and insects, elucidating such mechanisms is challenging because events that determine the strength of a cohort may occur at any stage or combination of life history stages (Wilbur 1980, Berven 1990, Booth and Brosnan 1995, Caley et al. 1996, Hunt and Scheibling 1997). Mortality may occur at a constant rate or during a series of critical periods corresponding to transitions between behavioral and developmental stages (Hjort 1914, Wilbur 1980, Balon 1985, Gosselin and Qian 1996, Twombly 1996). Metamorphosis between larval and juvenile stages is one such transitional stage and trait variability (condition, size, and developmental state) as well as mortality may be high at this time (Blakley 1981, Newman 1992, Keefe and Able 1993, Hunt and Scheibling 1997).

The growth–mortality hypothesis (sensu Anderson 1988) provides a theoretical framework to examine how traits expressed in one life history stage may affect the probability of survival in subsequent stages. This hypothesis is based on the idea that mortality is size selective (i.e., small individuals have a higher probability of mortality than larger individuals) and can be divided into three main concepts. The bigger is better concept states that if mortality is size-dependent, then larger individuals of a given age will have a lower probability of mortality than smaller individuals of the same age (see Leggett and Deblois 1994). Second, in the growth rate concept, if the probability of mortality is lower for larger individuals, then larvae with faster growth may gain a size advantage with respect to avoiding predation, obtaining food, and the ability to withstand starvation (Miller et al. 1988, Bailey and Houde 1989). Finally, the stage duration concept is based on the idea that an individual with shorter larval duration may avoid high mortality in this stage and have a higher chance of survival to become a juvenile (Anderson 1988, Cushing 1990). The growth–mortality hypothesis is supported by a variety of temperate field and labo-

Early life history traits such as larval growth rates, size-at-age, and body composition are initially controlled by genotype and maternal contribution to the egg yolk (e.g., George 1990, Kerrigan 1994, Jaeckle 1995). As larvae age, they are also influenced by a variety of environmental factors such as temperature and food availability (Alford and Harris 1988, Bertness and Gaines 1993, McCormick and Molony 1995). Larval trait variability at metamorphosis reflects the influence of these various environmental factors. The potential for selective mortality based on this variability as well as high mortality rates at this time have led to the recognition of metamorphosis as a critical period that may determine the strength of a cohort (e.g., Berven 1990, Keefe and Able 1993, Jarrett and Pechenik 1997).

Despite this recognition, very few studies have assessed how selective mortality acts during or immediately following metamorphosis. Researchers working with amphibians have determined that both larger size and shorter larval duration at metamorphosis confer higher survival to later stages (Semlitsch et al. 1988, Berven 1990). Studies of marine invertebrates have demonstrated that higher condition (lipid/protein content) also confers a survival advantage (Harms et al. 1991, Basch and Pearse 1996). Individuals with higher lipid reserves may be able to survive patchy food environments and periods of starvation, sustain higher maximum growth rates, and escape predation better than individuals with lower energy reserves (e.g., Jarrett and Pechenik 1997). Similar research for marine fishes has produced mixed results. Two laboratory studies addressed selective mortality of young fish following the larval–juvenile transition and found no evidence for selective mortality based on size, age, or condition (Bertram and Leggett 1994, McCormick and Kerrigan 1996). Alternatively, laboratory and field manipulations using newly settled damselfish fed high and low rations indicated that higher ration (better condition/faster growth) fish had higher survivorship than fish fed low rations (Booth and Hixon 1999). To date, no field studies have examined selection across the entire transitional period from pelagic larva to demersal recruit. Measuring early mortality schedules and identifying factors that may enhance survivorship are critical to understanding mechanisms that regulate abundance of later stages (McCormick and Kerrigan 1996).

We designed this field study to examine how variability in the early life history traits of two common Caribbean wrasses influenced survival during settlement, metamorphosis, and the early juvenile period. Coral reef fishes are ideal subjects for studying the relationship between larval traits and the survival of subsequent stages because multiple life history stages can easily be collected and many species have a record of age, relative growth rates, and relative length-at-age preserved on a daily basis in their otoliths (ear stones; e.g., Victor 1982). We examined selective mortality by measuring shifts in the distribution of early life history traits exhibited by juvenile fishes before and after particular time intervals. The period of time surrounding metamorphosis was used as a focal point to determine whether certain larval traits (expressed at settlement) as well as early juvenile traits confer a higher probability of survival.

**Materials and Methods**

**Study area**

Barbados is a small (15 by 25 km), geographically isolated (140 km east of the Lesser Antilles) island in the eastern Caribbean (Fig. 1). The current flows predominately northwest at 0.35–0.55 m/s and large-scale circulation around Barbados appears to be topographically steered along the coasts and then recirculated before continuing downstream (Cowen and Castro 1994). As a result of the relative isolation and predominant current patterns, it is thought that coral reef fishes recruiting to Barbados are spawned locally (Cowen and Castro 1994, Sponaugle and Cowen 1996).

We collected larval and juvenile reef fishes along the western coast of Barbados, which is characterized by a shallow (1–15 m depth) nearshore coral spur and grove system. Reef spurs of mostly dead coral are concentrated at small coastal headlands and are separated from each other by grooves of coral rubble and sand (Sponaugle and Cowen 1997). We sampled larvae with light traps (see Materials and methods: Collection methods) deployed off the Bellairs Research Institute and collected juveniles between 1 and 6 m depth offshore of Greensleeves, North Bellairs, the Bellairs Research Institute (Holetown), and Batts Rock (Fig. 1).

**Study species**

*Halicoreus bivittatus*, the slippery dick wrasse, and *Thalassoma bifasciatum*, the bluehead wrasse (Family Labridae), are two of the most common reef fishes throughout the Caribbean. Both species have been reported to spawn daily (Warner and Robertson 1978), yet recruitment does not reflect this pattern and occurs in pulses (Victor 1986a, Robertson 1992, Sponaugle and Cowen 1997). In Barbados, recruitment pulses are highest in the spring and fall (Sponaugle and Cowen 1997; S. Dorsey, unpublished data). *H. bivittatus* recruiting to Barbados settle near the time of the new moon (maximum amplitude tide) following a relatively
short and invariant larval duration of 18–27 d (Sponaugle and Cowen 1997; See Results). In contrast, after a longer, more variable larval duration of 34–76 d, *T. bifasciatum* recruiting to Barbados settle during minimum amplitude tides near the time of the third-quarter moon (Sponaugle and Cowen 1997; See Results). Upon return to the reef, both species settle (bury) into the sand for 3–5 d and undergo metamorphosis, a phenomenon characteristic of labrid fishes (Victor 1983, Sponaugle and Cowen 1997). After emergence, *H. bivittatus* can be found swimming low near the substrate in small to large groups depending on the size of the recruitment event, while *T. bifasciatum* recruits are initially found as solitary individuals swimming low in coral crevices, schooling in progressively larger groups with increasing age (Sponaugle and Cowen 1997).

**Collection methods**

We designed sampling methods to collect larvae and young juveniles of two cohorts of *H. bivittatus* and *T. bifasciatum* during each of two seasons (spring 1997 and fall 1997). In the spring (May 1997) we only were able to collect one cohort of each species (spring cohort), whereas in the fall we collected two cohorts of each species: August–September (fall-1 cohort) and September–October (fall-2 cohort).

We targeted late-stage larvae prior to settlement by deploying 3–4 replicate light traps (design described in Sponaugle and Cowen 1996) 1 m off the bottom at the reef–sand interface (depth 3–8 m). We deployed light traps nightly from one week prior to the third-quarter moon until several days after the new moon (encompassing the periods during which peak recruitment of *H. bivittatus* and *T. bifasciatum* occurs at Barbados; Sponaugle and Cowen 1997). Upon retrieval, we rinsed the light traps, sorted the samples to remove late-stage larvae, and preserved the larvae in 95% ethanol. Light traps were unsuccessful in collecting *T. bifasciatum*; however, we were able to collect late-stage larval *H. bivittatus* in relatively high numbers in the spring.

We used standard techniques (Scuba, hand nets, and the fish anesthetic Quinaldine [90%, Sigma Chemical Company, St. Louis, Missouri, USA]) to collect young
Plate 1. Sagittal otolith of *Thalassoma bifasciatum* showing daily increments at 400× magnification. Larval increments (closest to the otolith core) are separated from juvenile increments by settlement and emergence marks.

Juveniles of both species following their metamorphosis and emergence onto the reef. Each cohort was collected evenly among sites: the spring cohort at Bellairs, North-Bellairs, and Greensleeves; the fall-1 cohort at Bellairs and Batts Rock; and the fall-2 cohort only at Bellairs. Each collection was made on different areas of each reef (minimum of 25 m apart) to ensure that sampling would not bias later collections. We collected ~30 fish of each species every 2 d for 2 wk. After each collection, we immediately preserved the fishes in 95% ethanol.

**Otolith analysis**

To obtain a measure of larval duration, size-at-age, and growth rates, we analyzed the otolith record of each individual fish (e.g., see Plate 1). Daily deposition of concentric marks on the otolith has been validated for both species (Victor 1982). Furthermore, a clear settlement mark was evident on the otolith (Victor 1982, Sponaugle and Cowen 1997), followed by a wide, unreadable band that represents the metamorphic period (validated by Victor 1983 for *H. bivittatus*). The risks of back-calculating information (somatic growth rates and length-at-age) from otoliths are well known, as not all fish have a consistent relationship between otolith length and fish length (Thorrold and Milcich 1990, McCormick 1994, Paperno et al. 1997). In this study, the relationship between fish length and otolith length was strongly correlated for both study species (see Results, also Victor 1986b, Masterson et al. 1997, Sponaugle and Cowen 1997). We assumed a positive though not necessarily constant relationship between otolith and somatic growth, though most of our comparisons used only otolith traits rather than derived somatic traits (see below).

Prior to dissection, we measured the standard length of each fish to the nearest 0.1 mm using digital calipers. We then dissected each fish and extracted two pairs of otoliths, the sagittae and lapilli, using standard techniques (Brothers 1987). To facilitate interpretation and allow clearing of the otoliths, we placed otoliths on microscope slides in medium viscosity immersion oil for 30 d (Sponaugle and Cowen 1997). We read the sagittae using a Zeiss transmitted light microscope at

<table>
<thead>
<tr>
<th>Site comparison</th>
<th>Source of variation</th>
<th><em>Halichoeres bivittatus</em></th>
<th><em>Thalassoma bifasciatum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>df</td>
</tr>
<tr>
<td>Spring cohorts</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Bellairs</td>
<td>Between groups</td>
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<td>2</td>
</tr>
<tr>
<td>N. Bellairs</td>
<td>Within groups</td>
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<td>64</td>
</tr>
<tr>
<td>Greensleeves</td>
<td>Total</td>
<td>21</td>
<td>66</td>
</tr>
<tr>
<td>Fall-1 cohorts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bellairs</td>
<td>Between groups</td>
<td>18</td>
<td>1</td>
</tr>
<tr>
<td>Batts Rock</td>
<td>Within groups</td>
<td>37</td>
<td>53</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>54</td>
<td>97</td>
</tr>
</tbody>
</table>

Notes: Comparisons are made between 0–2 d postemergence juveniles (*H. bivittatus*) and 0–7 d postemergence juveniles (*T. bifasciatum*). A between-site comparison is not given for fall-2 cohorts as juveniles for both species were collected only at Bellairs. Abbreviation: NS, *P > 0.05*.
Table 2. Repeated-measures MANOVA of initial group vs. survivor group comparisons of larval otolith length and growth of *Halichoeres bivittatus* and *Thalassoma bifasciatum*.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Measure</th>
<th>Comparison†</th>
<th>df₁</th>
<th>df₂</th>
<th>Wilks’ λ</th>
<th>F</th>
<th>P</th>
<th>Trend</th>
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<td>Spring</td>
<td>length</td>
<td>LT vs. 0–1 d</td>
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<td>0.932</td>
<td>0.808</td>
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<td>length</td>
<td>LT vs. 6–9 d</td>
<td>9</td>
<td>78</td>
<td>0.787</td>
<td>2.343</td>
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<td>S &gt; I</td>
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<td></td>
<td></td>
<td>0.722</td>
<td>3.296</td>
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<td>S &gt; I</td>
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<tr>
<td></td>
<td>length</td>
<td>0–1 d vs. 6–9 d</td>
<td>9</td>
<td>82</td>
<td>0.863</td>
<td>1.450</td>
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<td>growth</td>
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<td>0.879</td>
<td>1.251</td>
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<tr>
<td>Fall-1</td>
<td>length</td>
<td>0–1 d vs. 6–9 d</td>
<td>9</td>
<td>62</td>
<td>0.760</td>
<td>2.171</td>
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<td>S &gt; I</td>
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<td>0.848</td>
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<tr>
<td>Fall-2</td>
<td>length</td>
<td>0–1 d vs. 6–11 d</td>
<td>9</td>
<td>61</td>
<td>0.758</td>
<td>2.168</td>
<td>*</td>
<td>S &gt; I</td>
</tr>
<tr>
<td></td>
<td>growth</td>
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<td></td>
<td></td>
<td>0.854</td>
<td>1.160</td>
<td>NS</td>
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</table>

Notes: Abbreviations are as follows: LT, late-stage larvae collected in light traps; df₁, hypothesis degrees of freedom; df₂, error degrees of freedom; Wilks’ λ, multivariate test statistic; I, initial group (younger fish); S, survivor group (older fish). Where significant, the trend for each comparison indicates which group exhibited higher otolith growth rates or larger otolith length-at-age.

*P < 0.05; **P < 0.01; NS, not significant (P > 0.05).
†Postemergence age is given in days (d).

250× with a rotating polarized filter placed between the light source and the first stage. We captured the microscope image with a frame grabber and then displayed the image on a computer screen (resolution was ~2 μm). We set the focal plane of the microscope so that the larval increments would be clear (nucleus to settlement mark). Typically with this focus the metamorphic and juvenile regions of the otolith were clear as well. We recorded measurements using the OPTIMAS image analysis system (Optimas 1996). We analyzed the otoliths along the longest radius from the core to the outer edge, and recorded otolith length (radius-at-age) for every day during the larval and juvenile periods. From this information, we determined daily growth during the larval and juvenile periods, the width of the otolith metamorphic band, as well as juvenile age. To account for the time between fertilization and the deposition of daily increments, we added two days to the total number of presettlement increments (reflecting a standard time to hatching; Victor 1982, Spinaugle and Cowen 1997) to obtain larval duration.

All otoliths were read by one person and all unclear, abnormally shaped (nonlinear growth axis), or pairs of unequally sized sagittae were discarded. Each pair of sagittae was read twice by randomly selecting one of the two otoliths for each independent reading. If the increment counts were within 5% of each other (typically one increment for *H. bivittatus* or two to three increments for *T. bifasciatum*), the reader randomly selected one measurement for analysis. If the increment counts differed by >5%, the otolith was analyzed again. If the increment counts from the third independent reading remained >5%, the otolith was discarded. If the difference on the third count was <5% of one

Table 3. Data and results of ANOVA of initial group vs. survivor group analysis of early life history traits of *Halichoeres bivittatus*.

<table>
<thead>
<tr>
<th>Cohort and Group†</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>ANOVA</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>ANOVA</th>
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<tbody>
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<td>Spring</td>
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<tr>
<td>Init.-1 (LT)</td>
<td>53</td>
<td>21–25</td>
<td>23.0</td>
<td>1.1</td>
<td></td>
<td>132.5–151.1</td>
<td>147.1</td>
<td>9.3</td>
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<tr>
<td>Surv.-1 (0–1 d)</td>
<td>35</td>
<td>21–27</td>
<td>22.8</td>
<td>1.3</td>
<td></td>
<td>130.8–164.2</td>
<td>147.5</td>
<td>7.9</td>
<td></td>
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<tr>
<td>Init.-2 (0–1 d)</td>
<td>35</td>
<td>21–27</td>
<td>22.8</td>
<td>1.3</td>
<td></td>
<td>130.8–164.2</td>
<td>147.5</td>
<td>7.9</td>
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<tr>
<td>Surv.-2 (6–9 d)</td>
<td>57</td>
<td>21–25</td>
<td>23.2</td>
<td>1.0</td>
<td>NS</td>
<td>133.9–168.4</td>
<td>148.8</td>
<td>6.9</td>
<td>NS</td>
</tr>
<tr>
<td>Fall-1</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Init. (0–1 d)</td>
<td>33</td>
<td>20–23</td>
<td>21.4</td>
<td>0.8</td>
<td></td>
<td>131.5–151.4</td>
<td>143.9</td>
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<tr>
<td>Surv. (7–14 d)</td>
<td>38</td>
<td>19–22</td>
<td>20.9</td>
<td>0.8</td>
<td>**</td>
<td>131.8–161.8</td>
<td>145.2</td>
<td>6.3</td>
<td>NS</td>
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<tr>
<td>Fall-2</td>
<td></td>
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<tr>
<td>Init. (0–1 d)</td>
<td>41</td>
<td>18–24</td>
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<td>1.2</td>
<td></td>
<td>122.4–159.8</td>
<td>142.5</td>
<td>9.1</td>
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</tr>
<tr>
<td>Surv. (7–14 d)</td>
<td>30</td>
<td>19–23</td>
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<td>1.0</td>
<td>*</td>
<td>123.7–153.3</td>
<td>140.2</td>
<td>6.9</td>
<td>NS</td>
</tr>
</tbody>
</table>

Notes: A single comparison was made for juveniles within each fall cohort. In the spring cohort, two comparisons were made (the Surv.-1 group is the same as the Init.-2 group). Abbreviations: init., initial group (younger fish); surv., survivor group (older fish); LT, late-stage larvae collected in light traps.

*P < 0.05; **P < 0.01; ***P < 0.001; NS, not significant (P > 0.05).
†Postemergence age is given in days (d).
of the former readings, then one of these two measurements was randomly chosen for analysis. A total of 172 _Thalassoma bifasciatum_ otoliths (26% of the total read) and 142 _H. bivittatus_ otoliths (21% of the total read) were discarded due to abnormal shape or inconsistent reading. For the data analysis, an additional selection was made to ensure that individuals were from the same cohort: we used only fish that emerged during an 8-d window of recruitment.

**Data analysis**

To avoid errors and assumptions of back-calculating somatic growth (Secor and Dean 1992, Hare and Cowen 1995), we based comparisons of size and growth primarily on otolith measurements. Hereafter, reference to growth or size measurements refers to otolith growth or size unless explicitly stated otherwise. To examine whether there was selective mortality based on early life history traits for either species, we compared the distribution and frequency of traits exhibited by groups of younger and older fishes collected (i.e., a presumed initial population vs. survivor population comparison). We selected particular comparisons for each cohort such that sample sizes and groups compared would be similar among cohorts.

Preliminary inspection of the length-at-age data revealed that measurements were not normally distributed, therefore a natural log transformation was applied to improve normality and homogeneity of variance. Because the measurements were longitudinal in nature (i.e., sequential measurements were made from otoliths of individual fishes), we used repeated-measures MANOVA (SYSTAT Version 5.1, Wilkinson 1992) for all comparisons of growth and size-at-age. For _H. bivittatus_ we compared average growth (μm/d) over 2-d intervals up to 20 d of age, and length-at-age (μm) at the end of each 2-d interval. Similarly, for _T. bifasciatum_ we compared 5-d intervals up to 35 d (spring) or 50 d (fall cohorts). These age limits were chosen to encompass the greatest numbers of individuals collected. As some individuals were older at settlement than the age cutoffs used, we also analyzed growth trajectories backward (hindcast) over 1-d intervals 10 d prior to settlement.

**Table 3.**

<table>
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<tr>
<th>Range</th>
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<th>SD</th>
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<td>**</td>
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<td>177.7–207.3</td>
<td>189.9</td>
<td>8.1</td>
<td>**</td>
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<td>169.4–192.9</td>
<td>178.5</td>
<td>6.5</td>
<td>**</td>
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<tr>
<td>171.1–198.1</td>
<td>183.3</td>
<td>6.8</td>
<td>**</td>
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<tr>
<td>157.4–201.2</td>
<td>181.3</td>
<td>10.2</td>
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<td>180.8</td>
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<tr>
<td>29.2–47.6</td>
<td>40.6</td>
<td>3.9</td>
<td>NS</td>
</tr>
</tbody>
</table>
MANOVA techniques enable comparisons to be made at the resolution of an individual fish (Chambers and Miller 1995, Meekan and Fortier 1996). Comparisons are then made among groups of individuals with the null hypothesis being that of no difference among groups. The statistic used is the interaction term for Wilks' λ, which is based on sample size, number of groups in the comparison, and number of intervals being analyzed.

To examine whether there was selective mortality of transitional stage fish based on larval traits, we compared the distribution of traits between groups of younger (initial group) and older (survivor group) juveniles. For *H. bivittatus*, we compared the distribution of traits between three groups in the spring cohort: late-stage larvae from light trap collections, ≤1 d old juveniles, and 6–9 d old juveniles. We did not collect late-stage larvae in the fall cohorts; thus comparisons from the fall are made solely between younger and older juveniles: fall-1, ≤1 d old juveniles vs. 7–14 d old juveniles; fall-2, ≤1 d old juveniles vs. 6–11 d old juveniles. Similar comparisons were made for *T. bifasciatum*: spring, ≤2 d old juveniles vs. 7–9 d old juveniles; fall cohorts, ≤1 d old juveniles vs. 7–14 d old juveniles.

To determine whether there was selective mortality based on age-at-settlement (pelagic larval duration), otolith length at settlement, or width of the otolith metamorphic band, we made initial group vs. survivor group comparisons using standard ANOVA techniques (because only a single measurement was obtained from each individual). Similarly, we used standard ANOVA techniques to compare selective mortality based on growth rates and length-at-age during the first day following emergence.

To confirm findings regarding selective mortality based on size, we used a second technique comparing the standard length of fishes that had been on the reef for ≤1 d postemergence with the back-calculated standard length of older fishes. For this analysis, the initial settler group consisted of the standard lengths of all individuals caught during their first day on the reef (day 1), and the survivor group consisted of individuals that had been on the reef for 7–14 d. For the survivor group (and initial group of the spring cohort of *T. bifasciatum*, which included 2–3 d old juveniles), we measured otolith growth between the emergence mark and the day of capture and converted this measure to somatic length (using the standard length to otolith length relationship). We then subtracted this value from the standard length at capture. We used a standard ANOVA to reveal if there was any evidence for selective mortality based on standard length at emergence.

To determine whether there was selective mortality based on otolith growth or length in older juveniles, we used repeated-measures MANOVA. We examined otolith growth and length for the first four days post-emergence for *H. bivittatus* and the first five days following emergence for *T. bifasciatum*. Two comparisons were made to determine whether selective mortality of smaller or slower growing juveniles would be immediately apparent (*H. bivittatus*, 1-d old juveniles vs. 2–3 d old juveniles; *T. bifasciatum*, 1-d vs. 2–4 d old juveniles) or apparent after a longer period of time (*H. bivittatus*, 1-d vs. 6–14 d old juveniles; *T. bifasciatum*, 1-d vs. 7–14 d old juveniles).

**Results**

The relationship between otolith length and body length was highly significant for both study species (Fig. 2), indicating that otolith growth was an accurate index of somatic growth. To ensure that collection methods did not bias results, we compared early life history traits (larval growth and length-at-age, larval duration, and width of otolith metamorphic band) for each cohort among collection sites for fishes of similar ages. There were no significant differences in any cohort traits examined among sites (e.g., width of the metamorphic band, ANOVA; Table 1). Results of the progressive otolith length and growth analyses are presented below for each species. Hind-cast otolith growth analyses (10 d prior to settlement; MANOVA) were not significant for either species and are not presented.

*Halichoeres bivittatus*

Survivors of *H. bivittatus* consistently exhibited faster growth than the presumed initial population (Fig. 3). This trend was significant for the spring cohort between light trap larvae (settlers) and 6–9 d old juveniles (see below), but not between these groups and ≤1 d juveniles (repeated-measures MANOVA; Table 2). The largest difference in larval otolith growth for all cohorts occurred between day 5 and 15 (Fig. 3). As a consequence of higher daily growth rates, otolith length-at-age (an alternate measure of larval growth) throughout the larval period was significantly higher for survivors than the initial group (repeated-measures MANOVA; Table 2; Fig. 3). Otolith length at settlement, however, was not significantly higher for survivors (ANOVA; Table 3). Our initial group vs. survivor group analysis of back-calculated standard length at emergence confirms this result. In only one case (spring cohort) was the initial group significantly smaller at emergence than the survivor group (Table 4). This apparent discrepancy between selective mortality of slower growing and smaller-at-age larvae, yet no selective mortality based on length at settlement, is explained by the fact that survivors (the two fall cohorts) generally spent a shorter period in the plankton than did the initial group (ANOVA; Table 3). Interestingly, the mean width of the metamorphic band in the otoliths (corresponding to the time when fish are buried in the sand undergoing metamorphosis) was 8.4–10.9% wider for survivors than the initial settler group (significant in the spring and fall-1 cohorts but not the fall-2 cohort, ANOVA; Table 3).
In the initial group vs. survivor group comparisons of juvenile early life history traits, there was no difference in otolith growth rate between survivors and the presumed initial population for either comparison (1 d vs. 2 d juveniles; 1 d vs. 6+ d juveniles) in all three cohorts (ANOVA $P > 0.05$; Fig. 4). Despite this lack of difference in otolith growth rates, mean otolith length at emergence (ANOVA $P < 0.05$; Table 3) and after the first day on the reef (ANOVA $P < 0.05$) was significantly longer for survivors than the initial group in the fall-1 and spring cohorts, but not the fall-2 cohort. However, after the first four days on the reef, there were no differences in juvenile otolith growth or length between the initial group (4–6 d) and survivor group (7+ d juveniles; repeated-measures MANOVA; Fig. 5).

**Thalassoma bifasciatum**

For *T. bifasciatum*, there was no significant difference in larval otolith growth or length-at-age between new settlers (0–1 d juveniles) and survivors (7–14 d juveniles) for any cohort collected (repeated-measures MANOVA; Table 2; Fig. 6). There was also no significant difference in pelagic larval duration or otolith length at settlement or emergence (ANOVA; Table 5). This result is confirmed by comparisons of back-calculated standard length at day of emergence, which revealed no difference between the initial and survivor groups (Table 4). Similar to *H. bivittatus*, however, the width of the otolith metamorphic band was significantly wider for survivors than settlers for all three cohorts (ANOVA; Table 5). Mean metamorphic band
Fig. 3. *Halichoeres bivittatus* mean larval otolith growth rate trajectories (open and closed symbols) and length-at-age (solid and dashed lines) for three cohorts. LT refers to late-stage larvae collected in light traps. Age (days on reef) of group is given in inset.

Widths (corresponding to the period of metamorphosis) of survivors were 8.9% (spring), 28% (fall-1), and 10.8% (fall-2) larger than the mean metamorphic band width of settlers.

Early juvenile otolith growth (emergence to 2 d) for all cohorts was faster for survivors (7+ d on the reef) than the new settlers (1 d on the reef; ANOVA $P < 0.05$; Fig. 7). The same groups used in growth comparisons were used to compare otolith length-at-age, although no significant differences were evident in otolith length at emergence and day one after emergence for any group (ANOVA $P > 0.05$; Table 5; Fig. 7). Comparing older juveniles (5–7 d vs. 8–14 d), neither spring nor fall-2 cohorts exhibited selective mortality based on otolith length during the first five days of the juvenile period. Although survivors of the fall-1 cohort had significantly different otolith growth rates than the presumed initial population (repeated-measures MANOVA), the pattern was mixed with no significant trend: initial fast growth followed by slower growth and then faster growth again (Fig. 8).

**Discussion**

Comparisons of early life history traits between younger and older recruits of two coral reef fishes (*Thalassoma bifasciatum* and *Halichoeres bivittatus*) revealed that recently settled juveniles are susceptible to strong selective mortality. Because we examined se-
TABLE 4. ANOVA of initial group vs. survivor group comparisons of standard length at emergence of *Halichoeres bivittatus* and *Thalassoma bifasciatum*.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Group</th>
<th>Mean length (mm)</th>
<th>SD</th>
<th>ANOVA</th>
<th>Mean length (mm)</th>
<th>SD</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>init.</td>
<td>25</td>
<td>12.3</td>
<td>0.28</td>
<td>***</td>
<td>28</td>
<td>10.7</td>
</tr>
<tr>
<td>Fall-1</td>
<td>surv.</td>
<td>20</td>
<td>12.9</td>
<td>0.77</td>
<td></td>
<td>58</td>
<td>10.9</td>
</tr>
<tr>
<td>Fall-1</td>
<td>init.</td>
<td>24</td>
<td>11.7</td>
<td>0.40</td>
<td>NS</td>
<td>14</td>
<td>11.4</td>
</tr>
<tr>
<td>Fall-2</td>
<td>surv.</td>
<td>37</td>
<td>11.6</td>
<td>0.80</td>
<td>NS</td>
<td>26</td>
<td>11.7</td>
</tr>
<tr>
<td>Fall-2</td>
<td>init.</td>
<td>20</td>
<td>11.6</td>
<td>0.32</td>
<td>NS</td>
<td>22</td>
<td>11.4</td>
</tr>
<tr>
<td>Fall-2</td>
<td>surv.</td>
<td>33</td>
<td>11.5</td>
<td>0.58</td>
<td>NS</td>
<td>27</td>
<td>11.8</td>
</tr>
</tbody>
</table>

*Notes:* The initial group consists of 1 d postemergence juveniles except for the spring cohort of *T. bifasciatum* in which 2–3 d postemergence juveniles were also used. Abbreviations: init., initial group (younger fish); surv., survivor group (older fish).

*** P < 0.001; ns, not significant (P > 0.05).

Fig. 4. *Halichoeres bivittatus* mean juvenile otolith growth (left column) and length (right column) for the first two days after emergence (E) for three cohorts. Age (days on reef) of each group is given in the insets. Nonsignificant (ns, P > 0.05) or significant (P < 0.05) difference between the initial group (1 d) and survivor group (≥6 d) was determined by ANOVA.
TABLE 5. Data and results of ANOVA of initial group vs. survivor group analysis of variables of *Thalassoma bifasciatum*.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Group†</th>
<th>n</th>
<th>Range (d)</th>
<th>Mean (d)</th>
<th>SD</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>init. (0–2 d)</td>
<td>18</td>
<td>38–49</td>
<td>42.3</td>
<td>2.7</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>surv. (7–9 d)</td>
<td>35</td>
<td>37–48</td>
<td>42.1</td>
<td>2.7</td>
<td>NS</td>
</tr>
<tr>
<td>Fall-1</td>
<td>init. (0–1 d)</td>
<td>34</td>
<td>45–66</td>
<td>56.5</td>
<td>5.5</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>surv. (7–11 d)</td>
<td>26</td>
<td>43–66</td>
<td>55.9</td>
<td>6.4</td>
<td>NS</td>
</tr>
<tr>
<td>Fall-2</td>
<td>init. (0–1 d)</td>
<td>43</td>
<td>34–66</td>
<td>53.6</td>
<td>9.0</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>surv. (7–11 d)</td>
<td>25</td>
<td>37–76</td>
<td>55.9</td>
<td>9.8</td>
<td>NS</td>
</tr>
</tbody>
</table>

*Notes:* A single comparison was made between younger (initial, init.) and older (survivor, surv.) juveniles.

* P < 0.05; ** P < 0.001; NS, not significant (*P* > 0.05).

† Postemergence age is given in days (d).

**Fig. 5.** *Halichoeres bivittatus* mean juvenile otolith growth (left column) and length (right column) for the first four days after emergence (E) for three cohorts. Age (days on reef) of each group is given in the insets. Nonsignificant difference (NS, *P* > 0.05) between initial group and survivor group was determined by MANOVA.
### Table 5. Extended.

<table>
<thead>
<tr>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>ANOVA</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>182.3–228.0</td>
<td>207.9</td>
<td>11.6</td>
<td>NS</td>
<td>21.2–31.1</td>
<td>25.9</td>
<td>3.4</td>
<td>*</td>
</tr>
<tr>
<td>192.9–227.7</td>
<td>210.4</td>
<td>9.6</td>
<td>NS</td>
<td>15.0–40.9</td>
<td>28.8</td>
<td>5.1</td>
<td>*</td>
</tr>
<tr>
<td>194.9–268.7</td>
<td>234.1</td>
<td>16.7</td>
<td>NS</td>
<td>11.8–33.9</td>
<td>19.2</td>
<td>4.9</td>
<td>***</td>
</tr>
<tr>
<td>203.8–301.2</td>
<td>240.4</td>
<td>20.7</td>
<td>NS</td>
<td>19.2–36.0</td>
<td>26.7</td>
<td>4.1</td>
<td>*</td>
</tr>
<tr>
<td>187.8–286.9</td>
<td>231.1</td>
<td>18.5</td>
<td>NS</td>
<td>9.0–27.1</td>
<td>18.9</td>
<td>4.3</td>
<td>*</td>
</tr>
<tr>
<td>197.7–272.4</td>
<td>239.9</td>
<td>18.5</td>
<td>NS</td>
<td>15.9–30.4</td>
<td>21.2</td>
<td>3.5</td>
<td>*</td>
</tr>
</tbody>
</table>

![Graphs](image)

**Fig. 6.** *Thalassoma bifasciatum* mean larval otolith growth rate trajectories (open and closed circles) and otolith length-at-age (solid and dashed lines) for three cohorts. Age (days on reef) of group is given in inset.

AS A CAVEAT, IT SHOULD BE NOTED THAT SOME OF THE SIGNIFICANT RESULTS ARE CLOSE TO OR BELOW THE RESOLUTION OF THE MICROSCOPE (LARVAL GROWTH; *H. BIVITTATUS*) OR BELOW ACCEPTABLE ERROR AS STATED IN THE METHODS SECTION (COUNT OF LARVAL DURATION; *H. BIVITTATUS*). DESPITE THIS, THE RESULTS WERE REPEATABLE WITHIN AND AMONG COHORTS AND EXHIBITED A CONSISTENT TREND. THIS OUTCOME SUGGESTS THAT THE RESULTS ARE REAL AND NOT SIMPLY DUE TO THE POWER OF THE STATISTICAL TESTS. FINALLY, IT MAY BE ARGUED THAT THE OBSERVED SHIFT IN TRAITS IS NOT THE RESULT OF SELECTIVE MORTALITY, BUT RATHER THE RESULT OF SMALL-SCALE PATCH DY-
Fig. 8. *Thalassoma bifasciatum* mean juvenile otolith growth (left column) and length (right column) for the first five days after emergence for three cohorts. Age (days on reef) of each group is given in the insets. Nonsignificant difference (NS, $P > 0.05$) between initial group and survivor group was determined by MANOVA.

Dynamics and collection methods (i.e., the initial group was collected from one site and the survivor group from another, which was only the case for the spring comparison of *H. bivittatus* larvae vs. juveniles). Our results indicate that this bias is unlikely to have occurred. Not only were there no significant differences in early life history traits among sites, but larval fish settlement to Barbados is typically synchronous along the entire west coast (Sponaugle and Cowen 1996), suggesting that larvae settling to one site are part of the same general pool of larvae recruiting to other west coast sites.

**Selective mortality**

In all three *H. bivittatus* cohorts, larvae with faster larval otolith growth and/or length-at-age and a shorter larval duration (fall cohorts) differentially survived the early juvenile period. However, there was no evidence for selective mortality based on otolith length at settlement. The fact that there was selective mortality of juveniles with slower otolith growth during the larval stage, yet no apparent selective mortality of smaller settlers (otolith length at settlement and back-calculated standard length at emergence), may be interpreted to mean that there was selective loss of individuals with
a growth-based characteristic other than length (i.e., physiological condition). This idea is supported by previous work demonstrating that faster otolith growth and better condition are correlated in fishes such as cod (Suthers et al. 1992), plaice (Hovenkamp and Witte 1991), goatfish (McCormick and Molony 1992), myctophids (Suthers 1996), and glassfish (Molony and Sheaves 1998). In addition, laboratory and field manipulations on another Caribbean reef fish, Stegastes partitus, have shown that condition can influence the probability of survival of newly settled juveniles (Booth and Hixon 1999).

We reach a similar conclusion when interpreting the result that survivors of both H. bivittatus and T. bifasciatum had wider otolith metamorphic bands. Metamorphosis at the time of settlement for both species generally is considered to be a period of food deprivation where larval characteristics such as coloration, behavior, physiology, and morphology change radically (as is common in other species; reviewed in Balon 1985, Youson 1988). Assuming that feeding ceases during metamorphosis (while fishes are buried under sand), then otolith accretion in the metamorphic band is likely the result of relative condition at settlement. The response of otolith accretion to starvation events (such as metamorphosis for the two study species) may be immediately apparent (Govoni et al. 1985), apparent after a few days (McCormick and Molony 1992, Molony 1996, Molony and Sheaves 1998), a week (Pepino et al. 1997), or even longer (Molony and Choat 1990). In the current study, higher otolith accretion during metamorphosis (broad band width) may therefore be a reflection of better physiological condition at the time of settlement. Due to the energetically costly nature of the metamorphic period, larvae settling in relatively poor condition (narrower metamorphic band) will likely emerge in a relatively depaupe state and thus be more susceptible to mortality (starvation or predation) than settlers in better condition. A second, though less parsimonious, interpretation of the width of the metamorphic band is that band width represents time spent buried. For example, larvae settling at a less developed state may require more time to undergo metamorphosis. While developmental state at settlement may vary for some fishes (Policansky 1983, Fukuhara 1991, McCormick 1993), recent physiological research on T. bifasciatum and H. bivittatus has shown that the developmental state of settling wrasse larvae is fairly uniform (low variability; Lara 1999). Thus, it is unlikely that some larvae would require more time than others to complete metamorphosis. Although we believe that the observed differences in width of the metamorphic band are not related to time spent buried, this interpretation is not mutually exclusive with our first interpretation regarding condition. If the width of the metamorphic band represents time, then survivors in better condition at settlement were energetically able to spend more time (extra energy available to sustain a nonfeeding period) undergoing metamorphosis. Clearly, future work is needed to disentangle these possibilities.

Although selective mortality appears to have acted primarily upon larval (H. bivittatus) and metamorphic characteristics (H. bivittatus and T. bifasciatum), there was also evidence for selective mortality based on juvenile traits (T. bifasciatum). Juvenile otolith growth immediately following emergence was faster for T. bifasciatum survivors than the overall population, yet there was no evidence for selective mortality of smaller fishes on day 1 (based on standard length or otolith length on day one). If otolith growth responds directly and immediately to feeding, then survivors were probably able to feed more effectively during their first day on the reef. Alternatively, if there is a lagged response between feeding and otolith growth (see previous discussion), then this faster growth may be the residual effect of settlement condition. Either way, evidence suggests that survivors were in better physiological condition at settlement, emergence, and the first day after emergence than the original population of settling larvae.

Very few significant differences and no consistent trends were found for later juvenile growth or length-at-age exhibited by older juveniles relative to younger recruits. These results suggest that no detectable size or growth selection occurs after the first few days on the reef. A previous field study of predation on juvenile T. bifasciatum also did not find evidence for size selective mortality, even though mortality levels of near 50% were reported over a one-month time period (Carr and Hixon 1995). Although there is no immediately apparent size-based selective mortality during this post-settlement period, size may be important in later competitive interactions as well as reproductive success (Forrester 1990, Kerrigan 1994, Tupper and Boutilier 1995).

Species-specific differences in selective mortality

The observed pattern of selective mortality for young juveniles was different for H. bivittatus and T. bifasciatum. Although the metamorphic band was wider for survivors of both species, selective mortality of juveniles with slower larval growth was observed only in H. bivittatus, and selective loss of slower growing juveniles was observed only in T. bifasciatum. This apparent dichotomy of selective mortality may be interpreted in light of species-specific differences in otolith growth patterns or juvenile ecology.

For example, larval duration and growth rates are significantly more variable for T. bifasciatum than H. bivittatus. Whereas H. bivittatus larvae had relatively invariant otolith growth trajectories, T. bifasciatum individuals with longer larval durations had maximum otolith growth rates consistently 50% slower than individuals with shorter larval durations and faster otolith growth (Searcy and Sponaugle 2000). Consequently,
whereas larval condition, growth rates, and metamorphic band width may be correlated in _H. bivittatus_, the same is not necessarily true for _T. bifasciatum_.

In contrast to _T. bifasciatum_ survivors that had faster juvenile growth the first day following emergence, there was no difference in juvenile growth rates immediately after emergence for _H. bivittatus_. Despite this pattern, survivors of the _H. bivittatus_ spring and fall-I cohorts had significantly larger otoliths at emergence and after the first day than the original population. These results should be interpreted cautiously, as there was no consistent trend in selective mortality based on standard length at emergence. Furthermore, because somatic growth is probably negligible during metamorphosis and there was no difference in post-emergence otolith growth rates between the population and survivor groups, these results probably do not indicate size selection. Rather the difference in otolith size between populations and survivor groups is more likely the residual effect of differential otolith accretion rates during metamorphosis (i.e., survivors had wider metamorphic bands than the overall population).

Selective mortality based on larval (_H. bivittatus_), metamorphic (_H. bivittatus_ and _T. bifasciatum_), and juvenile traits (_T. bifasciatum_ likely reflects the high vulnerability of both species immediately following the larval–juvenile transition. While it is possible that a highly variable larval life history in _T. bifasciatum_ masks any selective mortality based on larval traits (as discussed above), evidence for juvenile trait-based selective mortality in _T. bifasciatum_ and not _H. bivittatus_ suggests a dichotomy of selective mortality as these fishes age. Upon settlement, these species are ecologically distinct and may exhibit species-specific differences in how physiological condition is manifested, both in their behavior as well as in otolith growth patterns. In Barbados, recently emerged _T. bifasciatum_ juveniles are found as solitary individuals in reef areas whereas juvenile _H. bivittatus_ are more cryptic and are generally found in small groups in the sand/rubble areas between reefs. Risk of predation for juvenile fishes is thought to decrease with distance away from the reef (Shulman 1985) because there are more predators in the reef environment than in surrounding areas. Furthermore, predation of older juvenile _T. bifasciatum_ may be low as this species is a known cleaner (Carr and Hixon 1995). As a result of these contrasting ecologies, juveniles may be subjected to different species of predators, different rates of predation, and thus different rates of selective mortality. Higher settlement condition (wider metamorphic band width) in _T. bifasciatum_ may be translated into enhanced competitive abilities, better feeding, and higher early growth (higher otolith growth rates the first two days following emergence). In contrast, newly emerged, schooling _H. bivittatus_ individuals may have equal access to food (no difference in otolith growth following emergence);

thus, individuals of higher condition simply may be better able to detect or behaviorally avoid predators.

There was no consistent trend for selective mortality based on all larval traits either within or between species. This result is not surprising because by definition a critical period is one in which mortality is temporally variable (Thorisson 1994). Mortality in general and thus selective mortality may vary among cohorts for a number of reasons. For example, predation pressure has been shown to be highly variable among cohorts (e.g., Hixon 1991). Competitive interactions based on abundance of recruits as well as range of condition with which recruits settle may further compound among cohort differences in selective mortality. Therefore, due to the inherent variability of these processes it is not surprising that no consistent pattern in selective mortality was found.

_Demographic significance_

Evidence from this study suggests that physiological condition manifested as growth rate influences early juvenile survival of two coral reef fishes. We suggest that this pattern is general in taxa that have an energetically costly life history transition (i.e., a relatively long period of metamorphosis). Poor condition may increase mortality due to both starvation and enhanced risk of predation (Margules 1993, Planes et al. 1997). In marine invertebrates, a minimum condition level may be necessary to complete the physiological and morphological changes during metamorphosis (e.g., Fenaux et al. 1994, Guillou and Tortu 1994, Jarrett and Pechenik 1997) as well as to ensure initial juvenile feeding success (Whyte et al. 1992). The importance of physiological condition to the survival of new recruits will probably depend not only on the degree of variability in condition at settlement, but also on how quickly feeding can commence following settlement.

High mortality rates during and immediately following metamorphosis, as well as the potential for selective mortality based on metamorphic traits during this period has been widely recognized and metamorphosis has gained recognition as a critical interval for marine fishes (Anderson 1988, McCormick and Molony 1992, Keefe and Able 1993, Thorisson 1994), invertebrates (Gosselin and Qian 1996, Jarrett and Pechenik 1997, Pechenik et al. 1998), as well as amphibians (Wilbur 1980, Twombly 1996). Depending on the unique characteristics of a larva (variability in size, age, and condition) as well as that of the environment it enters (high or low mortality risk), this critical period may be as short as several hours to as long as several weeks.

The finding that selective mortality may occur during a relatively narrow temporal window highlights the importance of mortality of the youngest individuals in determining local population size. Recent work has shown that larval supply is often quickly decoupled from recruitment and later abundance (Jones 1990, Osman et al. 1992, Eggleston and Armstrong 1995, Hixon
and Carr 1997, Caselle 1999). Despite this pattern, most work examining post-settlement mortality does not often differentiate juvenile age on a sufficiently fine temporal scale, thereby missing the early transitional period when mortality is likely to be highest. Recruitment studies that begin counting young juveniles after this early period provide a measure of input to the population, yet the underlying processes and mechanisms of settlement generating these patterns are often entirely unknown. Recruitment peaks may be the result of either a large pulse in larval supply or relatively higher early juvenile survival. Variation in juvenile survival may be related not only to juvenile habitat and predator field, but also early life history traits (such as physiological condition) of settlers. Ultimately, the environment encountered by larvae may not only dictate initial supply of juveniles but also how well they survive to later stages. Teasing apart causal mechanisms that may operate across stage transitions is a prerequisite to a complete understanding of the population dynamics of organisms with complex life histories.

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