

## NOTE

## Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae)

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**ABSTRACT:** To test the hypothesis that pelagic larval duration (PLD) plays a role in the longitudinal dispersal of reef fishes, we examined the relationship between PLD and occupancy of oceanic islands among tropical eastern Pacific (TEP) snappers (Lutjanidae). We estimated PLD from analysis of the otolith microstructure of juveniles collected at 2 localities from the Pacific coast of Colombia. Otoliths had a distinct 1-increment settlement transition, along which increment width gradually decreased in 1 species examined (*Lutjanus guttatus*). PLD estimated from lapilli was relatively short (21.8 to 24.4 d) and invariant (3.1 to 9.6% coefficients of variation [CV]) in *L. argentiventris*, *L. guttatus*, *L. novemfasciatus*, and *Hoplopagrus guntheri*, but was relatively long in *L. viridis* (37.9 d, CV = 8.6%). Mean PLD was not correlated with the largest distance between any 2 localities occupied but was positively correlated with number of oceanic islands occupied. Consideration of the geographic isolation of each island improved the strength of the latter relationship. However, these patterns were largely due to *L. viridis*, which was present in all oceanic islands, including Clipperton Atoll, the most isolated island in the TEP. This study suggests that the longitudinal component of species' ranges (measured by occupancy of reefs around oceanic islands) reflect dispersal abilities, yet overall range size is independent of PLD because other factors determine other components of geographic range.

**KEY WORDS:** Early life history · Geographic range size · Lutjanidae · Otolith microstructure · Pelagic larval duration · Reef fishes

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Most tropical reef fishes have a life cycle that includes planktonic larvae and benthic adults (Thresher 1984, Leis 1991). Larval transport by currents is the most likely mechanism of dispersal because adults are relatively sedentary and the distribution of reef habitats is patchy (Sale 1978). Consequently, the

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hypothesis that dispersal ability and extent of geographic distribution are functions of pelagic larval duration (PLD) has received considerable attention (Victor 1991). Although intuitively appealing, this idea has only weak empirical support. Among Indo-Pacific reef fishes, Brothers & Thresher (1985) reported a threshold of approximately 45 d in PLD, above which species tended to be widespread. Widely distributed Indo-Pacific species, such as Pacific Plate endemics (Springer 1982) and those that range into isolated areas like Hawaii and the eastern Pacific, have longer PLDs than more geographically restricted species (Brothers & Thresher 1985, Victor 1986a, Thresher et al. 1989). Pomacentrid genera with restricted distributions tend to have shorter PLDs (Wellington & Victor 1989, Cowen & Sponaugle 1997), but the opposite tends to be true for labrids (Victor 1986a, Cowen & Sponaugle 1997). At the species level, there is no evidence of a correlation between PLD and range size among Indo-Pacific pomacanthids (Thresher & Brothers 1985) and pomacentrids (Thresher et al. 1989, Wellington & Victor 1989), or among tropical eastern Pacific (TEP) labrids and pomacentrids (Victor & Wellington 2000). Furthermore, recent findings regarding the strong swimming abilities of reef fish larvae (Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997, Stobutzki 1998, Fisher et al. 2000) and local larval retention in some coral reef fish populations (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000) suggest that passive larval transport by currents plays a minor role in determining the geographic distribution of reef fishes.

The TEP is a region with suitable reef-fish habitat along the American continental coast and in a few oceanic island groups (Allen & Robertson 1994, Glynn & Ault 2000). Geographic ranges of some species in this region have strong latitudinal and longitudinal components. Latitudinal limits of distribution are likely a function of thermal tolerances because this region is characterized by sharp temperature gradients both to

the north and to the south (Briggs 1974, Brusca & Wallerstein 1979). However, PLD may play a key role in the longitudinal dispersal of species. If so, the presence of species around oceanic islands at different distances from source populations of reef fishes should be related to PLD. In this study, we used otolith microstructure of TEP snappers (Lutjanidae) to estimate PLD and then examined the relationship between PLD and extent of geographic range on oceanic islands.

**Materials and methods. Pelagic larval duration:** We estimated PLD by examination and analysis of the microstructure of juvenile fish otoliths, which has become a standard methodology for the study of fish early life history (Victor 1991, Stevenson & Campana 1992, Secor et al. 1995). Using a combination of techniques, we collected juvenile snappers from coral and rocky reef areas of Gorgona Island (2° 56' N, 78° 11' W) between May 1997 and November 1999, and at Ensenada de Utría (6° 04' N, 77° 25' W) in September 1998. At Gorgona, individuals were also captured on clusters of coral rubble, similar to those previously used by Sweatman (1983). These were placed on sandy substrates far from reef areas to attract new settlers. After collection, specimens were preserved in 95% ethyl alcohol and transported to the laboratory.

We dissected the fish, and extracted, prepared and polished the otoliths following the methods described by Secor et al. (1992) with modifications by Wilson & McCormick (1997, 1999) and Wilson (2000). Otolith microstructure was examined using a light microscope (150 to 1200× magnification) connected through a digital video camera to a computer. Image analysis software (Q-Win, Leica) facilitated the observation and measurement of otolith increments, although increment counts were made visually while the otolith image was displayed on the computer screen and the focus could be adjusted to facilitate counting. After initial comparisons we found that both sagittae and lapilli yielded similar results, although lapilli were easier and less time consuming to prepare and interpret than sagittae. We therefore used lapilli for the estimation of PLD in all species.

Otoliths from 114 of the 123 individuals collected were sufficiently clear for interpretation and analysis. PLD for individual fish was estimated from 3 replicate counts of the growth increments present from the nucleus either outward to the edge of the otolith or to the settlement mark associated with the transition from a planktonic to a benthic habit (Wilson & McCormick 1997, 1999). Each otolith reading was assigned a score representing the degree of perceived confidence in its interpretation following the weighting method described by Campana & Jones (1992). Only 1 otolith had replicate readings that varied by >10%, resulting in its exclusion from further analysis.

Increment deposition was assumed to begin at the time of hatching (Radtke & Dean 1982) because incubation times of lutjanids are relatively short (Thresher 1984, Leis 1987, Doi et al. 1994). Preliminary validation experiments with tetracycline marking indicated that increments of sagittae are deposited at an average rate of 1.0 increment  $d^{-1}$  in *Hoplopagrus guntheri* and 1.2 increments  $d^{-1}$  in *Lutjanus guttatus* (Bárcenas 1999). The daily formation of otolith increments has also been demonstrated for other lutjanids (Ralston & Miyamoto 1983, Radtke 1987). Although subdaily increments were evident, generally in the zone of the greatest increment width (Fig. 1), these were easily discriminated following the recommendations of Victor (1986a) and Campana (1992).

Widths of growth increments were measured along a profile in 6 specimens of *Lutjanus guttatus* and were plotted using the 'transition-centered' method (Wilson & McCormick 1997) to examine the pattern of change in increment width around the transition zone (see also Victor 1986b, Fowler 1989, Cowen 1991). Statistical comparisons of increment widths along the profile, and before and after the settlement mark were made using a 1-factor repeated measures ANOVA. To examine interspecific differences in PLD, we used a 1-way ANOVA to compare mean individual estimates of PLD among species and a Tukey multiple comparison test to determine which species differed from the others (Zar 1996).

**Geographic distribution:** Geographic distribution information obtained from different sources (primarily López & Bussing 1982, Eschmeyer et al. 1983, Rubio et al. 1987, 1992, Goodson 1988, Humann 1993, Allen & Robertson 1994, Allen 1995, Grove & Lavenberg 1997, Chirichigno & Vélez 1998, Thomson et al. 2000) was used to document species occupancy in previously defined continental biogeographic provinces (Brusca & Wallerstein 1979, Hastings 2000) and oceanic islands of the TEP. Three measures of range size were used: (1) the greatest distance between any 2 occupied localities; (2) the number of oceanic islands occupied; and (3) the sum of the distances between each island occupied and its nearest land mass. The latter 2 measures were used to examine patterns of island occupancy in relation to PLD and differ in the explicit consideration of geographic isolation.

**Results and discussion. Otolith internal microstructure and PLD:** The microstructure of the otoliths was similar in all 5 species. The first increments around the nucleus were very narrow and progressively increased in width with distance from the nucleus (Fig. 1). In otoliths of older juveniles there was an evident transition in the optical contrast and resolution of the increments and a slight decrease in their width. A conspicuously dark increment usually marked the begin-

ning of such a transition, and this was considered to be the settlement mark (Fig. 1). Although occasionally other increments were also conspicuously dark, these were never consistently so around the entire circumference of the otolith. PLD estimates for *Hoplopagrus guntheri* and *Lutjanus guttatus* did not differ significantly between individuals with or without the presumed settlement transition (Table 1). PLD in individuals of *L. argentiventris* without a transition was on average 2 d longer than in other individuals, but the difference was not statistically significant (Student's *t*-test,  $p > 0.05$ ). This suggests that the transition mark coincides with the time of settlement in these 3 species. In contrast, mean PLD in individuals of *L. viridis* without a transition was significantly greater (4 d) than in individuals with the presumed settlement mark (Table 1). Using unweighted instead of weighted means did not change this result (Student's *t*-test,  $p = 0.008$ ). However, individuals of *L. viridis* without a transition were collected between July and August 1998 in the coral rubble clusters used to attract new settlers, while juveniles with a transition were collected between August and November 1997 at Gorgona's 2 main coral reefs. Because the 2 cohorts were separated in time by about 1 yr, the observed difference in PLD may have resulted from exposure to different environmental conditions, such as the strong El Niño warming event of 1997–98.

Increment profiles of *Lutjanus guttatus* showed a consistent, though not abrupt, decrease in increment width of lapilli after the presumed settlement mark (Fig. 2). There was significant variation in increment width across the profile (repeated measures ANOVA,  $F_{15,75} = 4.36$ ,  $p < 0.0001$ , considering only increments -10 to +6 for which replication was complete,  $n = 6$ ) with increment widths after the settlement mark being significantly narrower than those before it (planned comparison  $F_{1,5} = 150.6$ ,  $p < 0.0001$ ). The same result was obtained after excluding all replicate values corresponding to increment -9, which exhibited the greatest mean width. Considering all data (increments -10 to +10), increment widths before the mark (mean  $\pm$  SE:  $13.6 \pm 0.38 \mu\text{m}$ ) were greater than after the mark ( $10.1 \pm 0.37 \mu\text{m}$ ).

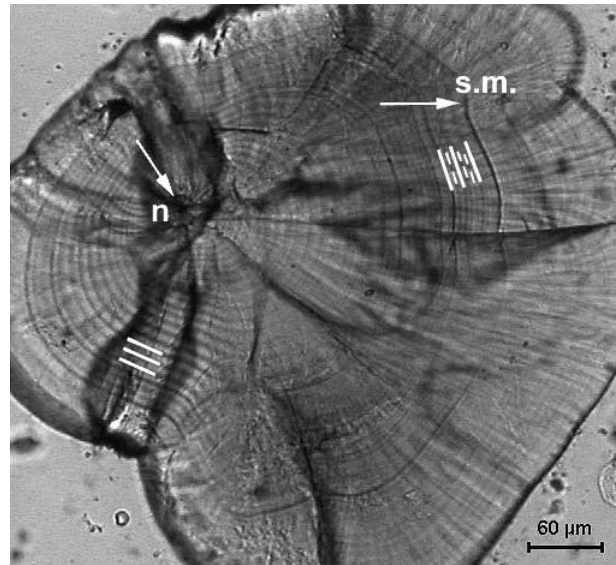


Fig. 1. *Lutjanus guttatus*. Microstructure of a lapillus after polishing procedure. Arrows indicate the position of the nucleus (n) and the settlement mark (s.m.). Solid lines indicate daily increments while finer, dashed lines indicate subdaily increments. Note the narrowing of increments after the settlement mark

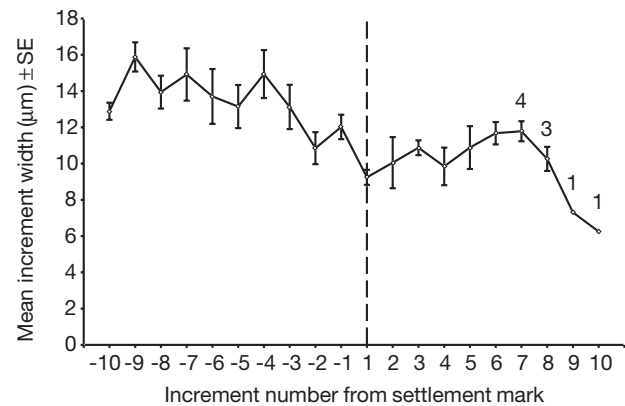


Fig. 2. *Lutjanus guttatus*. Increment width profile using the 'transition-centered' method (Wilson & McCormick 1997). Dashed line indicates the location of the settlement transition.  $n = 6$  at all points except where indicated

Table 1. Mean pelagic larval durations ( $\pm$ SE) of 4 Colombian Pacific lutjanids in individuals with and without a presumed settlement mark (SM) in their otoliths. Most individuals without a SM were collected on isolated clusters of coral rubble and appeared to be newly settled because they were smaller, translucent or lacked the coloration typical of older juveniles

Species	With SM		Without SM		<i>t</i> -test p-value
	Mean $\pm$ SE	n	Mean $\pm$ SE	n	
<i>Hoplopagrus guntheri</i>	21.9 $\pm$ 0.44	10	21.0 $\pm$ 0.33	9	0.326
<i>Lutjanus argentiventris</i>	21.3 $\pm$ 0.30	11	23.3 $\pm$ 0.46	4	0.053
<i>L. guttatus</i>	24.1 $\pm$ 0.57	26	24.7 $\pm$ 0.26	18	0.449
<i>L. viridis</i>	36.2 $\pm$ 0.42	11	40.4 $\pm$ 0.42	8	0.002

Table 2. Estimates of mean pelagic larval duration (PLD) ( $\pm$ SE) in 5 species of Lutjanidae from the Colombian Pacific Ocean based on the number of increments observed in lapilli. Means indicated by the same superscript letter did not differ significantly at  $\alpha = 0.05$  based on Tukey's test for unequal sample sizes involving samples from Gorgona Island only. CV%: coefficient of variation

Species	Location	PLD $\pm$ SE (d)	Range	CV%	n
<i>Hoplopagrus guntheri</i>	Gorgona Island	21.5 $\pm$ 0.40 <sup>a</sup>	18–24	8.56	19
<i>Lutjanus argentiventris</i>	Gorgona Island	21.9 $\pm$ 0.39 <sup>a</sup>	19–27	8.28	15
	Ensenada de Utría	23.7 $\pm$ 0.18	23–25	3.67	3
<i>L. guttatus</i>	Gorgona Island	24.4 $\pm$ 0.47 <sup>b</sup>	20–32	9.63	45
	Ensenada de Utría	24.1 $\pm$ 0.19	23–25	3.91	2
<i>L. novemfasciatus</i>	Gorgona Island	20.6 $\pm$ 0.26 <sup>a</sup>	20–23	6.00	5
	Ensenada de Utría	22.9 $\pm$ 0.15	22–24	3.14	6
<i>L. viridis</i>	Gorgona Island	37.9 $\pm$ 0.53 <sup>c</sup>	31–44	8.60	19

In the 5 lutjanids examined, the frequency distribution of PLDs did not differ from normal. *Lutjanus viridis* showed both the greatest mean and range in PLD followed by *L. guttatus* (Table 2). Mean PLD in these 2 species was significantly longer than in the other 3 species (ANOVA based on specimens from Gorgona Island,  $F = 136.10$ ,  $p < 0.001$ , Table 2), which in turn did not differ significantly in PLD. *L. guttatus* showed the highest intraspecific variability, although its variance in PLD only differed significantly from that of *L. novemfasciatus* from Ensenada de Utría ( $F = 10.78$ ,  $p < 0.02$ ). In general, coefficients of variation in PLD were relatively small, varying between 3.1 and 9.6% (Table 2).

TEP lutjanids had PLDs within the range of values reported for other lutjanids. Known PLDs are 25 d in newly settled, unidentified Indo-Pacific lutjanids (Brothers et al. 1983), 40 d in *Lutjanus sebae* (Brothers & Thresher 1985), 26.1 d in *L. fulviflamma* and 62 d in *L. gibbus* (Wilson & McCormick 1999). Richards & Saksena (1980) found a larval duration of 4 wk for the

western Atlantic *L. griseus* raised in captivity. However, our findings and most other estimates indicate that tropical lutjanids have relatively short PLDs; most values are within the lower third of the range reported for coral reef fishes (7 to 150 d; Cowen & Sponaugle 1997). Intraspecific variability in PLD of lutjanids appears to be low as well, but small sample sizes in most studies do not permit an adequate assessment of this trait. In TEP lutjanids, interspecific differences in PLD were greater among some congeners (e.g. *L. viridis* and *L. guttatus* vs other species of *Lutjanus*) than between at least 1 other genus (*Hoplopagrus*) and some species of *Lutjanus*, suggesting that PLD is not a phylogenetically conservative character within the family Lutjanidae.

**PLD and geographic range:** The 5 species studied here appear, at first, to have similar geographic distributions (Table 3) because they all inhabit rocky and coral reef habitats along the mainland coast throughout the TEP region. In fact, mean PLD was not corre-

Table 3. Pelagic larval duration (PLD) and geographic distribution of 5 lutjanids on continental biogeographic provinces and oceanic islands of the (primarily) tropical eastern Pacific Ocean. Continental biogeographic provinces are as follows: CAL, Californian (Point Conception, California to Punta Eugenio, Baja California Sur); COR, Cortezian (Bahia Magdalena and Gulf of California to Topolabampo, Sinaloa); MEX, Mexican (southwestern Mexico from Mazatlán, Sinaloa to Puerto Angel, Oaxaca); and PAN, Panamanian (Gulf of Fonseca, Honduras-Nicaragua border to Gulf of Guayaquil, Ecuador). Oceanic islands (and distance to nearest land) are as follows: MAL, Malpelo (362 km to Gorgona Island, Colombia); REV, Revillagigedo Islands (454 km to Cabo San Lucas); COC, Isla del Coco (501 km to Isla del Caño, Costa Rica); GAL, Galapagos Islands (750 km to Isla del Coco); and CLI, Clipperton Atoll (947 km to Revillagigedo Islands). Range size is the great circle distance between the 2 most distant localities. Minimum oceanic range is the sum of the distances between each island occupied and its nearest land

Species	Mean PLD (d)	Continental province				Oceanic Island					Range size (km)	Minimum oceanic range (km)
		CAL	COR	MEX	PAN	MAL	REV	COC	GAL	CLI		
<i>Hoplopagrus guntheri</i>	21.5		+	+	+				+		5158	750
<i>Lutjanus argentiventris</i>	22.2	+	+	+	+	+			+		5916	1613
<i>L. guttatus</i>	24.4		+	+	+	+			+		5385	863
<i>L. novemfasciatus</i>	21.8		+	+	+	+			+		5209	1112
<i>L. viridis</i>	37.9		+	+	+	+	+	+	+	+	4976	3014

lated with the greatest distance between any 2 occupied localities ( $r = -0.522$ ,  $p = 0.366$ ). However, mean PLD was significantly and positively correlated with the number of oceanic islands occupied ( $r = 0.889$ ,  $p = 0.043$ ; Table 3). The correlation was greater when the degree of geographic isolation of the islands was taken into account by considering the sum of the distances between each oceanic island occupied and its nearest land mass ( $r = 0.911$ ,  $p = 0.032$ ). Although suggestive, these results should be considered with caution due to the small number of species and oceanic islands considered. *Lutjanus guttatus* is not as widely distributed on oceanic islands as expected on the basis of its PLD, and the overall pattern is largely dependent upon the effect of only 1 species (*L. viridis*), which had a PLD 14 d longer than that of the other 4 lutjanids. This suggests that the greater PLD of *L. viridis* has allowed it to colonize oceanic islands within the TEP that the others have not.

The presence of *Lutjanus viridis* at Clipperton Atoll may be of particular significance because this is a small, remote island and has the most isolated coral reefs within the TEP region (~950 km from the Revillagigedo Islands; Robertson & Allen 1996). Also, it is located at the westernmost limit of the TEP and a large proportion (~55%) of its shorefish fauna is transpacific rather than TEP endemic, probably due to the strong influence of eastbound currents coming from Oceania (Robertson & Allen 1996). Based on differences in morphology and coloration, it is apparent that the nearest relatives of *L. viridis* are more likely to be species from the central and western Pacific than from the TEP or the Caribbean (G. R. Allen pers. comm.). Furthermore, most transpacific fishes have relatively long PLDs (Brothers & Thresher 1985, Victor 1986a). Thus, an alternative explanation consistent with the widespread geographic distribution and prolonged PLD exhibited by *L. viridis* is that an ancestor successfully crossed the East Pacific Barrier and first colonized the oceanic islands, from which it spread to the rest of the TEP. Both explanations (i.e. colonization from the mainland or a trans-Pacific ancestry) suggest that a relatively long PLD may have enabled *L. viridis* to colonize distant oceanic islands. Overall, this study suggests that the longitudinal component of species' ranges, reflected by occupancy of oceanic islands, correlates with dispersal abilities, yet overall range size is independent of PLD because other factors determine other components of a species' range.

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