

Regional differences in duration of the planktonic larval stage of reef fishes in the eastern Pacific Ocean

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Abstract. Regional variation in the duration of the planktonic larval phase of three species of reef fishes, *Thalassoma lucasanum* (Labridae), *Stegastes flavilatus*, and *Micropogonias dorsalis* (Pomacentridae) was investigated between 1982 and 1991 at several sites in the tropical eastern Pacific over a distance of 3500 km, encompassing virtually their entire range of distribution. Durations of the larval phase, determined from counts of daily otolith increments, were significantly different (1.3 to 1.6 x) between sites. Populations of all three species had a consistently shorter larval life at the most northern site, Cabo San Lucas (Mexico) compared to Panamá and the offshore islands of Galápagos and Cocos. Analyses of otolith increment width over the precompetent period revealed that this disparity in larval duration primarily reflected differences in larval growth rates: faster growing fish spent less time in the plankton. In *T. lucasanum*, some of the variation in larval duration between Panamá and offshore sites (Galápagos Islands and Cocos Island) may be accounted for by a higher frequency of individuals delaying metamorphosis at the offshore sites. These data indicate that conditions in the planktonic environment are not homogeneous throughout the tropical eastern Pacific and may have a profound effect on aspects of the larval ecology of reef fishes in this region.

Introduction

The larval life of nearly all reef fishes is spent in the plankton (Sale 1980, Doherty and Williams 1988). Since this habitat is still relatively unexplored, little is known about many of the basic aspects of the larval ecology of reef fishes. Direct assessment of the distribution and abundance of larvae has proven difficult, and problems of sampling have been further compounded by identifications limited to the familial or generic level (Leis and Rennis 1983). The most comprehensive information so far about the larval life of reef fishes has come from studies making use of aging by daily otolith increments

(Brothers et al. 1983, 1976, Victor 1986 a, b, c, 1987, Thresher and Brothers 1989, Thresher et al. 1989, Wellington and Victor 1989, Thorrold and Milicich 1990).

Studies of larval otoliths have proven useful in revealing several important aspects about larval and adult biology, such as the timing of settlement and geographic patch-size of recruitment events (Victor 1984, Wellington and Victor 1985), and the linkage between reproduction and recruitment (Robertson et al. 1988). Estimates of larval duration, combined with size at settlement, have been used to calculate overall growth rates of larvae during the planktonic phase (Victor 1986 b, 1987, Thresher and Brothers 1989, Thresher et al. 1989, Wellington and Victor 1989, Thorrold and Milicich 1990, Cowen 1991). Attempts have been made to relate larval duration with geographic range to explain patterns of species distribution (Brothers and Thresher 1985, Thresher et al. 1989, Wellington and Victor 1989). Yet, despite the potential wealth of information that can be derived from estimates of the length of time larvae spend in the plankton (i.e., the planktonic larval duration, hereafter referred to as PLD), very little is actually known about the ecological factors which influence the time larvae spend in the plankton. It is not known, for example, if environmental factors such as water temperature and food availability influence the PLD, or how much of the observed variation in PLD is genetically determined. This information would be fundamental to understanding the ecological significance of the variability in larval duration.

If planktonic larval duration varies temporally or spatially, inferences drawn from data collected from a locality at one time should not be generalized to other sites within the range of the species. Thus far, most estimates of planktonic larval duration for individual species are derived from collections from a single site (e.g. Brothers et al. 1983, Brothers and Thresher 1985, Thresher and Brothers 1985, Victor 1986 a, c, Robertson et al. 1988, Wellington and Victor 1989). There is usually an implicit assumption that the larval duration of a particular species varies little over time and space. Although studies

have not systematically addressed the variation of PLD over the broad range of a reef fish, some work has indicated that the larval duration in several species of wrasses (Victor 1986c) and damselfishes (Thresher et al. 1989, Thorrold and Milicich 1990) can differ significantly between sites.

In this study we examine regional geographic variation in planktonic larval duration in three species of reef fishes whose PLD spans periods from 3 wk to as long as 3 mo. To insure full sampling of the potential variation within a species, collections were made over a broad geographic range of 3 500 km that encompasses nearly the entire range of distribution of the three species. The survey covered a variety of both nearshore (continental and peninsular) and offshore (island) habitats that vary in temperature, productivity and current patterns (Hubbs and Roden 1964, Wyrski 1966, Forsbergh 1969, Zeitzschel 1969). We compared PLDs between regions, areas we define as broad subsets of the total geographic range of a species which, in this case, included an offshore island group along with coastline areas.

Materials and methods

Sites and species

We collected a series of juvenile reef fishes (from 9 to 30 mm standard length, SL) from several sites in the tropical eastern Pacific Ocean. The sites included the Galápagos Archipelago (Santiago, Marchena, Isabela and Fernandina islands), Ecuador; Cocos Island, Costa Rica; Contadora and Taboguilla islands, Panamá; and, Cabo San Lucas, Mexico (Fig. 1).

We examined the rainbow wrasse *Thalassoma lucasanum* (Labridae), and two damselfishes (Pomacentridae), the giant damselfish *Microspathodon dorsalis*, and the beaubrummel *Stegastes flavilatus*. *S. flavilatus* is confined to mainland shores from the Gulf of California to southern Ecuador, while *M. dorsalis* and *T. lucasanum* have distributions that extend to offshore islands (Thomson et al. 1979). *T. lucasanum* is reported to have a mean larval life of 74 d (Victor 1986c), while the larvae of *M. dorsalis* and *S. flavilatus* spend an average of about 30 to 35 d in the plankton (Wellington and Victor 1989). Specimens used in the present study were collected between 1982 and 1991; however, the majority were collected during the 1989–1990 settlement season. Details of locality, collection date and sample size are presented in Table 1.

Otolith analyses

Specimens were preserved in 95% ethanol. The standard length of preserved fish was measured to the nearest 0.1 mm. The otoliths (sagittae and lapilli) were extracted and mounted on microscope glass slides in immersion oil and, after a minimum period of 7 d, they were examined using transmitted light at 650× magnification, with a polarizing filter placed between the light source and the slide. For damselfishes, the lapilli were used for counting daily increments since increments of the lapilli were generally clearer than those on the sagittae. In the wrasse, however, increments on the sagittae were clearer. The daily nature of these increments has been demonstrated experimentally in juveniles for species in the genera *Thalassoma* (Victor 1982) and *Stegastes* (Robertson et al. 1988, Wellington and Victor unpublished data). We assume that these increments are also daily for species of *Microspathodon*. We make the assumption that the otolith increments formed during the larval stage are also daily; while no field studies have validated this assumption, evidence from

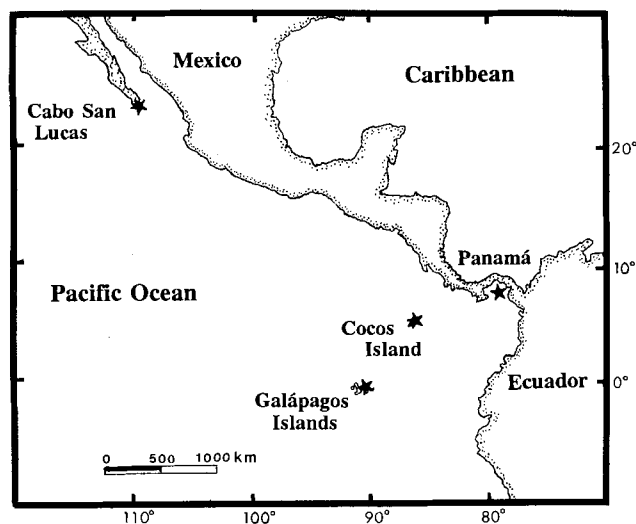


Fig. 1. Map of tropical eastern Pacific region showing location of study sites (stars). Coordinates for collecting sites: Galápagos Islands, 0°15'40"S, 91°26'20"N; 0°19'30"N, 90°24'00"W; 0°02'00"S, 91°33'40"W; 0°10'00"S, 90°49'52"W; Cocos Island, 5°33'20"N, 87°2'45"W; Panamá, 8°37'23"N, 79°02'31"W; 8°42'10"N, 79°30'00"W; Cabo San Lucas, 22°50'30"N, 110°00'00"W

Table 1. Localities, collection dates and sample sizes of study specimens. (*n*): numbers collected. Site coordinates are given in legend to Fig. 1

Locality	Date	(<i>n</i>)
<i>Thalassoma lucasanum</i>		
Galápagos	Dec. (1987)	(20)
	Apr. (1990)	(32)
Cocos	Nov. (1990)	(20)
Panamá	Nov. (1982)	(21)
	Apr. (1990)	(14)
Cabo San Lucas	Oct. (1989)	(20)
	Nov. (1991)	(20)
<i>Microspathodon dorsalis</i>		
Galápagos	Apr. (1990)	(10)
Cocos	Nov. (1990)	(6)
Cabo San Lucas	Oct. (1989)	(15)
<i>Stegastes flavilatus</i>		
Panamá	Dec. (1989)	(4)
	Apr. (1990)	(21)
Cabo San Lucas	Oct. (1989)	(32)

laboratory studies shows that increments are formed daily in larvae of temperate (Kingsford and Milicich 1987) and tropical (Thresher et al. 1989) reef fishes.

Repeated daily increment counts were made independently by two workers on otoliths, which were mixed blindly with respect to date and location. Several counts were made by each worker until consecutive counts were within ± 2 increments (generally 2 to 4 counts were required). Counts made on the same otolith by different observers varied by <10%. The final value represented the mean of four counts.

For *Thalassoma lucasanum*, presettlement increments were defined as those which occurred from the center of the otolith to the settlement mark, which was identified as a wide band with either wide and faint increments, or clear and lacking increments entirely (Victor 1982, and present Fig. 2). Since wrasses release fertilized eggs into the plankton and their otoliths do not form until 1 to 2 d

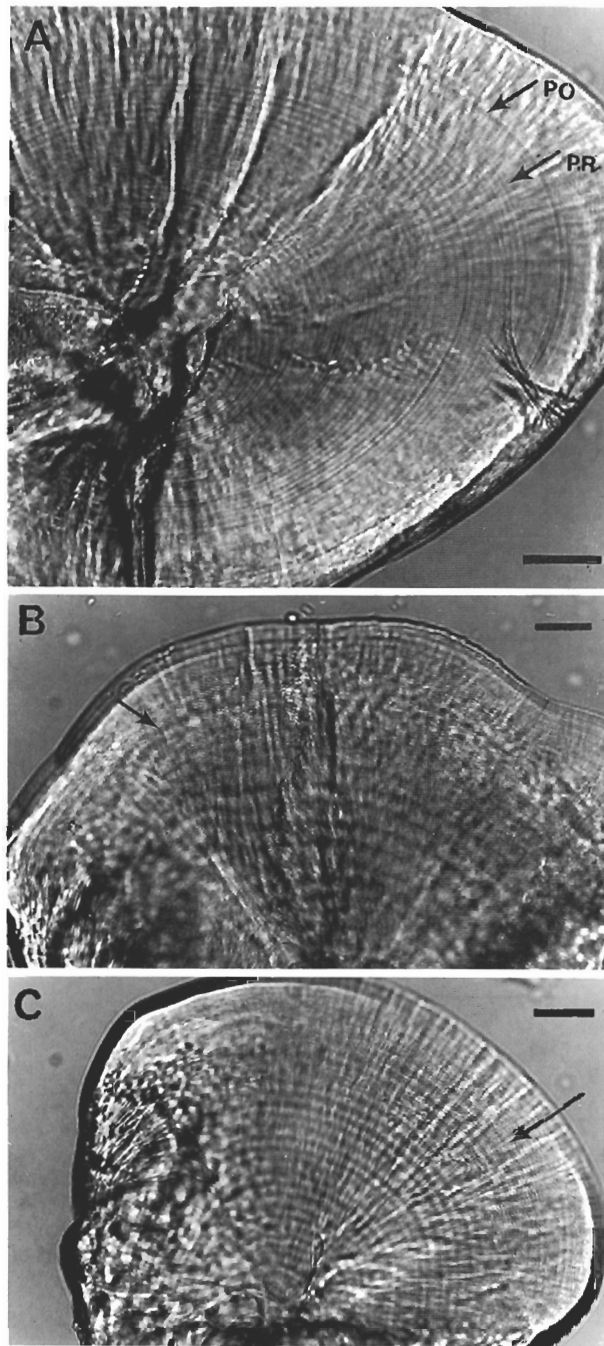


Fig. 2. *Thalassoma lucasanum* (A), *Microspathodon dorsalis* (B), and *Stegastes flavilatus* (C). Photomicrographs showing presettlement increments on otoliths. (A) Sagitta from 12.7 mm standard length (SL) *T. lucasanum* collected from Galápagos Island, Ecuador; arrows indicate end of presettlement period (PR) and beginning of postsettlement period (PO), with settlement mark in-between. (B) Lapillus from 15.9 mm SL *M. dorsalis* from Cabo San Lucas, Mexico; arrow indicates transition from wide (presettlement) to narrow (postsettlement) increments. (C) Lapillus from 11.3 mm SL *S. flavilatus* from Taboguilla Island, Panamá; arrow as in (B). All scale bars = 40 μ m

later, we added 2 d to the presettlement increment number in order to arrive at an estimate of the total time spent in the plankton (Victor 1982). For damselfishes, presettlement increments were identified as the wide increments that precede an abrupt transition to narrow increments. Justification for using this transition as a

Table 2. *Thalassoma lucasanum*, *Microspathodon dorsalis* and *Stegastes flavilatus*. Results of statistical analyses performed on \log_{10} -transformed data for planktonic larval duration and mean otolith increment width at various localities in tropical eastern Pacific. Descriptive statistics are shown in Figs. 3 and 4. Post-hoc comparison are based on Tukey's HSD test for *T. lucasanum* and *M. dorsalis* and Student's two tailed *t*-test for *S. flavilatus*. Locations with different letters indicate significant differences in mean values ($\alpha=0.05$). nd: no data

Locality	<i>T. lucasanum</i>	<i>M. dorsalis</i>	<i>S. flavilatus</i>
Planktonic larval duration			
Statistic	$F_{3,123}=50.48$	$F_{2,29}=52.05$	$t_{45}=10.72$
Significance	$p<0.001$	$p<0.001$	$p<0.001$
Cabo San Lucas	A	A	A
Panamá	B	nd	B
Cocos Island	C	B	nd
Galápagos Island	C	B	nd
Mean otolith increment width			
Statistic	$F_{3,123}=50.84$	$F_{2,29}=9.20$	$t_{45}=10.45$
Significance	$p<0.001$	$p<0.001$	$p<0.001$
Cabo San Lucas	A	A	A
Panamá	B	nd	B
Cocos Island	B	B	nd
Galápagos Island	B	B	nd

settlement mark is based on the fact that newly-settled individuals lack the narrow increments while those collected after settlement have narrow increments between the transition and the edge of the otolith (Wellington and Victor 1989, and present Fig. 2). The presence of a transition in the sequence of otolith increments corresponding to settlement has been found in other damselfishes also (Pitcher 1988, Thorrold and Milicich 1990). Since damselfishes incubate their eggs until they hatch and the otoliths form just prior to hatching, pretransition increment counts were used as a direct estimate of PLD without any adjustment (Wellington and Victor 1989).

We measured increment widths in two ways. Mean otolith increment widths were calculated simply by dividing the maximum radius of the otolith between the center and the settlement mark by the number of increments. In addition, we made individual measurements of increment widths on a subsample of *Thalassoma lucasanum* to determine if regional variation in the PLD was influenced by the ability of this species to delay metamorphosis, as has been documented in its Caribbean congener (Victor 1986b). These measurements were made along the maximum radius of the otolith from enlargements of photographs taken through a microscope. In delayed metamorphosis, some individuals reach settlement size and then continue to live in the plankton but grow at a much reduced rate. Regional differences in PLD could, of course, be accounted for by varying proportions of individuals delaying settlement, rather than by simple differences in larval growth rate.

Results

Major differences in larval duration were found between sites for all three species (Fig. 3; Table 2). For *Thalassoma lucasanum*, the mean PLD ranged from a low of 44.7 d at Cabo San Lucas to a high of 72.3 d at Cocos Island (70.0 d at Galápagos Islands). Populations in Panamá have an intermediate mean PLD of 63.0 d. Individuals PLDs ranged from a low of 37 d at Cabo San

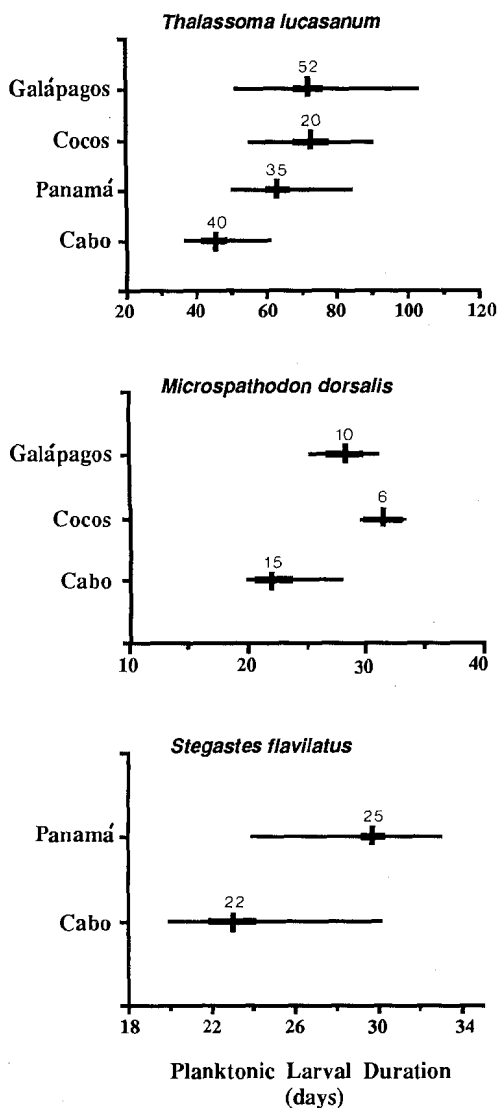


Fig. 3. *Thalassoma lucasanum*, *Microspathodon dorsalis*, and *Stegastes flavilatus*. Duration of planktonic larval period from various localities in tropical eastern Pacific. Vertical bars show means, horizontal bars 95% confidence interval of the mean, and horizontal lines range in values. Numbers above means are sample sizes. Note different scales on abscissas

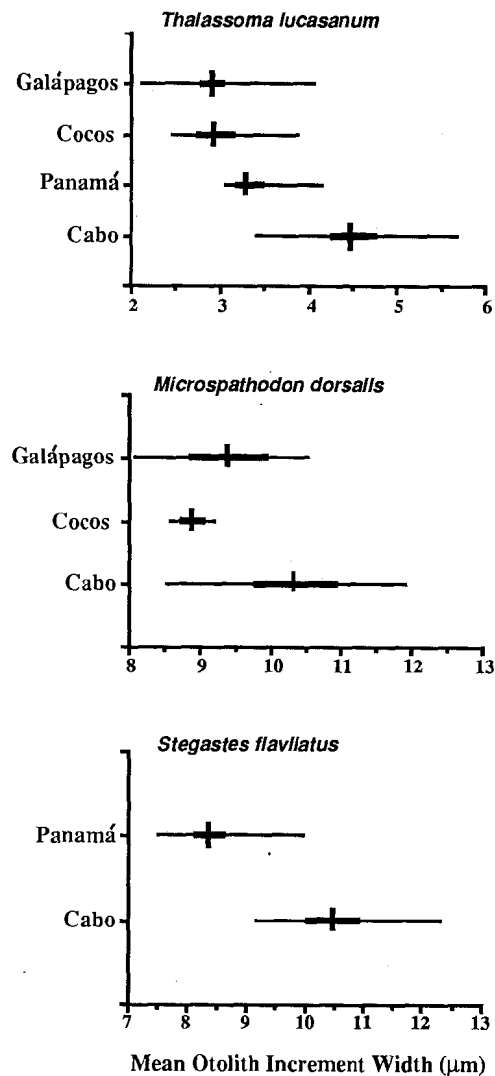


Fig. 4. *Thalassoma lucasanum*, *Microspathodon dorsalis* and *Stegastes flavilatus*. Mean otolith increment widths (µm). For *T. lucasanum*, measurements were derived from maximum radius of sagitta from center of otolith to beginning of settlement mark; for *M. dorsalis* and *S. flavilatus*, otolith increment widths were derived from maximum radius of lapillus from center of otolith to end of presettlement period

Lucas to a high of 102 d at Galápagos. While the range of values overlap extensively, the mean PLDs were significantly different between island and mainland populations, and between Panamá and Cabo San Lucas. Mean planktonic larval duration for the widely distributed damselfish *Microspathodon dorsalis* was 22.2 d at Cabo San Lucas in contrast to 28.2 d and 31.5 d at the offshore sites of Galápagos and Cocos, respectively. Individual PLDs for this species ranged from 33 d at Cocos to 20 d at Cabo San Lucas, a difference of nearly 2 wk. A similar range in PLD (20 to 33 d) was observed for *Stegastes flavilatus*, a species limited to the mainland. At the two sites sampled for *S. flavilatus*, the mean PLD in Panamá was 30.3 d, in contrast to 23 d in Cabo San Lucas. The largest magnitude of difference in mean PLD between sites was comparable for all three species: 1.6, 1.4 and 1.4

fold, for *T. lucasanum*, *M. dorsalis* and *S. flavilatus*, respectively (Fig. 3; Table 2).

If the size of larvae at settlement were similar between sites, the variation in larval duration would reflect differences in larval growth rates. The assumption that fish settled at about the same size at all sites is supported by the finding that the otolith size at settlement (a likely measure of size at settlement) varied little between sites. In fact, the maximum radius of the otolith at settlement ranged among sites from a mean of 200 to 212 µm (sagitta) for *Thalassoma lucasanum*, 256 to 279 µm (lapillus) for *Microspathodon dorsalis*, and 241 to 253 µm (lapillus) for *Stegastes flavilatus* – a difference of only 5 to 8%.

Fish settling at Cabo San Lucas grow up to one and a half times faster than conspecifics at other locations in

