

# Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae)

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**ABSTRACT:** Records of age and growth stored within otoliths were used to compare early life history traits with patterns of light trap catches for the damselfish *Stegastes partitus* (Poey). Otoliths provided strong evidence that fast growing cohorts of *S. partitus* larvae had higher survivorship than slow growing cohorts. Average growth rates during the larval phase accounted for 83% of the variability in the magnitude of catches in light traps on a monthly basis. This result suggests that fast growing cohorts of larvae contribute more to the replenishment of benthic populations than slow growing cohorts of this species. Multiple regression identified water temperature, rainfall and wind component as important determinants of larval growth, age at capture and monthly catches of this species. These variables accounted for 7 to 36% of the variance in growth rates, while water temperature was moderately correlated ( $r^2 = 0.48$ ) with catches. If such correlations between larval growth rates and replenishment are a general phenomenon, then this may provide a simple means of predicting year-class success in a range of reef fishes.

**KEY WORDS:** Coral reef fish · Larval growth · Otolith · Survivorship · Replenishment · Environmental variables · Water temperature · Light traps

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## INTRODUCTION

The 'growth-mortality' theory suggests that survivorship of fish larvae during the planktonic stage is selective due to a range of size-related effects on predator-prey interactions (Anderson 1988, Bailey & Houde 1989, Leggett & DeBlois 1994). Size selection may occur because fast growing larvae reach the point of developmental competence to settle into juvenile habitats much quicker than slow growing larvae (Houde 1987) and will spend less time in the plankton, where they are exposed to high levels of predation (Houde 1987, Cushing 1990, Bailey et al. 1995, Suthers

1998). Fast growing fish within a cohort gain a size advantage with respect to avoiding predation (Miller et al. 1988, Bailey & Houde 1989, Litvak & Leggett 1992). Due to the great fecundity of marine fishes and the very high rates of mortality suffered by planktonic larvae, under conditions of size-selective survivorship only small changes in growth rates are necessary to create large fluctuations in the number of fish surviving to reach settlement. The combination of these processes is thought to account for the highly variable nature of the replenishment process in stocks of marine fishes (Houde 1987, 1989, 1997, Leggett & DeBlois 1994).

If growth rates are an important determinant of survivorship in the plankton, as suggested by the growth-mortality theory, then we would expect to find a strong positive correlation between the numbers of new individuals arriving in benthic habitats (replenishment)

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and larval growth. Some recent studies provide support for this prediction. For example, Campana (1996) found that size at age of pelagic juvenile cod *Gadus morhua* was strongly correlated with year-class strength and that variation in growth at this stage could account for a 4-fold difference in abundance among cohorts of adults. Similarly, Bergenius (1998) examined growth of a common tropical surgeonfish *Acanthurus chirurgus*, and found that the magnitude of settlement and recruitment of this species over 3 yr was strongly correlated with planktonic growth rates of larvae from 6 to 22 d after hatching. Further support for links between larval growth and recruitment success of marine fishes is derived from studies that show that fast growing larvae are more likely to survive than slow growing fish in the plankton (e.g. Hovencamp 1992, Meekan & Fortier 1996, Hare & Cowen 1997, Fortier & Quinonez-Velazquez 1998, Rilling & Houde 1999, Sirois & Dodson 2000).

Growth of planktonic larvae is influenced by water temperature (Houde 1989, Fukuhara 1990, Polo et al. 1991, Suthers & Sundby 1993, Jenkins & May 1994, McCormick & Molony 1995, Bailey & Haoude 2001), food availability (McCormick & Molony 1992, Theilacker et al. 1996, Jordan et al. 2000) and other intrinsic factors such as genotype and maternal contribution (Chambers et al. 1993, Chambers 1997). In poikilotherms such as fishes, temperatures determine metabolic rates, while food availability will not only depend on the number and quality of potential items of food and thus productivity of planktonic food chains, but also on the environmental variables that can influence the supply of this food to larval fish. For example, feeding success has been linked to spatial variability in turbulence levels, which can enhance encounter rates of larval fish with prey and lead to higher rates of ingestion (Kiorboe & MacKenzie 1995, Gallego et al. 1996).

In this study, we use fish otoliths to examine the extent to which planktonic growth rates influence the replenishment of a common Caribbean reef fish, *Stegastes partitus*. In this species, increments are deposited on a daily basis within otoliths (Robertson et al. 1988), allowing back-calculation of size-at-age and daily growth rates where there is a linear correlation between otolith and fish size (Francis 1990, Campana & Jones 1992, Hare & Cowen 1995; but see Murdoch & Doherty 1997). In order to identify the environmental factors that determine the growth of larvae in the plankton, a range of physical variables including water temperature, wind speed and direction, turbulence, tides, solar radiation and rainfall were measured and compared with growth and replenishment patterns using multiple correlation analyses.

Light traps (Doherty 1987) were used to measure replenishment of *Stegastes partitus*. In many previous

studies, replenishment has been estimated from counts of newly settled fish (Doherty & Williams 1988), which may be confounded by the effects of post-settlement processes such as mortality and migration (Robertson & Kaufmann 1998). This problem is avoided by the use of light traps, as the technique captures fish immediately prior to their settlement into the benthic habitats of juveniles (Milicich et al. 1992).

## MATERIALS AND METHODS

**Study species.** The bicolor damselfish *Stegastes partitus* is common throughout the Caribbean from the Florida Keys south to Brazil (Lieske & Myers 1996) and is an abundant component of light trap catches in the San Blas Archipelago (9°34' N, 78° 58' W; Wilson 2001). This species provided a useful model for study, as the family occurs throughout tropical oceans and it shares a number of life history traits with other reef species, such as planktonic larvae, sedentary adult phases and sex reversal.

**Sampling protocol.** Around the time of the new moon, throughout the year, *Stegastes partitus* settles on the reefs of San Blas (Wilson 2001). Patterns of replenishment of this species were measured using light traps over 18 consecutive lunar months from December 1996 to June 1998. A detailed description of the sampling protocol is provided in Wilson (2001). Briefly, 3 traps were deployed in each of the exposed, lagoon and back-reef habitats. Within a habitat, traps were moored ca. 100 m apart and at a distance of 50 to 100 m from the reef margin. Traps were sampled for a period of 19 consecutive nights centred on the new moon in each lunar month, which encompassed the time when the majority of larvae (90%) settled into benthic habitats (Robertson 1992, Wilson 2001). Each day, traps were deployed prior to dusk and retrieved the following morning at dawn. Catches were immediately preserved in alcohol. In the laboratory, *S. partitus* were sorted from the samples and their standard lengths (SL) were measured using a dissecting microscope.

**Otolith preparation and analysis.** As catches on any individual night of sampling were usually low, samples were pooled into monthly cohorts and a subset selected for otolith analysis. Within each month, catches were divided into 0.2 mm SL size classes and individuals were selected for analysis (n = 281) in proportion to the abundance of fish collected by the traps in each size range. A minimum of 15 fish were sampled from each cohort, although during several months <15 fish were collected, in which case all fish were sampled. The sagittae were extracted from each fish selected for otolith analysing, cleaned of endolymph

tissue and stored dry. One sagitta was selected from each fish and mounted on a glass slide using thermoplastic cement (Crystal Bond™), so that the distal end protruded over the edge of the slide. The otolith was then ground using 12 to 0.3 µm lapping films. The polished face of the otolith was then mounted face down on the slide and the rostral end of the otolith ground down to produce a thin transverse section incorporating the nucleus. Otoliths were viewed under transmitted light using a compound microscope at 1000× magnification. The microscope was equipped with a polarising filter, an Ikegami ICD-290 high-resolution video camera and an image analysis system. These were used to measure the width of increments along the longest axis of the otolith, which is the most sensitive to changes in growth during planktonic larval life (Wilson & McCormick 1997, 1999).

**Environmental variables.** Hourly measurements recorded at the San Blas Research Station were used to calculate daily averages of wind speed and direction, water temperature, rainfall and solar radiation (see Wilson & Meekan 2001). Prior to these data being compared to nightly light trap catches, the wind speed and direction data were combined into a single coarse wind component in addition to the non-directional wind speed variable. For this analysis, wind speeds originating from 315.1° to 90° (i.e. onshore), were identified as positive, and winds from 90.1° to 315° (i.e. offshore), were identified as negative (Milicich 1994). Mean daily water temperatures were measured at a depth of 6 m with a precision of 0.25°C. A daily average was calculated from the hourly readings. Rainfall data were measured as a daily total (mm). Total solar radiation was recorded ( $W\ m^{-2}\ h^{-1}$ ) and a daily average calculated. Tidal range was calculated as the maximum minus the minimum tidal height each night.

Estimates of wind-induced turbulence (MacKenzie & Leggett 1993, Dower et al. 1997) were calculated for each day of sampling using a boundary layer model (Oakey & Elliott 1982, Oakey 1985, Agrawal et al. 1992) where dissipation rates ( $\epsilon$ ,  $W\ m^{-3}$ ) scaled with wind and depth:

$$\epsilon = (\rho_a/\rho_w C_D)^{3/2} \times [w^3/(0.4z)] \times (1\ W\ m^{-3}/0.001\ m^2\ s^{-3}) \\ = (5.82 \times 10^{-9}) w^3/z$$

where  $w$  = daytime wind speed ( $m\ s^{-1}$ );  $z$  = sampling depth (1.5 m);  $\rho_a$  = density of air ( $1.2\ kg\ m^{-3}$ ; Loder & Greenberg 1986);  $\rho_w$  = density of seawater ( $1025\ kg\ m^{-3}$ ; Lueck 1988);  $C_D$  = coefficient of drag between the water surface and the wind (0.0015; Loder & Greenberg 1986); and 0.4 = von Karmann's constant; Lumley & Panofsky 1964).

**Early life history characteristics and monthly replenishment.** As the proportion of fish selected for analysis varied among lunar months, weighted aver-

ages of planktonic larval durations (PLD) and sizes at capture (SL) were calculated using the formula given in Zar (1996). Means were compared among months using non-parametric Kruskal-Wallis tests followed by Tukey-type multiple comparisons (Zar 1996) as the data set failed to meet the assumptions of parametric tests, even after transformation. The relationships of PLD and SL to monthly catches in light traps were examined using Pearson correlation coefficients. In this analysis, partial correlations were used to examine the effect of each variable independently.

An examination of larval growth rates over the duration of the PLD was undertaken in an attempt to determine whether fast growth throughout the PLD resulted in an increase in larval survivorship and thus enhanced replenishment. Otolith growth was calculated at different intervals of the PLD and compared to monthly catches in light traps using regression analysis. The mean PLD of this species was  $33.9 \pm 3.4$  d (Wilson & Meekan 2001). Thus, in order to include as many larvae as possible in analyses, the average age minus the standard deviation was chosen as the cut-off point for otolith examination (30 d). In the first analysis, monthly averages of otolith growth from 1 to 30 d after hatching were calculated and correlated with monthly catches in light traps. In all analyses, light trap catches were averaged among habitats (exposed, lagoon and back-reef). As the first 2 d of growth of pomacentrid larvae are probably sustained by food reserves in the yolk sac (M. McCormick pers. comm.) these increments were removed and the analysis repeated. Data sets were then divided into wet and dry seasons and reanalysed. Finally, analyses were repeated using partial correlation analysis (SPSS statistical package) to control for the effects of water temperature. These analyses compared monthly averages of otolith growth from 1 to 30 d and from 3 to 30 d with monthly catches in light traps.

In addition, otolith growth during different parts of the PLD was compared with light trap catches averaged among habitats. Examination of the mean otolith increment profile for *Stegastes partitus* revealed 2 distinct growth phases: from 1 to 13 d, and from 14 to 30 d after hatching. After removal of the first 2 increments after hatching (see above) monthly averages of otolith growth during both of these intervals were correlated with monthly catches in light traps. The PLD was then divided into 8 intervals: 1–2, 3–6, 7–10, 11–14, 15–18, 19–22, 23–26 and 27–30 d after hatching. The duration of these intervals corresponded to the error in age estimates from otoliths (2 to 3 d), with the exception of the first interval, which encompassed the likely duration of nutrition from the yolk sac. Average monthly increment width during each interval was then correlated against monthly catches in traps to determine whether

any portion of the PLD was a critical determinant of replenishment. Lastly, monthly averages of otolith radius from 3 d after hatching and then on successive days until 30 d after hatching were correlated with monthly catches in traps. Lastly, monthly averages of otolith radius from 3 d after hatching and then on successive days until 30 d after hatching were corrected with monthly catches in traps.

**Seasonal growth differences.** We compared the otolith growth profiles of fish that were collected in light traps in the wet season with those from the dry season using repeated measures MANOVA (Chambers & Miller 1994). The 8 growth intervals of the PLD (see preceding section) were used as response variables in these analyses. MANOVA compared average otolith growth rate ( $\mu\text{m d}^{-1}$ ), specific growth rate (% growth  $\text{d}^{-1}$ ) and radius at age, between fish collected in the wet and dry seasons. Repeated-measures MANOVA were used as the growth of larval otoliths is autocorrelated among time intervals (i.e. the fastest growing fish during 1 interval tend to be the fastest growing fish in the next interval) (Chambers & Miller 1994). Average otolith growth rate ( $\mu\text{m d}^{-1}$ ) was a measure of daily otolith growth throughout the larval phase. Specific growth rate (% growth  $\text{d}^{-1}$ ) measured the change in otolith growth during one period as a proportion of growth during the previous period, providing information on the relative growth rates of larvae. Average otolith radius at age ( $\mu\text{m}$ ) measured the combined growth to the point of measurement, thus providing information on size at age throughout the larval stage.

Examination of the data revealed that variance in measurements among individuals increased with age. Consequently, data were either arcsine or  $\log_{10}$  transformed to improve homogeneity of variance. Pillai's Trace was used as the test statistic. Planned comparisons of means were used to identify intervals where there were significant differences in otolith growth of fish between seasons. These tests were adjusted for multiple comparisons using Bonferroni correction (significance level  $\alpha = 0.006$ , 8 comparisons). As differences among individuals were likely to be small, these analyses used otolith growth rather than back-calculated fish growth to avoid errors that were likely to be introduced by back-calculation of fish size from otoliths (Chambers & Miller 1994). Data sets were analysed using STATISTICA.

**Environmental variables and larval growth.** Rainfall, solar radiation, turbulence, water temperature, wind speed and wind component were compared with 3 larval traits: age at capture, otolith radius from age 3 to 13 d and from 3 to 30 d, using multiple regression analysis. As the date of hatching was known for each fish, the average of each environmental variable could

be calculated over the period corresponding to the PLD of each individual fish. These values were then averaged for each month, giving 17 data points (i.e. months) for analysis, since in 1 lunar month no *Stegastes partitus* were captured. These data sets (age at capture, otolith radius from 3 to 13 d and from 3 to 30 d and monthly catches) were compared with the set of environmental variables for both wet and dry seasons and for data pooled between seasons. As some of the variables in these analyses were highly correlated, partial correlations were sometimes calculated between the dependent and independent variables. For similar reasons, correlation matrices were calculated for environmental variables. Where a model selected 2 highly correlated variables, the variable that contributed most to the model was retained and the other discarded. This procedure ensured that the final estimate of correlation was not inflated due to the interdependence of some variables. These analyses also used STATISTICA.

## RESULTS

### Early life history characteristics and monthly replenishment

The age at capture in light traps of pre-settlement *Stegastes partitus* ranged from 28 to 44 d (weighted mean = 33.91 d, SD = 3.0) (Fig. 1a). Fish collected during the wet season were on average younger than fish collected during the dry season ( $t$ -test,  $p = 0.001$ , weighted means of 33.46 d, SD = 2.7 and 34.95 d, SD = 3.5 respectively, Fig. 1b,c). Mean size at capture of fish over the duration of the study was 12.22 mm (SD = 0.83) and ranged from 9.1 mm to 14.4 mm (Fig. 2a). The frequency distributions of SL in wet and dry seasons showed similar patterns to age at capture (Fig. 2b,c). Generally, fish collected in light traps immediately prior to settlement during the wet season were smaller than those from the dry season ( $t$ -test,  $p = 0.009$ , Fig. 2b,c). Coefficients of variation for age and SL showed that age was slightly more variable than SL at capture in light traps (CV of 0.090 and 0.068 respectively). As there were strong seasonal differences in the size and age at capture, these variables also differed among lunar months (age: Kruskal-Wallis  $H = 79.132$ ,  $p \leq 0.0001$ ,  $df = 17$ , Fig. 3a; size: Kruskal-Wallis  $H = 67.918$ ,  $p \leq 0.0001$ ,  $df = 17$ , Fig. 3b). Age and size at capture were not correlated with light trap catches ( $r = -0.42$ ,  $p > 0.05$  and  $r = -0.04$ ,  $p > 0.05$  respectively). However, the partial correlation between age at capture and catches, when controlled for SL, was significant ( $r = -0.54$ ,  $p = 0.031$ ), while the partial correlation between SL and catches when controlled for the effect of age at capture was not significant ( $r = 0.37$ ,  $p \geq 0.05$ ).

### Average otolith growth throughout the pelagic larval duration

Otolith increment profiles of *Stegastes partitus* varied little among individuals. Typically, an initial period of rapid growth up to 12 to 13 d was then followed by a slight reduction in growth rate. Once fish attained the age of 30 d after hatching, growth rates declined slightly until the point of capture prior to settlement (Fig. 4a). The average otolith increment profiles for both wet and dry season fish are shown in Fig. 4b.

Monthly catches in light traps were strongly correlated with average otolith growth from 1 to 30 d after hatching ( $r^2 = 0.79$ ,  $p < 0.001$ , Fig. 5a). After removal from datasets of the first 2 d of growth after hatching, when larvae utilise yolk for nutrition, the strength of

the correlation increased slightly (Table 1, Fig. 5b). When data for wet and dry seasons were analysed separately, the correlation between otolith growth and monthly catches remained highly significant (Table 1, Fig. 5a,b). An analysis of covariance (ANCOVA) did not detect any significant differences between regression slopes calculated for wet and dry seasons (1 to 30 d:  $F = 0.229$ ,  $p = 0.640$ ; 3 to 30 d:  $F = 0.230$ ,  $p = 0.639$ ). When partial correlations were calculated that controlled for the effects of water temperature, the correlations remained strongly significant ( $r^2 = 0.69$ ,  $p \leq 0.001$  and  $0.67$ ,  $p \leq 0.001$  for otolith growth from 1 to 30 d and 3 to 30 d after hatching respectively).

Analysis of correlations between otolith growth at different intervals during the PLD and light trap catches are summarised in Table 1. Otolith growth dur-

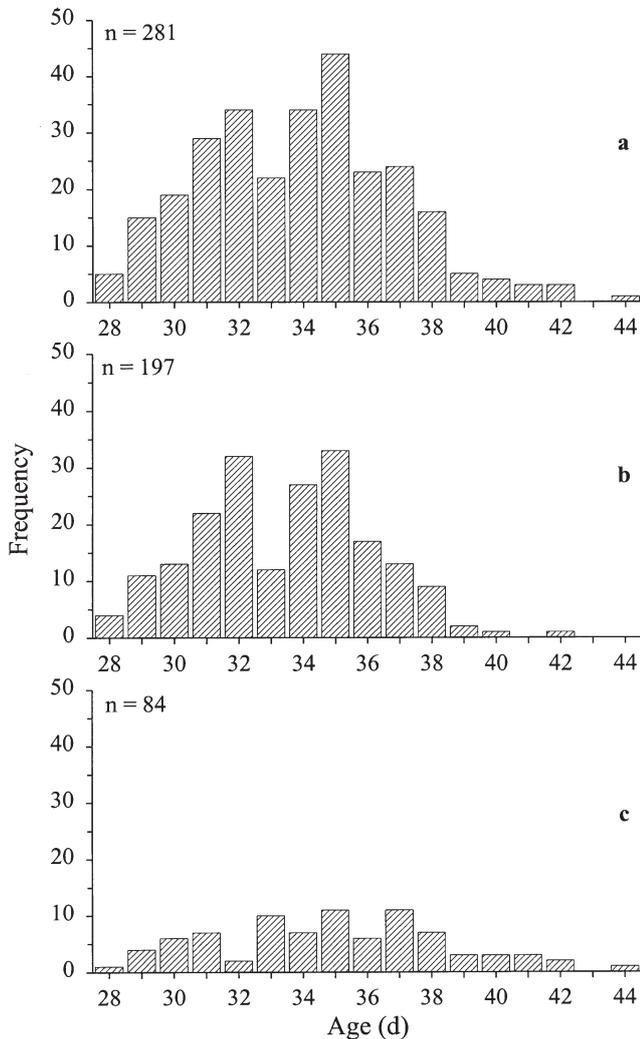


Fig. 1. *Stegastes partitus*. Age frequency at capture of pre-settlement fish collected by light traps sampled for 19 nights in each of 18 consecutive lunar months. (a) All months, (b) wet and (c) dry season months

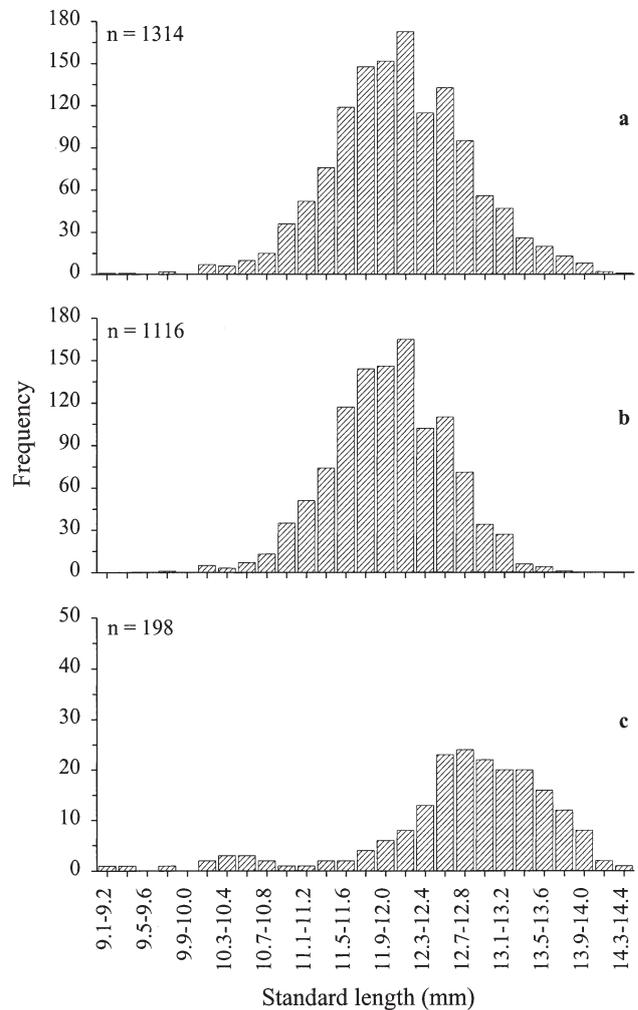


Fig. 2. *Stegastes partitus*. Standard length (SL) at capture of pre-settlement fish collected by light traps sampled for 19 nights in each of 18 consecutive lunar months. (a) All months, (b) wet and (c) dry season months

ing the first 2 d after hatching was not correlated with catches in the wet or dry seasons, or when data sets were pooled (Table 1). In the dry season, growth from 3 to 6 d after hatching was not significantly correlated with catches; however, in the wet season and pooled analyses, growth during this period accounted for 62% and 48% of the variance in catches respectively. All remaining growth intervals were correlated with light trap catches (Table 1). The strongest correlation between growth and catches in data sets pooled between seasons occurred from 7 to 10 d after hatching and accounted for 80% of the variance in catches. Similarly, growth in the wet season was highly correlated with

Table 1. *Stegastes partitus*. Coefficients of determination ( $r^2$ ) between mean daily otolith growth and catches of pre-settlement fish in light traps sampled for 19 nights in each of 18 consecutive lunar months in the San Blas Archipelago. Nightly catches were pooled and monthly averages calculated giving 17 data pairs in the pooled analysis, as in one month no *Stegastes partitus* were captured by traps. Coefficients were calculated for otolith growth averaged over different portions of the PLD. The same analyses were then repeated on data sets split into wet (n = 9) and dry (n = 8) season months

Growth interval (d)	Pooled $r^2$	Pooled p	Wet $r^2$	Wet p	Dry $r^2$	Dry p
1–30	0.79	<0.001	0.59	<0.001	0.76	<0.001
3–30	0.83	<0.001	0.59	<0.001	0.78	<0.001
3–13	0.79	<0.001	0.60	<0.001	0.57	<0.001
14–30	0.78	<0.001	0.50	<0.001	0.82	<0.001
1–2	ns	ns	ns	ns	ns	ns
3–6	0.48	<0.01	0.62	<0.01	ns	ns
7–10	0.80	<0.001	0.63	<0.01	0.53	<0.01
11–14	0.70	<0.001	0.38	<0.01	0.56	<0.01
15–18	0.64	<0.001	0.45	<0.01	0.52	<0.05
19–22	0.62	<0.001	0.50	<0.01	0.39	<0.05
23–26	0.68	<0.001	0.40	<0.01	0.68	<0.01
27–30	0.68	<0.001	0.55	<0.01	0.45	<0.05

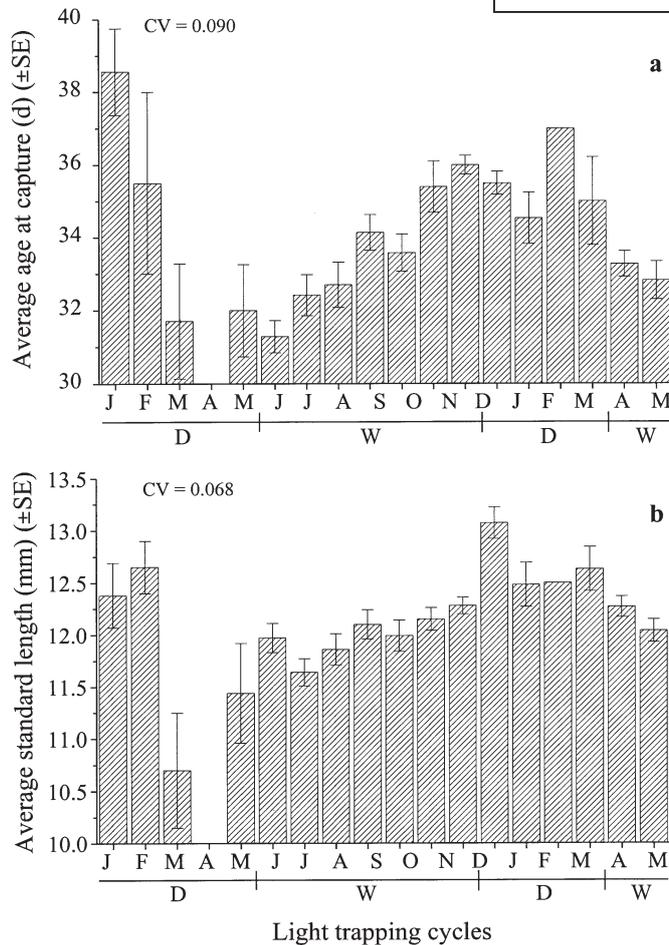


Fig. 3. *Stegastes partitus*. (a) Average monthly age and (b) standard length (SL) at capture of pre-settlement fish collected by light traps sampled for 19 nights in each of 18 consecutive lunar months. W = wet season, D = dry season. Calendar months shown

catches from 3 to 6 d and from 7 to 10 d after hatching (Table 1). In contrast, otolith growth and catches were most strongly correlated in dry season samples from 23 to 26 d after hatching (Table 1).

These growth patterns were supported by analysis of otolith radii measurements at successive increments from 3 to 30 d after hatching (Fig. 6a,b). The pooled data sets indicated a period between 3 to 13 d that accounted for most of the variance in the relationship between growth and catches. The addition of the otolith growth profile from 14 to 30 d contributed little extra information to the analysis (Fig. 6a). When data sets were divided between seasons, growth of larvae between 3 to 8 d after hatching accounted for up to 68% of the variance in catches during the wet season (Fig. 6b), while otolith growth during the remainder of the PLD contributed little to the relationship. In contrast, analysis of dry season samples displayed the opposite pattern. Larval growth of fish collected during the dry season was not significantly correlated with catches during the first week after hatching, while correlations between otolith radius and catches increased throughout the remainder of the PLD (Fig. 6b).

**Seasonal growth patterns in pre-settlement stage *Stegastes partitus***

The interaction between season and growth interval was highly significant for all 3 variables in the repeated-measures MANOVA analyses (aver-

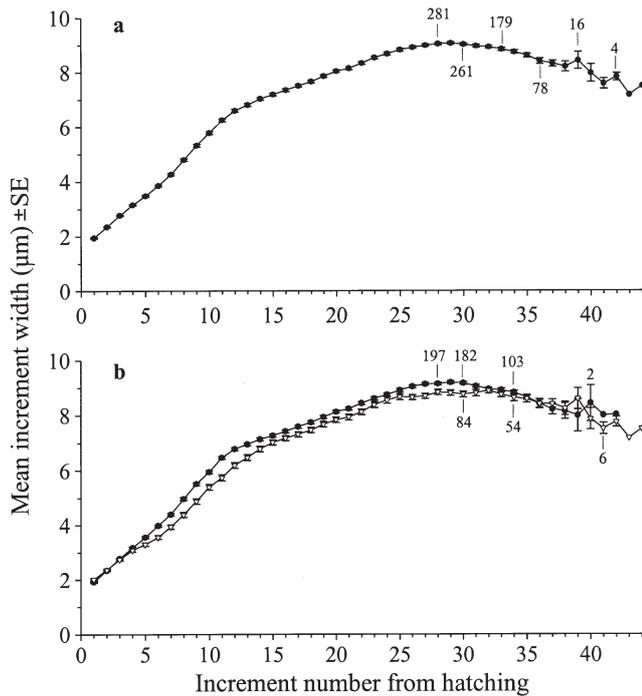


Fig. 4. *Stegastes partitus*. Mean otolith growth increment profiles of pre-settlement fish collected by light traps sampled for 19 nights in each of 18 consecutive lunar months. (a) All fish ( $n = 281$ ), (b) fish captured in wet ( $\bullet$ ,  $n = 197$ ) and dry seasons ( $\nabla$ ,  $n = 84$ ). Numbers on profiles show sample sizes

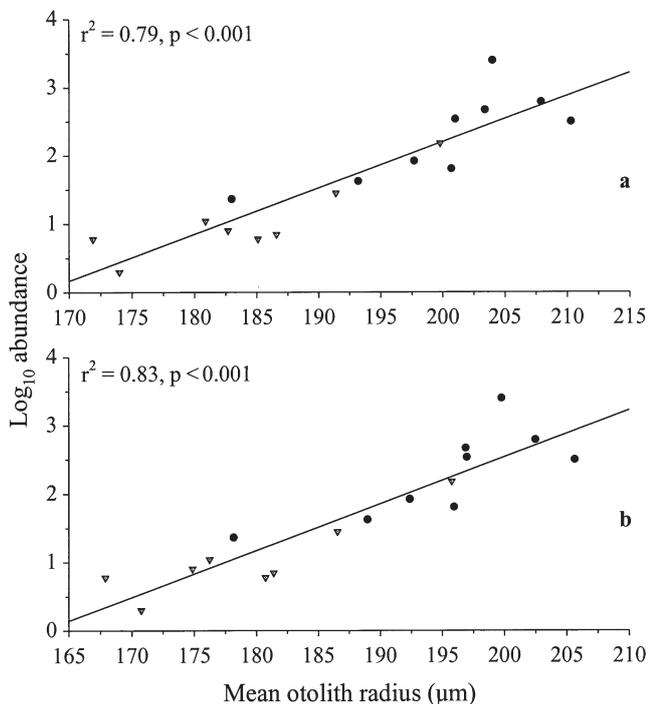


Fig. 5. *Stegastes partitus*. Relationship between monthly light trap catches and monthly averages of otolith radius ( $\mu\text{m}$ ) from (a) 1 to 30 d after hatching and (b) 3 to 30 d after hatching. ( $\bullet$ ) = wet season. ( $\nabla$ ) = dry season

age daily growth: Pillai's Trace  $F = 6.24$ ,  $p = 0.0001$ ; specific growth: Pillai's Trace  $F = 6.26$ ,  $p = 0.0001$ ; radius at age: Pillai's Trace  $F = 6.24$ ,  $p = 0.0001$ ) indicating significant differences in the growth profiles of otoliths of fish collected in the wet and dry seasons.

Average otolith growth rate ( $\mu\text{m d}^{-1}$ ) of wet and dry season fish diverged 7 to 10 d after hatching, with fish collected during the wet season growing faster than those collected in the dry season (Fig. 4b). Growth rates from 23 to 26 d after hatching did not differ between seasons, but from 27 to 30 d, fish collected in the wet season again grew faster than those collected in the dry season (Table 2, Fig. 7a).

Specific growth ( $\% \text{d}^{-1}$ ) of both wet and dry season fish declined throughout the PLD (Fig. 7b). Fish collected during the wet season had a higher specific growth rate than those collected in the dry season from 3 to 10 d after hatching (Table 2). Significant differences in the otolith radius ( $\mu\text{m}$ ) at age between fish

Table 2. *Stegastes partitus*. Summary of results of repeated-measures MANOVAs that compared mean daily otolith growth ( $\text{mm d}^{-1}$ ), specific otolith growth ( $\% \text{d}^{-1}$ ) and otolith radius at age ( $\text{mm}$ ) of fish collected in wet and dry seasons. Growth was averaged over 4 d intervals in order to reduce the number of response variables in the analysis (Chambers & Miller 1995). Data were either arcsine or  $\log_{10}$  transformed to improve homogeneity of variance. Pillai's Trace was used as the test statistic. Planned comparisons of means were used to identify intervals where there were significant differences in otolith growth of fish between seasons. Tests were adjusted for multiple comparisons using a Bonferroni correction.

\*significant at  $\alpha = 0.006$

Variable	Growth interval (d)	$F$	$p$
Mean growth rate ( $\mu\text{m d}^{-1}$ )	1-2	6.692	0.011
	3-6	7.597	0.007
	7-10	27.493	<0.001*
	11-14	28.834	<0.001*
	15-18	11.218	0.001*
	19-22	8.699	0.004*
	23-26	5.024	0.026
Specific growth rate ( $\% \text{d}^{-1}$ )	27-30	10.103	0.002*
	1-2	1.068	0.303
	3-6	23.169	<0.001*
	7-10	23.161	<0.001*
	11-14	1.252	0.265
	15-18	4.784	0.030
	19-22	5.762	0.018
Otolith radius at age ( $\mu\text{m}$ )	23-26	7.618	0.007
	27-30	1.076	0.301
	1-2	6.696	0.011
	3-6	2.893	0.091
	7-10	18.354	<0.001*
	11-14	27.634	<0.001*
	15-18	26.199	<0.001*
19-22	23.644	<0.001*	
23-26	20.898	<0.001*	
27-30	22.757	<0.001*	

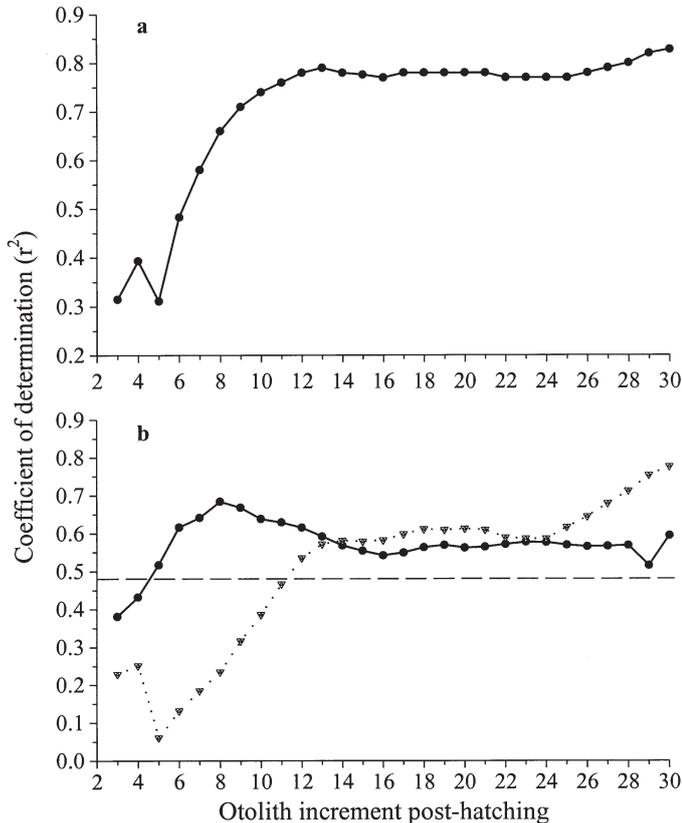


Fig. 6. *Stegastes partitus*. Pearson coefficients of determination ( $r^2$ ) between monthly light trap catches and otolith radius calculated for each successive increment from 3 to 30 d after hatching. (a) Data sets pooled between seasons and (b) wet and dry season data sets analysed separately. (●) = wet season, (▼) = dry season. Coefficients above horizontal line statistically significant at  $p < 0.05$

collected in wet and dry seasons first occurred at 7 to 10 d after hatching and then gradually increased during the PLD (Table 2, Fig. 7c).

#### Correlations between larval traits, light trap catches and environmental variables

Age at capture (PLD) of *Stegastes partitus* was correlated with different environmental variables in the wet and dry seasons. In the dry season this trait was weakly but significantly correlated with solar radiation and turbulence (Table 3). As these environmental variables were themselves only weakly correlated (Pearson correlation,  $r^2 = 0.25$ ), both were included in the model. During the wet season, age of capture was weakly correlated with water temperature. As different variables were identified for the models of wet and dry season data sets, the analysis could not identify a 'best fit' model for data pooled between seasons (Table 3).

Otolith growth from 3 to 13 d after hatching was correlated with rainfall and water temperatures during the dry season and these variables accounted for 22% of the variance in data sets during this period (Table 3). When rainfall was removed from the model, daily water temperature accounted for only 16% of the variance in otolith growth during this period. In the wet season, otolith growth (Partial correlation,  $r = 0.40$ , Table 3) from 3 to 13 d after hatching was weakly correlated (0.07) with rainfall and wind component. When data sets of otolith growth from 3 to 13 d after hatching were pooled between seasons, the multiple regression analysis selected the variables that accounted for the most variance in the dry and the wet season samples (i.e. water temperature and wind component respectively), which together accounted for 16% of the variance in otolith growth.

The results of the analysis of growth over the entire PLD were similar to those recorded in the analysis of growth from 3 to 13 d after hatching (Table 3). During the dry season rainfall and water temperature accounted for 36% of the variance in otolith growth (Table 3). Otolith growth was weakly correlated ( $r = 0.13$ ) with the wind component during the wet season, while water temperature and wind component were positively correlated with growth and accounted for 27% of the variance in the data set of growth pooled between seasons (Table 3).

Monthly catches pooled between seasons were positively correlated with water temperature ( $r^2 = 0.48$ ; Table 3). No other environmental variable contributed significantly to light trap catches. Data sets of catches in wet and dry seasons could not be analysed separately due to limited within-season (monthly) replication (Sokal & Rohlf 1981).

## DISCUSSION

Our results were consistent with the predictions of the growth-predation hypothesis. Growth rates of *Stegastes partitus* during planktonic life were strongly correlated with the magnitude of monthly catches in light traps, so that cohorts of fish that grew quickly were more abundant immediately prior to settlement than those that grew slowly. As the numbers of larvae arriving from the plankton can have a profound influence on the dynamics and population size of adult reef fishes (Doherty 1991, Doherty & Fowler 1994), these results suggest that fast growing cohorts may contribute more to the replenishment of benthic populations than those that are slow growing.

Mortality rates in the plankton decline as fish grow, since fewer predators are capable of consuming larvae of larger sizes (Anderson 1988, Bailey & Houde 1989). For this reason, the growth-predation theory predicts

that growth rates during the early part of larval life should be a more important determinant of survivorship than at later times. This idea was supported by analysis of the otolith radii of fish captured during the wet season, where correlations between otolith radii and catches increased rapidly after hatching and were strongest after 7 to 8 d of planktonic life. Correlations then declined slowly for the rest of the PLD. However, for fish captured in the dry season, correlations between otolith radii and catches were initially weak and only became significant almost 2 wk after hatching. Correlations then slowly increased or remained stable for another 10 d, after which time they rapidly increased towards the end of the PLD. Although this result should be treated with caution, since dry season correlations were based on fewer individuals than those of wet seasons, a potential explanation for this pattern is that fish hatching in each season may face different predators in the plankton. Many of the predators of larval fishes display seasonal blooms or cycles in abundance (Purcell 1985, Purcell et al. 2000). Similarly, fishes such as mackerels and tunas, which prey on fish larvae, have seasonal patterns of spawning (Jenkins et al. 1984, Fortier & Villeneuve 1996, Farley & Davis 1998). Additionally, freshwater runoff during the wet season may increase the productivity of food chains, increasing the abundance of zooplankton capable of attacking and consuming very young fish larvae (Heath 1992). At present, little is known of the identity of organisms that prey on larval fishes in the nearshore waters of San Blas, or of their seasonal patterns in abundance.

Differences in larval environments, predators and potentially in the mechanisms underlying size-selective mortality, may also account for variation in the timing of selective mortality recorded among studies. Campana (1996) found that the abundance of year classes of adult cod *Gadus morhua* was correlated with growth averaged over the entire larval phase, but not with growth rates of larvae prior to 40 d after hatching. In our study, catches of *Stegastes partitus* in light traps were correlated with larval duration and growth rates during early larval life in the wet season, but during the latter part of the PLD in the dry season. Bergenius (1998) examined a tropical surgeonfish *Acanthurus chirurgus* at San Blas and found that larval growth rates from 6 to 22 d after hatching were correlated with settlement and recruitment of young fish to benthic populations. Growth during the remainder of the

PLD, which averaged 52 d, had little influence on the magnitude of settlement or recruitment of this species.

Settlement of *Stegastes partitus* occurs largely during the wet season, while most *Acanthurus chirurgus* settle to reefs during the dry season in San Blas (Wilson 2001). As noted above, larval environments during wet and dry seasons may differ due to the seasonal changes in the identity and abundance of predators. Such changes are likely to be more extreme when comparisons are made between the tropical environments of reef fishes and the cool temperate waters inhabited by cod larvae. Additionally, Houde (1989) suggests that as a consequence of the relatively short stage durations and high growth rates of tropical fish larvae, they may be more susceptible than those in temperate environments to mortality during critical periods (*sensu* Hjort 1914) in early planktonic life.

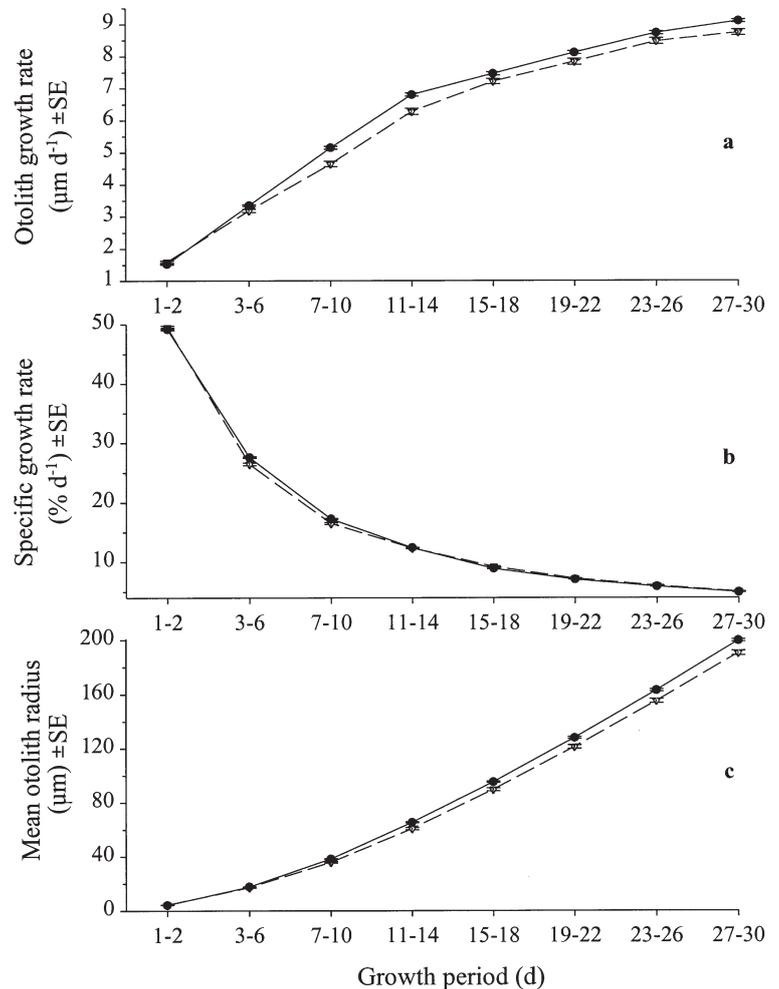


Fig. 7. *Stegastes partitus*. (a) Otolith growth (b) specific growth and (c) otolith radius averaged for each of 8 intervals during the larval stage. Solid lines = wet season samples ( $n = 197$ ). Dashed lines = dry season samples

Table 3. *Stegastes partitus*. Optimum predictive models from multiple regression analyses that compared early life history characteristics with a range of environmental variables. As the date of hatching was known for each fish, averages of environmental variables could be calculated over the period corresponding to the PLD of each individual fish. These values were then averaged for each lunar month of sampling, giving 17 data points (i.e. months) for analysis, since in 1 lunar month no *Stegastes partitus* were captured (See 'Materials and methods' for details). Analyses were then repeated using data sets split into dry (n = 8) and wet (n = 9) season months. Partial correlations shown for environmental variables selected in each model. ns = no significant model identified

Dependent variable	Season	r <sup>2</sup>	p	Independent variable(s)	Partial correlations	n
Plankton larval duration	Dry	0.19	0.0002	Solar radiation Turbulence	-0.32 -0.36	84
	Wet	0.09	<0.0001	Water temperature	0.30	197
	Pooled	ns	ns	–	–	281
Otolith growth 3–13 d	Dry	0.22	<0.0001	Rainfall Water temperature	-0.21 0.40	84
	Wet	0.07	0.0013	Rainfall Wind component	0.26 -0.22	197
	Pooled	0.16	<0.0001	Water temperature Wind vector	0.27 0.27	281
Otolith growth 3–30 d	Dry	0.36	<0.0001	Rainfall Water temperature	-0.30 0.55	84
	Wet	0.13	<0.0001	Wind vector	0.36	197
	Pooled	0.27	<0.0001	Water temperature Wind vector	0.34 0.36	281
Replenishment	Pooled	0.48	0.0021	Water temperature	0.69	17

Variation in larval growth rates between tropical and temperate regions may also influence the ability of studies to detect correlations at young ages. In *S. partitus* larvae, increment widths in otoliths are relatively large compared to those of young cod. At hatching *S. partitus* have increments that are ~3 µm wide and then rapidly increase in width to ~8 µm after 20 d of larval life, while in cod larvae increment widths remain less than 3 µm for many weeks after hatching (Campana 1996, Suthers et al. 1999). The wide increments in otoliths of tropical species (Wilson & McCormick 1997, 1999) are likely to enhance the power of statistical tests to detect correlations, particularly in the first days or weeks after hatching (Bergenius 1998).

As mortality rates in the plankton are very high, those larvae that grow rapidly to become juveniles may escape some of the mortality suffered by slow growing individuals (the 'stage-duration' hypothesis; Houde 1987, Anderson 1988, Cushing 1990). A theoretical study by Houde (1989) examined the effects of temperature on larval growth and mortality rates and concluded that larval duration was inversely related to growth rate and that variability in growth increased with temperature, while variability in stage duration declined. Under these conditions, he suggested that differences in stage duration were far less likely to contribute to mortality of larvae at low latitudes than high latitudes, since warm water temperatures in the tropics resulted in relatively fast larval growth rates. The results of our study and those of Bergenius (1998)

show that despite this prediction, larval growth is correlated with settlement and recruitment in tropical species, implying that mechanisms other than the stage-duration hypothesis may underlie the selective mortality of tropical larvae.

In addition to a reduction in stage duration, the larger size-at-age of fast growing fish may also provide a survival advantage, by reducing vulnerability to predators (the 'bigger-is-better' hypothesis, Miller et al. 1988, Bailey & Houde 1989). While laboratory evidence to support this idea is equivocal (Rosenberg & Haugen 1982, Leggett & DeBlois 1994), some field studies have found that larval and juvenile fish that have larger size-at-age have a higher probability of survival than smaller individuals (Post & Prankevicius 1987, Meekan & Fortier 1996, Hare & Cowen 1997). It remains difficult however, to determine if the bigger-is-better mechanism was responsible for the correlations between growth rate and catches found in *Stegastes partitus*. Growth rate and size of larval *S. partitus* were correlated, suggesting that the stage-duration and bigger-is-better mechanisms will not act independently (Hare & Cowen 1997). Furthermore, there was a significant negative correlation between the duration of the larval phase and catches in light traps when the analysis controlled for SL. This implied that fish that had short larval durations were more abundant at the end of the planktonic phase than fish with relatively long larval durations, as predicted by the stage-duration hypothesis. No significant correla-

tion was found between SL and catches when the analysis controlled for differences in age at capture, as would have been expected if the bigger-is-better mechanism were important in the days immediately prior to settlement.

While our results were consistent with the predictions of the growth-predation hypothesis, it is possible that correlations between growth rates and replenishment of *Stegastes partitus* actually reflected independent responses to other causal variables. For example, if spawning was maximised during periods when larval growth was greatest, then replenishment and growth rates might appear to be linked. However, this scenario would require a strong relationship between the magnitude of spawning and recruitment, which does not occur in this species (Robertson et al. 1988). The potential influence of other biological and physical variables on larval growth and replenishment of *S. partitus* are examined below.

#### Environmental determinants of larval duration and growth rates

Both environmental (McCormick & Molony 1992, 1995, Bergenius 1998, Wilson & Meekan 2001) and intrinsic (genetic, maternal; Kerrigan 1997, McCormick 1999) factors can drive variation in larval duration and growth rates of reef fishes. In our study, we found that solar radiation, turbulence and water temperature were weakly correlated with larval duration (age at capture in light traps), while water temperatures, in combination with wind direction, accounted for approximately 27% of the variance in growth rates of larval *Stegastes partitus* in the San Blas Archipelago. While comparative data for reef fishes are rare, our results are similar to those of McCormick & Molony (1995), who found that water temperatures could account for 30% of the variance in larval growth rates of newly metamorphosed goatfishes *Upeneus tragula* on reefs around Lizard Island, GBR. In contrast, Bergenius (1998) found that water temperature was not correlated with larval growth of *Acanthurus chirurgus* in San Blas, although wind direction had a moderate influence on growth patterns, as was the case in our study.

Temperature and food availability are argued to be the primary determinants of the growth rates of larval fishes (Batty 1987, Blaxter 1992, Heath 1992, Houde & Zastrow 1993, Rilling & Houde 1999). At large spatial and temporal scales, water temperature is often correlated with both larval growth rate and stage duration (e.g. Campana & Hurley 1989, Hovenkamp & Witte 1991, Rilling & Houde 1999, Bailey & Heath 2001), while other factors such as prey availability and turbu-

lence may appear more important at smaller scales, possibly because the range of temperature variation often declines with the scope of the study (Bailey & Heath 2001). However, the scale of sampling cannot explain the variation in environmental correlates of larval growth between our study and that of Bergenius (1998), since both collected fish over spatial scales of 1 to 10 km and at temporal scales of 1.5 and 3 yr respectively. Furthermore, McCormick & Molony (1995) obtained larvae at spatial scales comparable to the present study, but the duration of their sampling lasted only a few months.

In addition to larval growth, water temperature was also moderately correlated ( $r^2 = 0.48$ ) with the magnitude of monthly catches of *Stegastes partitus* in light traps. Although similar correlations have been recorded in a number of other species in San Blas (Wilson & Meekan 2001) they may, in reality, reflect the action of other factors that are themselves correlated with temperature. For example, warmer water temperatures are often associated with higher primary and secondary production and thus better feeding conditions for larvae (e.g. Heath 1992, Bailey & Heath 2001). In our study, correlations between larval growth and light trap catches were still significant in analyses that controlled for the effect of water temperature using partial correlations, implying that other, unmeasured variables such as food availability and maternal contributions (Kerrigan 1997, McCormick 1999) may indeed influence replenishment patterns of *S. partitus*.

In summary, our study adds to growing evidence that shows that variation in the larval duration, growth rate and development of the planktonic larvae of reef fishes is considerable (e.g. Wellington & Victor 1992, McCormick 1994, McCormick & Molony 1995, Kerrigan 1997, Sponaugle & Cowen 1997, Searcy & Sponaugle 2000, Wellington & Robertson 2001). Although this provides the raw material on which selective mortality can act, until recently relatively few studies have attempted to examine the effects of variation in these traits on the survivorship of larvae in the plankton. For newly settled fishes, growth, size and condition may be important determinants of mortality (Booth & Hixon 1999, Searcy & Sponaugle in press, but see McCormick & Kerrigan 1996). In *Stegastes partitus*, fish in better condition at settlement have a higher chance of survival in the first few weeks of benthic life (Booth & Hixon 1999). Similarly, Vigliola & Meekan (in press) found that fish that survived size-selective mortality one month after settlement were those individuals that were fast growing during planktonic life. This suggests that fast growth may not only provide a survival advantage in the plankton, but also has the potential to influence post-settlement survivorship in reef fishes.

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