Delayed Metamorphosis with Reduced Larval Growth in a Coral Reef Fish (*Thalassoma bifasciatum*)

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Analyses of daily otolith increment sequences in the bluehead wrasse, *Thalassoma bifasciatum*, from the San Blas Islands of Panama indicated that (1) the duration of the planktonic larval period of this species ranges from 38 to 78 d, (2) those larvae with extended larval durations reach settlement size at the same age as average individuals but then remain planktonic for several more weeks, and (3) the estimated larval growth rate during this period of delayed metamorphosis (0.08 mm·d^{-1}) is distinctly lower than both the estimated growth rate before attaining settlement size (0.26 mm·d^{-1}) as well as the growth rate of juveniles after settlement (0.31 mm·d^{-1}). The ability to delay metamorphosis, the first documented for a vertebrate, may be an adaptation for maximizing the return of planktonic larvae to coastal waters.

L'analyse de séries de croissance quotidiennes des otolithes chez le labre *Thalassoma bifasciatum* des îles San Blas de Panama a montré que : (1) la durée de la période larvaire planctonique variait de 38 à 78 jours chez cette espèce, (2) les larves à stade larvaire plus long atteignaient la taille de retour aux coraux au même âge que les individus à période larvaire moyenne, mais qu'ils continuaient d'être planctoniques pendant plusieurs autres semaines et (3) le taux estimé de croissance larvaire au cours de cette période de retard de la métamorphose ($0,08$ mm·jour^{-1}) était distinctement inférieur au taux de croissance estimé avant le moment où la taille de retour était atteinte ($0,26$ mm·jour^{-1}) ainsi qu'au taux de croissance des juvéniles après le retour ($0,31$ mm·jour^{-1}). Cette capacité de retarder la métamorphose, la première à être décrite chez un vertébré, peut s'expliquer par une adaptation visant à maximiser le retour des larves planctoniques vers les eaux côtières.

Larval settlement and metamorphosis in a number of invertebrate phyla do not have to occur at a fixed age but can be delayed, especially in the absence of suitable settlement cues (see review in Jackson and Strathmann 1981). The period of delay can last for weeks in many cases, and for months in various gastropods (Scheltema 1971; Pechenik et al. 1984), enteropneusts (Hadfield 1978), asteroids (Domanski 1984), and corals (Richmond 1985). Some of these species are able to disperse over great distances, presumably as a result of this flexibility in their timing of settlement and metamorphosis (Scheltema 1971; Scheltema and Williams 1983; Pechenik et al. 1984; Richmond 1985). Some widely dispersing, or teleplanic, larvae apparently experience a marked reduction in their growth rate after becoming competent to settle, perhaps because a larger size in the plankton would reduce survival (Scheltema 1971; Pechenik et al. 1984).

Although the delay of larval settlement and metamorphosis is apparently widespread among invertebrates, it has not yet been documented in a vertebrate, despite the fact that virtually all tropical marine fishes and most temperate marine fishes have planktonic larvae (Breder and Rosen 1966; Sale 1980). This is most likely a result of the general lack of information on the early life history of marine fishes, and, furthermore, the difficulties in manipulating captive larvae of nonpelagic species (laboratory studies of marine fish larvae have typically been performed on pelagic species, see Lasker 1981).

As a result of the recent development of the daily otolith increment aging technique, it is now possible to examine aspects of the planktonic life and the timing of settlement of fish larvae under natural conditions. The presence of distinct daily incremental marks on the otoliths of bony fishes permits one to age individual fishes with remarkable precision as well as to estimate the increment of growth for each day of their life (Panella 1980; review in Campana and Neilson 1985). In addition, both daily increments and a conspicuous mark corresponding to settlement of the planktonic larva have been experimentally verified to be on the otoliths of some coral reef wrasses (Victor 1982, 1983). In this study, I use this new technique to ascertain first whether larvae of the Caribbean bluehead wrasse, *Thalassoma bifasciatum*, are capable of delaying settlement after becoming competent to settle (defined here as attaining settlement size), and second, whether these fish larvae also exhibit reduced growth rates during the period of delay.

Materials and Methods

I collected 1125 bluehead wrasses, mostly juveniles, from various patch reefs at the western end of the San Blas Archipelago on the Caribbean coast of Panama between 1981 and

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1983. In addition to this broad sample, I captured 47 newly settled bluehead wrasses from Ukubtupo Reef in the San Blas Islands. To ensure that these new recruits were caught on the first day of their appearance on the reef, I censused the bluehead wrasse population on a number of coral outcrops in a seagrass bed each day over an 18-mo period in 1981 and 1982. Recruits of this species avoid sand and seagrass and prefer to settle onto coral outcrops, where they tend to remain for at least several weeks (Victor 1986a). I collected new recruits only when they first appeared on an outcrop that was isolated from other outcrops and had not had a bluehead wrasse resident for weeks prior to the new recruit's arrival.

The fish were captured by hand with an aquarium dipnet and immediately preserved in 95% ethanol. They were later measured to the nearest 0.1 mm standard length (SL) and two of the three pairs of otoliths were extracted from each individual. The larger pair, the sagittae, were removed with fine forceps from their pockets at the base of the cranium, while the midsized pair, the lapilli, were removed from the lateral walls of the brain case. The otoliths were subsequently cleaned and dried and placed in a drop of immersion oil on a glass microscope slide.

I examined the otoliths under a compound microscope with transmitted light at magnifications of from 400 to 1000×. Daily increments are clearly visible on the otoliths of both larval and juvenile wrasses without any special preparation. The increments are more distinct if the otoliths have remained in immersion oil for at least several weeks and if a polarizing filter is placed between the light source and the slide. I calculated the planktonic larval duration for each of the fish by counting the number of daily increments between the center of the otolith and the settlement mark and adding 2 d, the estimated time between fertilization and the first formation of the otoliths (Victor 1982). The growth rate of recently settled juveniles was derived from the relationship between the age since settlement and fish length (individuals <50 d postsettlement, $n = 694$). I estimated the age since settlement by counting the number of daily increments between the settlement mark and the edge of the otolith (Victor 1982).

The width of each increment from within the larval period was recorded for 10 fish with the modal larval duration (47 d) and 15 fish with extended larval durations (>62 d), drawn from the entire sample of bluehead wrasses from Panama. I measured increment widths to the nearest 0.1 μm along the longest radius of one of the sagittae (center to posterior tip) with the aid of a computerized digitizing board overlay on a videoscreen image of the otolith at a microscope magnification of 1000×.

The daily growth rate of bluehead wrasse larvae was estimated by back-calculating larval lengths from observed otolith radii. The mean otolith radius for each day of the larval life was derived by summing the sequence of mean daily increment widths leading up to that day (means of the 25 individuals whose otolith increment widths were recorded). Assuming that bluehead wrasses have a linear relationship between fish length and sagitta radius, one can predict the length of a larva at any previous age from the corresponding otolith radius if the equation for this line were known. Bluehead wrasse larvae hatch at 1.1 mm SL, at about the time their otoliths first appear (pers. obs.). Furthermore, new recruits with a larval duration of 42 d had a mean SL of 11.0 mm (this study) and a mean sagitta radius of 135.6 μm up to the settlement mark at the edge of their otoliths. The relationship between fish standard length and sagitta radius is therefore
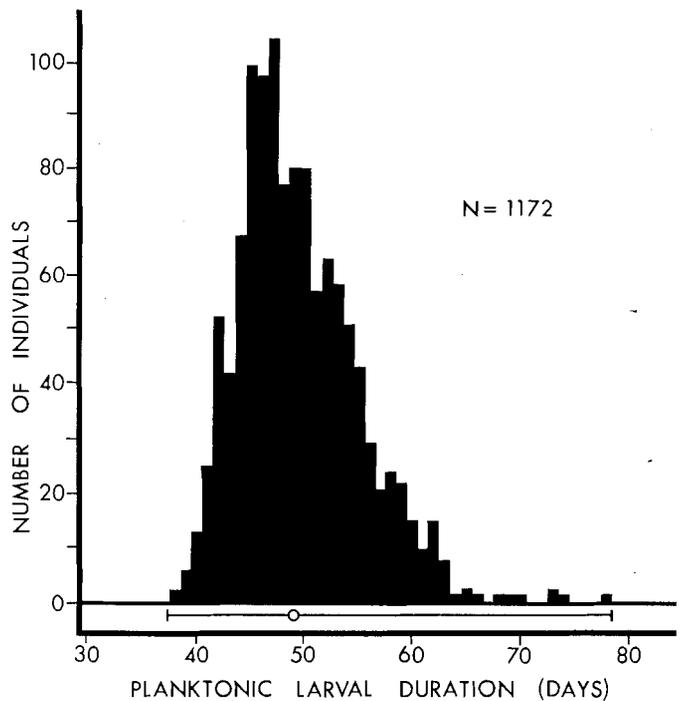

FIG. 1. Distribution of durations of the planktonic larval phase of bluehead wrasses from the San Blas Islands of Panama. Mean and range are represented below the horizontal axis. The sample includes 1125 juveniles and adults from San Blas patch reefs and 47 newly settled individuals from Ukubtupo Reef.

Standard length (mm) = 0.073 (sagitta radius (μm)) + 1.1.

This equation was used to estimate standard lengths for the mean sagitta radii corresponding to each day in the life of bluehead wrasse larvae.

Results

The larval durations of bluehead wrasses from the San Blas Islands ranged from 38 to 78 d, with a mean of 49.3 d and a mode at 47 d (SD = 5.5 d). The distribution was skewed, with a number of individuals having distinctly longer larval durations (Fig. 1). The widths of the daily increments steadily increased during the larval period until the beginning of the seventh week of larval life, at which point the daily increments narrowed abruptly (Fig. 2). This transition occurred in larvae with average larval durations as well as in those that had extended larval durations (Fig. 3). The mean width of the increments after the seventh week, 1.7 μm, was significantly narrower than the mean width for the first 6 wk, 3.4 μm (calculated from those individuals with larval lives longer than 62 d, paired t-tests, $n = 15$, $p < 0.0001$). Furthermore, the mean increment width for the first 47 d of larval life of those individuals with an extended larval duration was not significantly different from the mean width for that same period of fish with average larval durations (means of 3.3 and 3.4 μm, SD = 0.5 and 0.6 μm, $n = 15$ and 10, respectively; t-test $p > 0.63$).

Since the widths of the daily increments corresponding to the first 47 d for fish with extended larval durations were no different from those of fish with average larval durations, one can infer that within an age class (at least up to day 47), larvae that were destined to remain in the plankton longer were similar
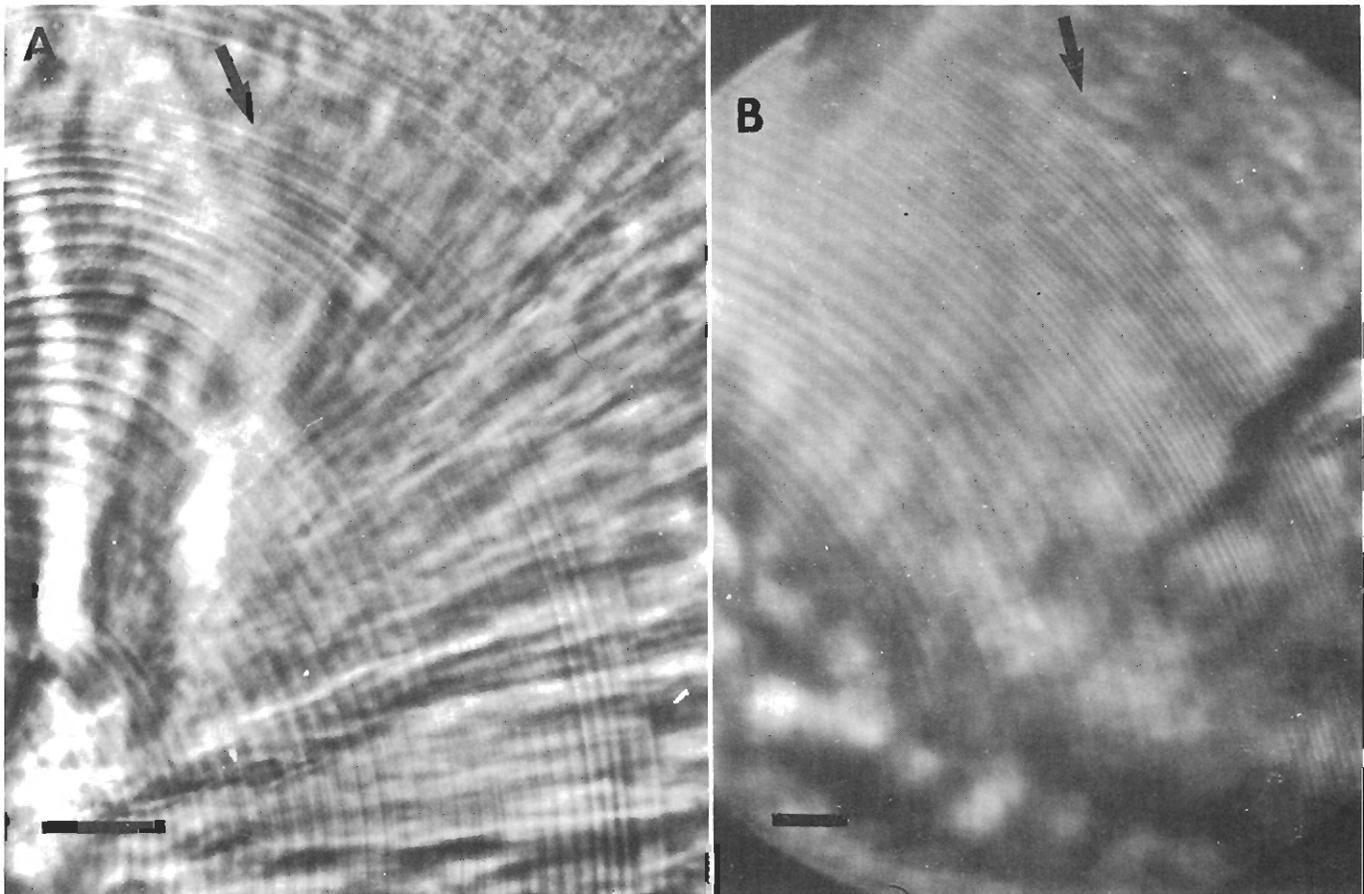
FIG. 2. (A) Sagitta of a 14.3 mm SL bluehead wrasse with the modal larval duration; (B) sagitta of a 16.1 mm SL bluehead wrasse with an extended larval duration of 63 d. Bars = 25 μm. The arrows indicate the settlement transition. The centers of the sagittae are out of the frame to the lower left.

in size to those that were settling. Given that both kinds of larvae attained a competent size at the same age, the observed change in size at settlement with increasing larval duration would therefore be one estimate of the rate of growth during the period of delay. The size of newly settled bluehead wrasses on Ukubtupo Reef ranged from 10.4 to 13.0 mm SL ($\bar{x} = 11.6$ mm, sD = 0.7 mm, $n = 47$). There was a significant increase in the size of new recruits with increased larval duration, indicating a growth rate of 0.08 mm·d^{-1} during the delay period ($y = 0.083x + 7.522$, $p < 0.0001$, $r^2 = 0.52$; Fig. 4B, solid line).

Back-calculations of fish length corresponding to previous otolith radii can provide a second, and independent, estimate of daily growth rates in the plankton. Indeed, this method is the only way of estimating daily larval growth rates before competency, since wild-caught larvae were not available for this study (a crude estimate of the overall precompetent larval growth rate can also be derived simply by dividing the change in size over the precompetent larval period, 11.0 − 1.1 mm, by the length of the period, 42 d, yielding 0.24 mm·d^{-1}). On the other hand, larval growth rates during the period of delay after competency can be estimated both by the back-calculation method as well as by the change in size of new recruits with increased larval duration described above (Fig. 4B). Back-calculations indicated that the growth rate of bluehead wrasse larvae after hatching started out at about 0.18 mm·d^{-1} and reached 0.26 mm·d^{-1} as they approached settlement size (Fig.

4A). Back-calculations also indicated that the growth rate of larvae during the delay period was 0.13 mm·d^{-1} (Fig. 4B, broken line). The growth rate of juvenile bluehead wrasses for the first 50 d after settlement (estimated by the change in size with age since settlement) was 0.31 mm·d^{-1}, distinctly higher than the estimated rates of larval growth (Fig. 4C). The larval duration did not affect subsequent growth rates on the reef; individuals with larval durations more than one standard deviation from the mean (55 d or longer and 43 d or shorter) grew at an identical rate to fish within one standard deviation from the mean (0.31 mm·d^{-1} for all three groups, total $n = 694$).

Discussion

The relative ease with which invertebrate larvae can be maintained and manipulated in captivity has resulted in a large body of research detailing the duration of larval development, the feeding and growth of larvae, and the cues for metamorphosis and settlement of a wide variety of marine invertebrates (e.g. Chia and Rice 1978). In comparison, information on the ecology of marine fish larvae is scarce. The recent development of the daily increment aging technique, however, should permit access to even more precise and valuable information than is obtainable by the methods currently employed by invertebrate zoologists. The otolith can contain a daily record of the growth and, in some cases, even subtle changes in the life history of individual fish in the field. It is the acquisition of information

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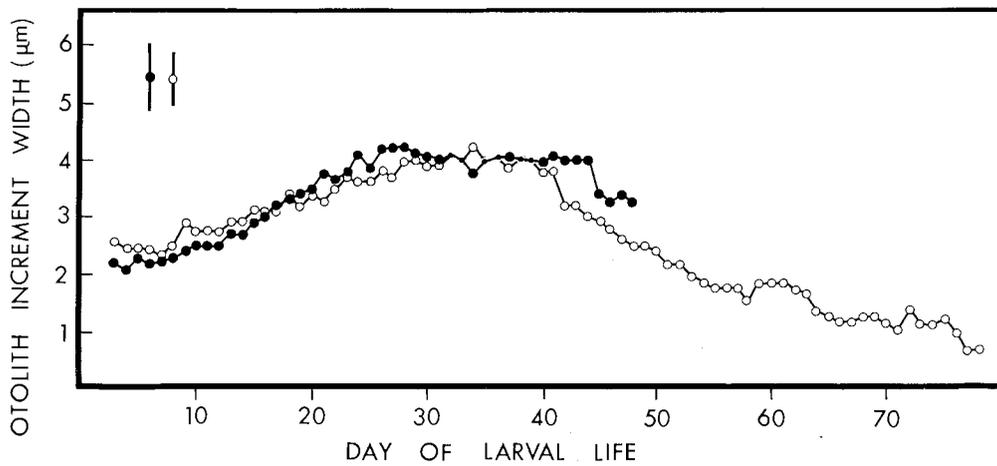*Can. J. Fish. Aquat. Sci., Vol. 43, 1986*

FIG. 3. Mean increment width along the longest radius of the sagitta for each day of the larval life of bluehead wrasses with modal larval durations (solid circles, $n = 10$) and with extended larval durations (open circles, $n = 15$). The average 95% confidence intervals of the means of both samples for the first 48 d are indicated at the upper left.
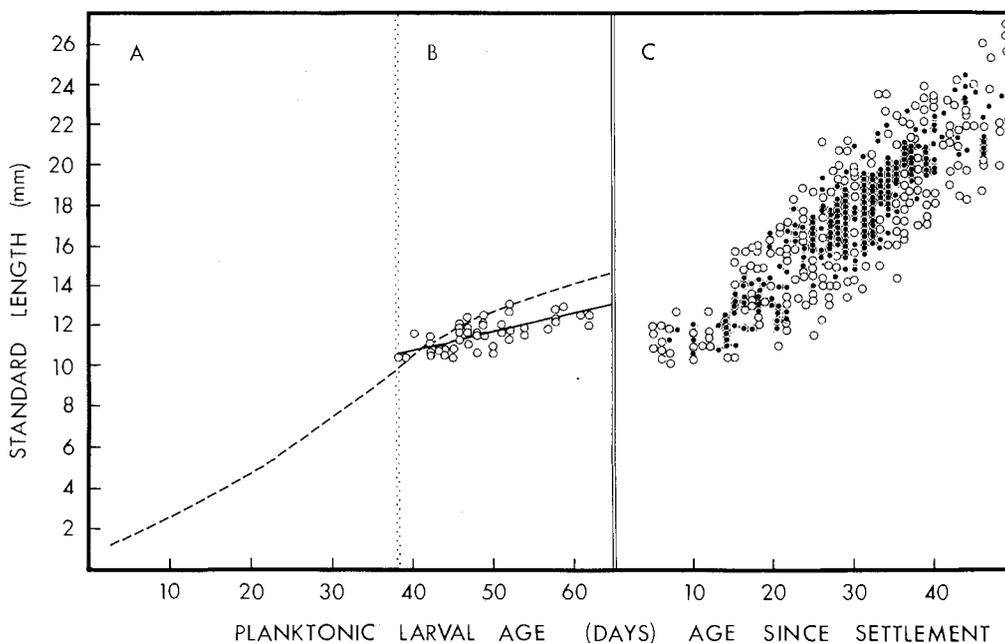

FIG. 4. Relationship between length and age for three phases in the life of bluehead wrasses. (A) Growth curve of larvae before a competent size is reached (back-calculated from the mean otolith radius for each age, $n = 25$ individuals, 10 with modal larval durations and 15 with extended durations combined); (B) growth curve of larvae after a competent size is reached was similarly back-calculated, as well as directly estimated from the change in size with increased larval duration of newly settled fish (solid line and open circles, $n = 47$); (C) growth rate after settlement was estimated by the relationship between the length of juveniles on the reef and their age since settlement (open circles, half-solid circles represent multiple points, $n = 694$).

directly from undisturbed natural populations that holds great promise for advancing our understanding of larval processes of both temperate and tropical fish species.

Planktonic Larval Duration

Many invertebrates are capable of extending their larval life after reaching a competent size in the absence of suitable settlement cues (see Jackson and Strathmann 1981). Whether fish larvae exhibit similar behavior has been an open question, since direct information on larval durations has been generally un-

available. Randall (1961) found in Hawaii that the larvae of convict surgeonfish, *Acanthurus triostegus*, which transformed after the main peak in settlement tended to be larger than those settling during the peak, and thus inferred that some larvae remain planktonic and continue to grow after reaching a size capable of settlement. Pearcy et al. (1977) observed occasional very large larvae of dover sole, *Microstomus pacificus*, well beyond normal settlement sizes in the plankton off of Oregon, and thus suggested that some larvae may be delaying settlement. Although the planktonic larval durations of a number of nonpelagic marine fishes have now been directly estimated

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with the use of daily otolith increments, the sources of variability within species have not been examined (Brothers and McFarland 1981; Laroche et al. 1982; Victor 1982, 1983, 1984, 1986b; Brothers et al. 1983).

The length of the planktonic larval phase in the bluehead wrasse is extremely variable, with some individuals experiencing larval durations twice as long as the observed minimum. Furthermore, back-calculations of larval lengths indicate that those individuals with an extended larval duration reach a competent size at the same age as individuals with normal larval durations. While it has yet to be demonstrated, it is certainly plausible that size confers competency in most marine fish larvae. These results are in accord with the prediction of Jackson and Strathmann (1981) that coastal organisms with planktonic larvae subject to offshore mixing should have a competent period (delay period) greater than or equal to the precompetent period. The basis for this prediction is that species with long larval durations are subject to offshore dispersal of their larvae and therefore require long competent periods to allow for their return to a suitable habitat. Leis (1983) has recorded *Thalassoma* larvae in waters up to 1200 km east of the nearest coral reefs in the central Pacific, and I have found *Thalassoma* larvae several hundred kilometres east of the Galapagos Islands (the nearest reefs), confirming that wrasse larvae do disperse into offshore waters.

The methodology employed in this study can certainly be used in studies of temperate fish larvae as well. Estimates of the duration of the planktonic larval period of northern fishes are probably minimum estimates, since the potential for delayed metamorphosis has not been explored for these fishes. It is highly likely that at least some temperate fish species will be found to exhibit similar larval behavior. If they do, there may be important implications for recruitment success and subsequent population dynamics. Delayed metamorphosis can extend the season of settlement far beyond the window suggested by a narrow spawning season. Furthermore, if larvae are capable of remaining planktonic for extended periods, then short-term fluctuations in larval food supplies or oceanographic conditions may have less of an effect on future stock size than might otherwise be expected.

Larval Growth

Field estimates of the growth rates of larval fishes are becoming increasingly common as the daily otolith increment aging technique becomes more popular. Population estimates of growth rates are typically derived from length at age curves of wild-caught larvae. Alternatively, growth curves can be back-calculated from otolith widths, since the otolith length to fish length relationship tends to be close for marine fish larvae (correlation coefficients typically greater than 0.90, e.g. Lough et al. (1982) and Radtke and Dean (1982)). Campana and Neilson (1985) reported that linear fish length — otolith radius relationships are usual for juvenile fishes but that many larval fishes have a curvilinear relationship. However, other than for some flatfishes of the family Pleuronectidae, which undergo great morphological changes during metamorphosis (Laroche et al. 1982; Campana 1984), and the northern anchovy, *Engraulis mordax* (Methot 1981), the relationship has been reported to be linear (Methot 1981; Lough et al. 1982; Radtke and Dean 1982). I have found that for four species of planktonic tropical eastern Pacific wrasse larvae the fish length — otolith radius relationship is linear and close (cor-

relation coefficients greater than 0.93, unpubl. data).

There is, at present, an absence of field data on growth rates of tropical fish larvae of nonpelagic species. My estimates of the growth rates of larval bluehead wrasses before competency $(0.18-0.26 \text{ mm} \cdot \text{d}^{-1})$ are well within the range that has been reported for other marine fish larvae. These estimates typically lie between 0.1 and 0.3 $\text{mm} \cdot \text{d}^{-1}$ (Boehlert 1981; Bailey 1982; Laroche et al. 1982; Lough et al. 1982), but can reach 0.55 $\text{mm} \cdot \text{d}^{-1}$ in some northern anchovy (Methot and Kramer 1979).

The back-calculated estimate of the larval growth rate of bluehead wrasses during the period of delay was higher than the estimate derived from the change in size of new recruits with increased larval duration (0.13 versus 0.08 $\text{mm} \cdot \text{d}^{-1}$). The back-calculated estimate was, however, based on the equation for larval fish before competency, which are relatively fast-growing. As a result, it is probably an overestimate, since delaying larvae are growing relatively slowly and slow-growing fish are known to have larger otoliths (and therefore wider otolith increments) for their size than normal fish (Marshall and Parker 1982). This is corroborated by the evidence that new recruits with extended larval durations are smaller than predicted by the equation (Fig. 4). This method of estimation cannot be further refined without direct information on the effect of reduced growth rates on the fish length — otolith radius relationship.

Teleplanic (widely dispersing) invertebrate larvae often have a reduced growth rate during the period of delay after attaining a competent size (Scheltema 1971; Pechenik et al. 1984). In some planktonic gastropod larvae the cause of this reduction is considered to be either shifts in metabolism (a probable adaptation to limit size and shell weight for a prolonged oceanic migration) or food limitation in the open ocean (Pechenik et al. 1984). Since fish larvae have air bladders to control buoyancy, it is unlikely that increased size and weight carry a similar cost. The reduction in growth found in bluehead wrasse larvae after reaching a competent size could be a result of a shortage of food for larvae above a certain size, although the abruptness of the transition and the relatively small size of planktonic wrasse larvae (Leis and Rennis 1983; Richards and Leis 1984) argue against this explanation. Alternatively, once a competent size is reached, a larva may shift its behavioral repertoire from one that maximizes food intake and minimizes predation to one maximizing the chance of return to coastal waters, perhaps by altering patterns of vertical migration or some active movement. If this change results in lower food intake or increased energy expenditure, the rate of growth will be reduced. Since even the most fundamental aspects of the ecology of planktonic fish larvae are unknown, these questions must remain unanswered.

The first transition in the widths of otolith increments is often ascribed to settlement of the planktonic larva and has thus been used as a settlement mark (Panella 1980; Brothers et al. 1983). My results demonstrate that this transition can correspond to the onset of competency (the attainment of settlement size) rather than settlement itself. This finding reinforces the need for verification in the field of assumed life history markers in otolith increment sequences. Furthermore, the ability of fish larvae to delay metamorphosis demands that biogeographers recognize that the potential for delayed metamorphosis may be more relevant than average larval duration in studies assaying the role of dispersal ability in the biogeography of fishes.

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Acknowledgments

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