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Population Ecology

Larval growth predicts the recruitment success of a coral reef fish

Mikaela A. J. Bergenius[1], ✉, Mark G. Meekan[2], D. Ross Robertson[3] and Mark I. McCormick[1]

Abstract. While growth rates of pelagic larvae have been argued to be one of the principal determinants of the recruitment success of temperate marine fishes, it is not known if this is the case in the tropics. Here, we use larval growth histories derived from otoliths of a Caribbean reef fish to show that monthly variation in the intensity of settlement and recruitment of pelagic juveniles onto reefs is positively correlated with variation in growth rates 1-2 weeks after larvae begin feeding. Our results suggest that the processes thought to underlie recruitment of marine fishes in temperate regions may also operate in the tropics and contrasts with current research on the causes of recruitment variability in coral reef fishes, which emphasises the role of larval transport.

Keywords. Critical period - Growth - Otolith - Plankton - Settlement

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Introduction

Variability in the recruitment of the pelagic young of marine fishes, which often is extreme, has major biological effects and substantial implications for management of fish stocks (Rothschild 1986). Identification of the processes that determine these fluctuations in recruitment has been a long-standing and central goal of fisheries research. Recent theories highlight relationships between larval growth and predation to the variability in survival of cohorts. Collectively termed the growth-predation hypothesis, they propose that mortality is size selective, with small fish having lower survivorship than large fish of the same age (Anderson 1988). This occurs because fast-growing fish become juveniles first and are thus exposed to pelagic predators for less time than slow-growing individuals (the stage duration hypothesis; Leggett and DeBlois 1994). Additionally, fast-growing fish are also larger than slow-growing fish of the same age and thus less vulnerable to predators (the bigger-is-better hypothesis; Miller et al 1988; Bailey and Houde1989). Under these conditions, small changes in growth rates produce large variations in survivorship and thus recruitment (Houde

1987; Cushing and Horwood 1994).

The evidence supporting these concepts originates almost exclusively from temperate regions and some theoretical work suggests that they may not apply in the tropics, where warm water temperatures result in relatively fast larval growth rates (Houde 1989). Whether this is the case is unclear, because until very recently, most tropical studies of the causes of recruitment variability have focused on larval traits related to dispersal, rather than patterns of planktonic growth and survivorship (Cowen and Sponagule 1997).

Unlike many temperate species of importance to fisheries, tropical reef fishes undergo a distinct habitat change at the end of larval life, settling from the plankton into the benthic habitats of adults. This allows settlement and recruitment patterns to be easily measured. If correct, the growth-predation hypothesis predicts that there should be a strong correlation between the magnitude of settlement and growth rates of larvae during planktonic life. We used growth records from the otoliths of newly settled fish to test this prediction for a common, widely distributed Caribbean reef fish, *Acanthurus chirurgus*.

Methods

Settlement and recruitment

Pelagic juveniles of *Acanthurus chirugus* settle to benthic reef habitats at night (Robertson et al. 1988). To estimate settlement, newly-settled fish were collected each morning from January 1984 to January 1987 from small (40-60 m^2 area) patch reefs in the San Blas Archipelago, Caribbean Panama (see map in Robertson et al. 1999). These reefs were isolated by sand and seagrass from continuous areas of reef to reduce the potentially confounding effects of migration of fish on our estimates of settlement. Recruitment patterns were measured by monthly censuses of recently settled fish at sites near the patch reefs. Censuses were made on eight reefs during the week before full moon, when settlement peaks (Robertson 1992). Counts recorded the number of recruits per month.

Otolith analysis

As *A. chirurgus* has a lunar pattern of settlement, with peak activity around new moons (Robertson 1992), collections of settlers were grouped into lunar cohorts (between successive full moons) and fish were selected for otolith analysis from each cohort. Typically, 30% of the fish from each lunar cohort of settlers were sampled for otolith analysis. Within each cohort, catches were subdivided among 1 mm size classes of standard length and sub-samples removed in proportion to the abundance of fish in each size class. Where a cohort included <15 settlers all individuals were processed. In total, 623 fish were selected for analysis.

Sagittal otoliths were removed from each fish, mounted on a glass slide, ground on lapping film to produce a thin transverse section that contained the nucleus, and viewed under immersion oil with a compound microscope using transmitted light at 1,000 × magnification.

Measurements of the width of each increment along the longest axis of the otolith were made using an image analysis system (OPTIMAS). We assumed that the increment closest to the nucleus of the otolith was formed at or within a day of hatching, as is the case in many temperate and tropical species (Campana and Neilson 1985; Wellington and Victor 1989). Otoliths from 11 haphazardly selected individuals were analysed 3 times in order to estimate errors associated with age and size measures. The errors in age estimates ranged from 0 to 3 days (median 2 days), while errors in radii measurements from the core to the edge of the otolith ranged from 2 to 13 µm (i.e. ±0.57% of the mean otolith radius).

Validation of daily increments

To validate daily patterns of increment formation 10 newly settled *A. chirurgus* were placed in aquaria and acclimated for several days. They were then immersed for 24 h in a solution of 500 mg/l oxytetracyline in seawater, returned to the aquaria for 16 days under a normal light regime with flow through seawater and algal food, then sacrificed. Sagittal otoliths of these fish were viewed under a microscope at 1,000 ×

magnification using a UV light source. As oxytetracyline deposits a fluorescent mark in the otolith (Stevenson and Campana 1992), the number of increments following the mark could be counted and compared to the number of days since treatment. Three independent counts were made of the otoliths of each individual. Counts of increments corresponded to the number of days since treatment of the fish by oxytetracyline and averaged 16.7±0.3 SE, where the expected number of increments was 17. Hence we assume that increments were deposited at daily intervals throughout the larval life.

Data analysis

Correlation analyses were used to compare larval growth rates and settlement and recruitment patterns. Prior to analysis, data sets of otolith growth were divided into 4-day periods to accommodate the 2-3 days error in age estimates. Since low-settlement months provided few individuals for analyses of otolith growth, data sets were pooled to 2-monthly intervals to increase samples sizes during such months. Settlement and recruitment data sets were also transformed to $\log_{10}$ values to accommodate the patchy nature of settlement at small spatial scales (Doherty and Williams 1988).

Results

Settlement and recruitment

Settlement of *Acanthurus chirugus* to patch reefs was seasonal and peaked around December each year (Fig. 1). There was a strong correlation between settlement and recruitment data sets (r=0.75, P<0.05) indicating that collections from patch reefs were a good estimate of larger-scale (15 km^2) recruitment patterns.

Growth

Measurement of increment width provided a daily record of growth of *A. chirurgus*, as an increment is formed each day and there was a strong linear relationship between sagittal radius and standard length of settlers (regression analysis, r^2=0.85, P<0.001, n=623) suggesting proportionality between growth of the otolith and somatic growth of the fish. As Fig. 2 shows, otolith-increment growth was initially slow, rapidly accelerated to a peak ~22 days after hatching, then declined slowly until settlement, which occurred 52 days±0.2 SE) after hatching for the average fish.

Growth versus settlement and recruitment

Comparisons of growth during each 4-day portion of the larval phase shows that between 6 and 25 days after hatching there were strong positive correlations between average growth and monthly settlement (Fig. 3). This corresponds to the time when increment growth rates are rapidly increasing and reaching their peak. Before and after this period there were very weak and/or non-significant correlations between these variables. A similar pattern was evident in correlations between otolith growth and recruitment (Fig. 3). Correlations were strongest from 10 to 13 days after hatching, when there was a moderately strong linear relationship between monthly growth and settlement (Fig. 4). Growth from 6 to 25 days after hatching was significantly correlated with both the raw data set of recruitment and the data set after seasonal trends were removed. Settlement and recruitment of *A. chirurgus* was not significantly correlated with growth averaged over the whole planktonic phase (regression analysis, r=0.32, P>0.05, n=38). In contrast, larval duration was significantly correlated with settlement and recruitment, (regression analysis, r=-0.33, P<0.05, n=38) although this relationship was largely driven by a single data point and became non-significant when it was removed from the analysis. There was no significant correlation between larval duration and settlement when the analysis controlled for size (partial correlation analysis r=-0.19, P>0.05), or between size and settlement when the analysis controlled for age (partial correlation analysis, r=-0.23, P>0.05, n=38).

Discussion

The precise number of days required for yolk sac absorption in *Acanthurus chirurgus* is not known. However, yolk reserves of a tropical congeneric species are exhausted 5-6 days after hatching (Randall 1961). Thus, the onset of the positive correlation between growth rate and recruitment of *A. chirurgus* occurs a few days after larvae are likely to begin feeding. Our results suggest that growth rates during the subsequent 2 weeks may be a major determinant of the success of both settlement and early recruitment of this species, a result that is consistent with the predictions of the growth-predation hypothesis.

There were no significant correlations between settlement (or recruitment) of *A. chirurgus* and either growth averaged over the entire larval phase, or the duration of that phase, or the size at settlement. Thus, enhanced early growth did not increase settlement success either by reducing the total amount of time fish spent as larvae or by increasing their final size. Rather, early growth per se simply had much more important effects on mortality than later growth, effects that were preserved till settlement and extended into recruitment. This situation contrasts with that in temperate species such as cod, where recruitment is correlated with both growth averaged over the entire larval phase and larval duration, but not with growth of larvae up to 40 days after hatching (Campana 1996). Our ability to detect correlations involving early growth was likely to be enhanced by rapid otolith growth in *A. chirurgus*: newly hatched fish have increments ~3 µm wide, and increment width increased to 16 µm at ~20 days. In temperate fishes, increment widths remain at or smaller than the minimum found in *A. chirurgus* for many weeks after hatching (Campana 1996; Suthers et al. 1999). When growth is rapid and increments are wide, variation in rates among individuals can be great and measurement errors are relatively small, allowing statistical tests to readily detect differences among cohorts at young ages (Meekan 1997; Meekan et al. 1998).

The idea that periods exist during the larval phase of marine fishes that are critical to survival has a long history in fisheries science. Nearly 100 years ago, Hjort (1914) proposed that year class size in temperate fishes was determined by the feeding success of larvae that have just exhausted their yolk supplies. Despite support from theoretical and laboratory studies of larval biology (e.g. Bailey and Houde 1989), there has been little unambiguous field evidence consistent with Hjort's theory, which is now termed the "critical-period" hypothesis (Leggett and DeBlois 1994). Some of the best evidence is derived from multi-year surveys of walleye pollock larvae, which show that young fish can be very vulnerable to starvation in the first 2 weeks after they begin feeding (Theilacker et al. 1996). Reasons why field studies have not provided clear results include the difficulties of accurately measuring the availability of food for larvae and disentangling the effects of dispersal and mortality within the plankton (Heath 1992; Helbig and Pepin 1998a, b). In our study, we avoided these problems by measuring patterns of larval growth, a variable that integrates the effects of differences in prey abundance, quality and the physical environment. Counts or collections of newly-settled fish, which can provide good estimates of recruitment to adult populations (Doherty and Williams 1988; Doherty and Fowler 1994), were used to as an alternative to standard techniques for the measurement of larval mortality. This approach allowed us to identify periods during the early life history of *A. chirurgus* that appeared to be critical to the survival of larvae.

Recent studies have documented variation in the growth rate, planktonic duration, condition and developmental state of tropical fish larvae (Wellington and Victor 1992; McCormick 1994; Kerrigan 1997; Sponagule and Cowen 1997; Searcy and Sponagule 2000; Wellington and Robertson 2001). Both maternal (Kerrigan 1997; McCormick 1999) and environmental factors can influence these characteristics (McCormick and Molony 1992, 1995). However, the influence of this variability on settlement or recruitment has rarely been examined and, consequently, these studies do not explicitly test predictions of the growth-predation hypothesis. Our results are consistent with the suggestion that larval growth and condition may be an important determinant of survivorship in the plankton (Suthers 1998), as has recently been shown to be the case in post-settlement reef fishes (Booth and Hixon 1999; Searcy and Sponagule 2002; Vigliola and Meekan 2002; but see McCormick and Kerrigan 1996). Our findings contrast with much of the current research on recruitment variability in tropical fishes, which has typically emphasised the role of larval transport (Shenker et al. 1993; Milicich 1994; Kingsford and Finn 1997; Robertson et al. 1999). Such studies have had little success in predicting recruitment intensity. Our results suggest that investigation of the factors that determine patterns of survivorship during larval life may provide a better basis for prediction of recruitment and thus management of resources.

Acknowledgements. We acknowledge financial support from the Smithsonian Tropical Research Institute, Panamá, and James Cook University, Townsville, Australia. Numerous assistants aided field work. Thanks to David Wilson for running the validation experiments at the San Blas Research Station. David Cushing, Louis Fortier, Iain Suthers and an anonymous reviewer provided useful comments on early drafts of the manuscript. This is AIMS publication no. 1104.

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Mikaela A. J. Bergenius[1], ✉, Mark G. Meekan[2], D. Ross Robertson[3] and Mark I. McCormick[1]

(1) James Cook University, School of Marine Biology and Aquaculture, Townsville, QLD 4811, Australia
(2) Australian Institute of Marine Science, Tropical Fisheries, Building 42, Northern Territory University, Casuarina Campus, Darwin, NT 0909, Australia
(3) Smithsonian Tropical Research Institute, Panamá, c/o Unit 0948, APO AA 34002-0948, USA

✉ E-mail: mikaela.bergenius@jcu.edu.au
Phone: +61-7-47814508
Fax: +61-7-47814099

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Introduction

Variability in the recruitment of the pelagic young of marine fishes, which often is extreme, has major biological effects and substantial implications for management of fish stocks (Rothschild 1986). Identification of the processes that determine these fluctuations in recruitment has been a long-standing and central goal of fisheries research. Recent theories highlight relationships between larval growth and predation to the variability in survival of cohorts. Collectively termed the growth-predation hypothesis, they propose that mortality is size selective, with small fish having lower survivorship than large fish of the same age (Anderson 1988). This occurs because fast-growing fish become juveniles first and are thus exposed to pelagic predators for less time than slow-growing individuals (the stage duration hypothesis; Leggett and DeBlois 1994). Additionally, fast-growing fish are also larger than slow-growing fish of the same age and thus less vulnerable to predators (the bigger-is-better hypothesis; Miller et al 1988; Bailey and Houde1989). Under these conditions, small changes in growth rates produce large variations in survivorship and thus recruitment (Houde 1987; Cushing and Horwood 1994).

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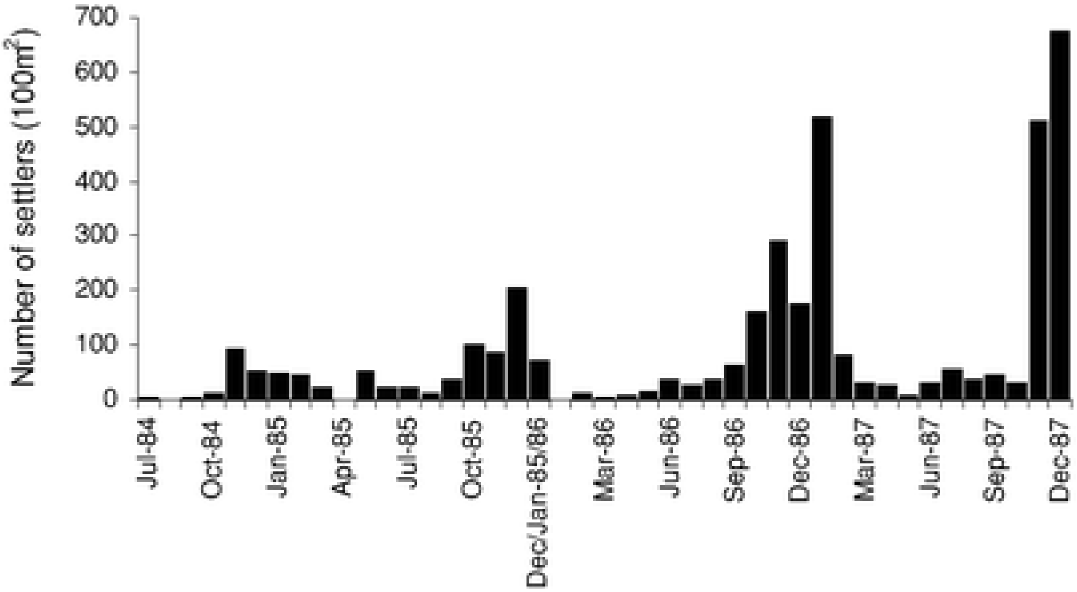

Fig. 1. Settlement patterns of *Acanthurus chirurgus* in the San Blas Archipelago, Caribbean Panamá

Growth

Measurement of increment width provided a daily record of growth of *A. chirurgus*, as an increment is formed each day and there was a strong linear relationship between sagittal radius and standard length of settlers (regression analysis, $r^2=0.85$, $P<0.001$, $n=623$) suggesting proportionality between growth of the otolith and somatic growth of the fish. As Fig. 2 shows, otolith-increment growth was initially slow, rapidly accelerated to a peak ~22 days after hatching, then declined slowly until settlement, which occurred 52 days±0.2 SE) after hatching for the average fish.

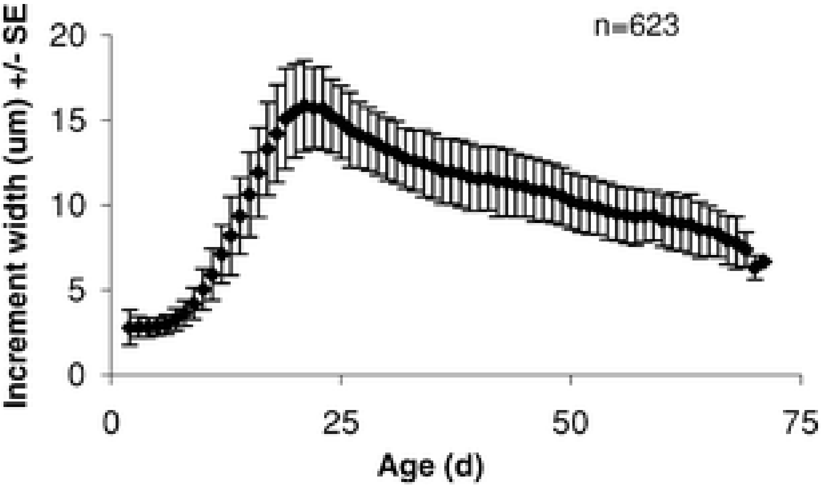

Fig. 2. Age versus average increment width during the planktonic larval phase of *A. chirurgus*. $n=623$

Growth versus settlement and recruitment

Comparisons of growth during each 4-day portion of the larval phase shows that between 6 and 25 days after hatching there were strong positive correlations between average growth and monthly settlement

(Fig. 3). This corresponds to the time when increment growth rates are rapidly increasing and reaching their peak. Before and after this period there were very weak and/or non-significant correlations between these variables. A similar pattern was evident in correlations between otolith growth and recruitment (Fig. 3). Correlations were strongest from 10 to 13 days after hatching, when there was a moderately strong linear relationship between monthly growth and settlement (Fig. 4). Growth from 6 to 25 days after hatching was significantly correlated with both the raw data set of recruitment and the data set after seasonal trends were removed. Settlement and recruitment of *A. chirurgus* was not significantly correlated with growth averaged over the whole planktonic phase (regression analysis, r=0.32, P>0.05, n=38). In contrast, larval duration was significantly correlated with settlement and recruitment, (regression analysis, r=-0.33, P<0.05, n=38) although this relationship was largely driven by a single data point and became non-significant when it was removed from the analysis. There was no significant correlation between larval duration and settlement when the analysis controlled for size (partial correlation analysis r=-0.19, P>0.05), or between size and settlement when the analysis controlled for age (partial correlation analysis, r=-0.23, P>0.05, n=38).

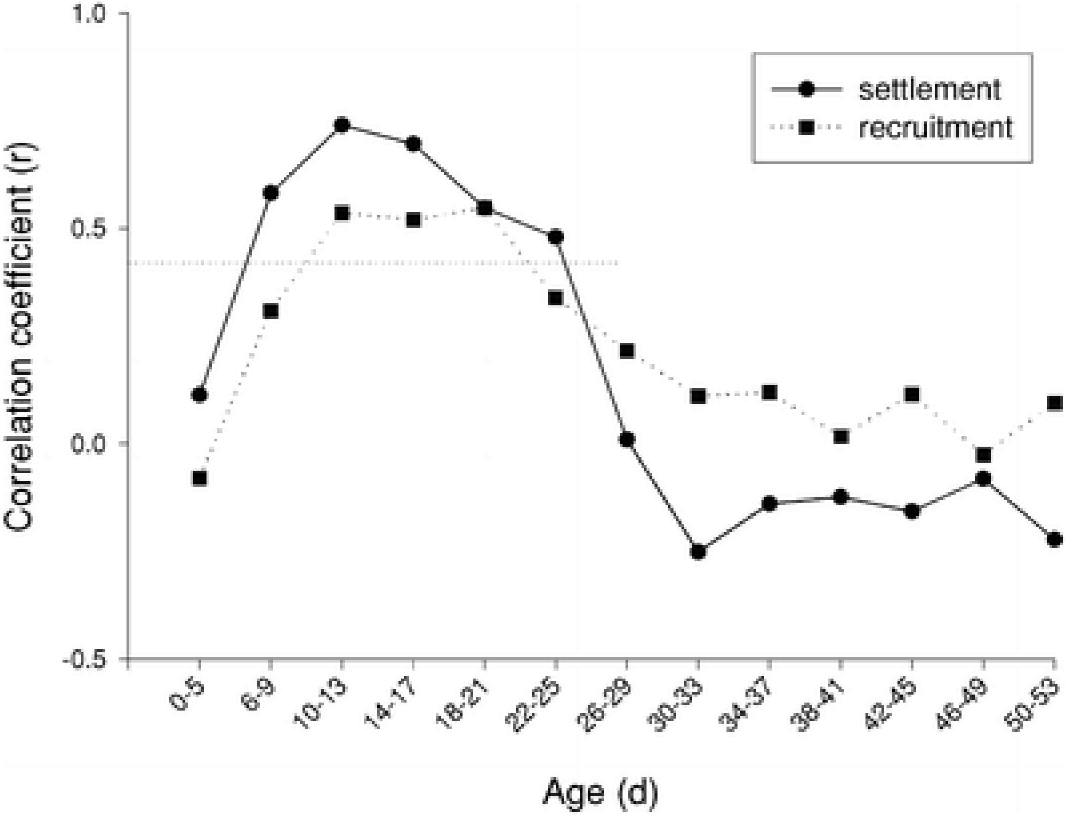

Fig. 3. Coefficients (r) from correlation analyses between average growth rate during pelagic life and monthly settlement and recruitment of *A. chirurgus*. Correlation coefficients above *horizontal dashed line* significant at P<0.05. n=19 for all analyses

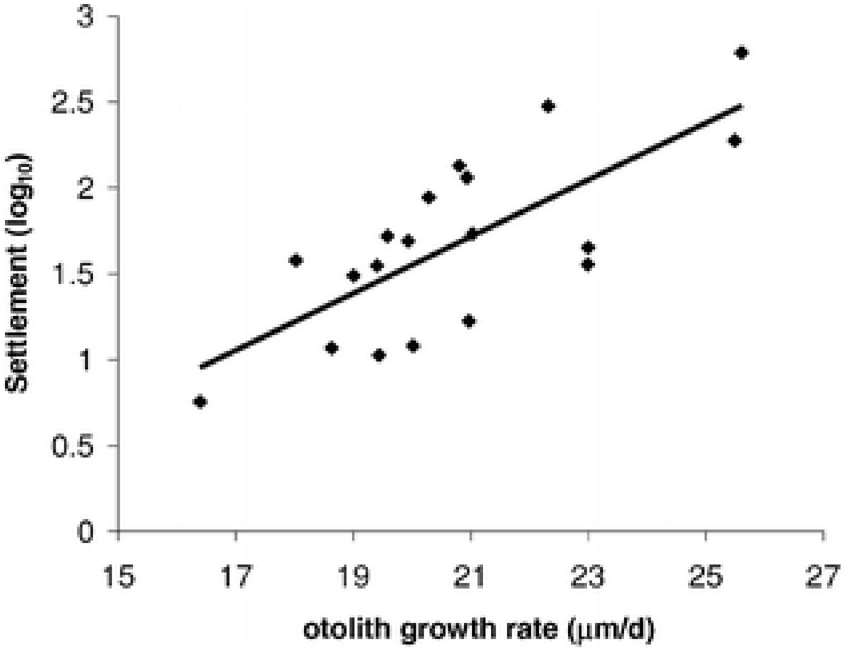

Fig. 4. Average increment width from 10 to 13 days after hatching versus monthly settlement (log transformed) of *A. chirurgus* to patch reefs. *Regression line* shown on plot (y=4.0301x-1.8989, r^2=0.49, n=19)

Discussion

The precise number of days required for yolk sac absorption in *Acanthurus chirurgus* is not known. However, yolk reserves of a tropical congeneric species are exhausted 5-6 days after hatching (Randall 1961). Thus, the onset of the positive correlation between growth rate and recruitment of *A. chirurgus* occurs a few days after larvae are likely to begin feeding. Our results suggest that growth rates during the subsequent 2 weeks may be a major determinant of the success of both settlement and early recruitment of this species, a result that is consistent with the predictions of the growth-predation hypothesis.

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