

# Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean

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## Abstract

Planktonic larvae of six genera of labrid and pomacentrid reef fishes were captured in March 1985 in the eastern Pacific Ocean several hundred kilometers from the nearest reefs. The larvae were identified to genus by fin-ray counts as well as by comparison of their larval otolith morphology with that of known species. The larval otolith morphologies of known species were derived from measurements of the larval otolith embedded within the otoliths of settled juveniles (as delineated by the daily otolith-increment marks corresponding to the late larval period). The body morphology and melanophore patterns of the eastern Pacific labrid and pomacentrid larvae closely matched those of congeneric larvae described from other oceans. Growth rates of larvae less than about 70 d old were similar between taxa (from 0.13 to 0.19 mm d<sup>-1</sup>). After about 70 d in the plankton, labrid larvae grew much more slowly (0.06 mm d<sup>-1</sup> in *Xyrichtys* sp.). Labrid larvae had long larval durations (up to 131 d in *Xyrichtys* sp.), while the larval lives of the pomacentrids appeared to be shorter and much less variable. Larvae of many different ages occurred within the same water mass, and young cohorts of larvae appeared continuously over the sampling period. Some larvae were as young as 21 d, indicating that reef-fish larvae are capable of rapid long-distance dispersal (at least 18 km d<sup>-1</sup>).

## Introduction

It is becoming increasingly apparent that processes occurring in the plankton affect the survival of fish larvae and may thus ultimately determine the distribution and abundance of coral-reef fish populations (Williams, 1980; Doherty, 1983; Victor, 1983 a, 1986 a; Wellington and Victor, 1985). With very few exceptions, coral-reef fishes have a planktonically-dispersed larval stage which remains in the

plankton for a period of weeks or months (Sale, 1980). The great fecundity of these fishes (many release thousands of eggs each day) and the relatively low mortality rates of juveniles and adults (Doherty, 1982; Victor, 1983 a, 1986 a) indicate that the rates of mortality during the planktonic larval period are enormous. It would therefore not be surprising were reef-fish population dynamics to be controlled to a large degree by rates of recruitment (successful settlement of larvae). Despite the importance of this stage in the life history of these fishes, very little is known about even the most basic aspects of the planktonic life of reef-fish larvae (Sale, 1980).

A major obstacle to resolving some of the questions concerning the ecology of reef-fish larvae in tropical waters has been the difficulty of identifying these larvae (Leis and Rennis, 1983). The larvae of most reef species are, furthermore, relatively uncommon in plankton tows (Leis, 1982 a; Richards, 1984), and those that have been captured are usually preserved in formalin, making age determination from daily otolith increments impossible (formalin dissolves otoliths). As a result, our knowledge of the larval ecology of reef fishes is presently limited to the distributional patterns of some larval fishes (Leis and Miller, 1976; Leis, 1982 a, b; Leis and Goldman, 1984; Richards, 1984) and some estimates of the duration of the larval stage, usually derived from otolith-increment counts of settled juveniles (Brothers and McFarland, 1981; Victor, 1982, 1983 b, 1986 b, c; Brothers *et al.*, 1983). Although there has been some recent discussion on the general dispersal abilities of reef-fish larvae (Leis, 1983; Doherty *et al.*, 1984; Williams *et al.*, 1984; Brothers and Thresher, 1985; Thresher and Brothers, 1985), growth and life history strategies of larval reef fishes (Victor, 1986 c), and the mechanisms by which reef-fish larvae are returned to coastal waters (Johannes, 1978; Victor, 1984; Lobel and Robinson, 1986), little critical information on these subjects has been obtained directly from planktonic larvae in the field.

In March 1985, I collected a series of daily samples of tropical fish larvae at a single point in the eastern Pacific

Ocean, many hundreds of kilometers from the nearest reefs (and directly above the Galápagos Rift valley hydrothermal vents). Reef-fish larvae comprised a very small fraction of the samples but were, nevertheless, obtained in moderate numbers. In this study, I describe the larvae of two of the major reef-fish families in this area (the wrasses, Labridae, and the damselfishes, Pomacentridae), using otolith morphology and daily otolith increments to assist in identification. Since the ages of individual larvae can be derived from counts of daily otolith increments, I have also estimated (1) the larval growth rate and larval duration of some of these fishes, (2) the distance and speed of dispersal, and (3) the degree of mixing of cohorts of larvae in this region of the eastern Pacific Ocean.

### Materials and methods

A series of 14 daily plankton tows was performed between 2 and 19 March, 1985 in the tropical eastern Pacific Ocean at a single site on the equator about 400 km east of the nearest Galápagos Islands and 680 km west of the coast of Ecuador (00°48'N; 86°13'W). Oblique tows were conducted at night at variable speeds (typically about 3 km h<sup>-1</sup>) to depths of between 100 and 200 m with a 2 m × 3 m trawl net with 2 mm mesh. The cod-end was refrigerated overnight and the fish larvae were then sorted and preserved in 95% ethanol. The labrid and pomacentrid larvae ( $n=81$  and 8 respectively; no scarid larvae were captured) were separated and subsequently measured to the nearest 0.1 mm standard length.

Two of the three pairs of otoliths, the lapilli and the sagittae, were extracted from each larva under a dissecting microscope and cleaned and dried. After a period of weeks in immersion oil, the otoliths were examined with transmitted light under a compound microscope equipped with a polarizing filter at magnifications from 400× to 1 000×. The age of each larva was estimated by counting the number of daily incremental marks between the center and the edge of the otolith and adding two days to account for development before the formation of the otolith (Victor, 1986c). The sagittae of the labrid larvae and the lapilli of the pomacentrid larvae tended to have the clearest increments.

Three measurements were taken to characterize the otolith morphology of the larval types examined; the maximum radius of the lapillus, the maximum radius of the sagitta (the radius from the center, the starting point of the incremental rings, to the pointed end of this arrowhead-shaped otolith), and the radius directly opposite the maximum radius of the sagitta. The maximum radius of the sagitta was measured for both sagittae from each larva. These paired measurements differed on average by only 2.3% (replicate measurements of the same sagitta typically varied by less than 1%). The other measurements were then made on a randomly-chosen member of the pair of otoliths of each kind. All measurements were made to the nearest micrometer from a videoscreen image of the otolith at a magnification of 400×.

I also captured a series of settled juveniles of known eastern Pacific labrid species from reefs in the Perlas Islands in the Bay of Panamá between 1982 and 1984. The otoliths were processed as described above and comparable measurements were made on the portion of the otolith corresponding to the larval otolith. The outline of the larval otolith can be recognized because there is a prominent mark on the otoliths of labrid fishes that is produced at settlement. The mark consists of a transition from very distinct larval increments to a band of faint increments which are laid down during metamorphosis after settlement (Victor, 1982, 1983b). The last distinct increment before the band of faint increments thus represents the outline of the otolith of the planktonic larva just prior to settlement (analogous to inferring the shape of a tree trunk in some previous year from the outline of the annual ring corresponding to that year).

### Results

#### Larval identification

Five types of labrid larvae and one type of pomacentrid larvae were captured (Figs. 1, 2; Table 1). Larvae were assigned to types based on clear differences in body mor-

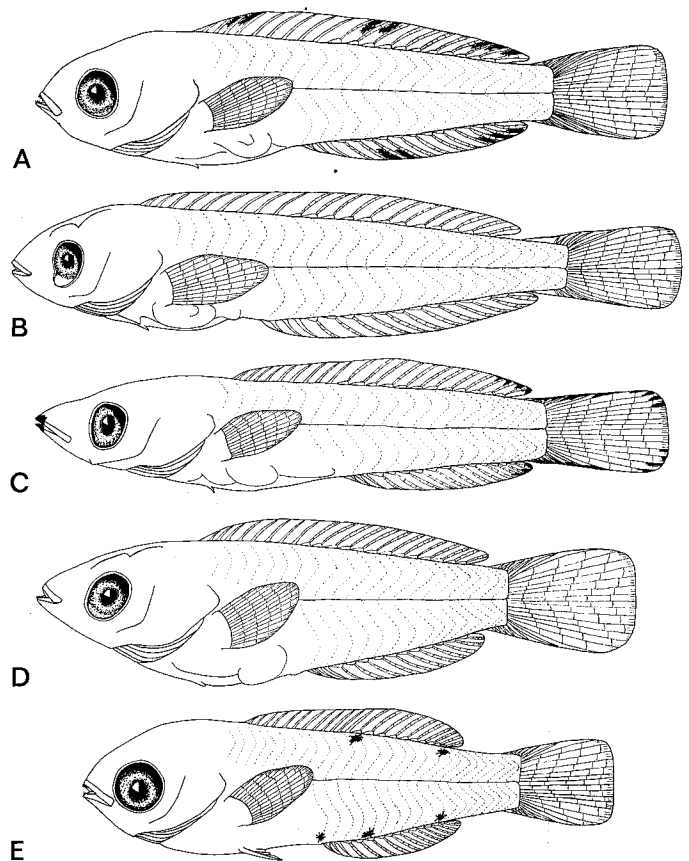
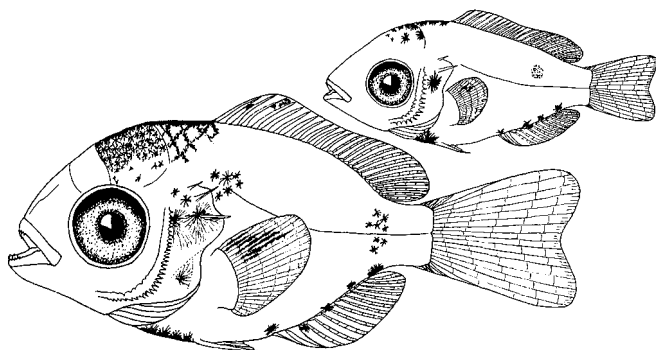


Fig. 1. Planktonic larvae of five genera of labrids from eastern Pacific Ocean. (A) *Halichoeres* sp., 11.8 mm standard length, SL; (B) *Xyrichtys* sp., 12.6 mm SL; (C) *Pseudojulis* sp., 11.7 mm SL; (D) *Thalassoma* sp., 10.6 mm SL; (E) *Bodianus* sp., 9.9 mm SL.

**Table 1.** Characteristics of the six types of planktonic labrid and pomacentrid larvae captured during March 1985 in the eastern Pacific Ocean, 0+ denotes extrapolated growth rates for ages younger than those collected, assuming hatching occurs at 1.1 mm SL. is: insufficient samples available

Putative genus	n	Dorsal rays	Anal rays	Size range (mm)	Age range (d)	Growth rate (mm d <sup>-1</sup> ) at:		
						0+	< 67 d	> 67 d
<i>Halichoeres</i>	4	IX, 11	III, 12	9.4–13.5	50– 81	0.17	is	is
<i>Xyrichtys</i>	36	IX, 12	III, 12	9.9–16.7	46–131	0.20	0.16	0.06
<i>Pseudojulis</i>	31	IX, 12	III, 12	7.7–14.1	27– 83	0.28	0.13	is
<i>Thalassoma</i>	9	VIII, 13	III, 11	7.7–11.7	47–101	0.15	0.16	is
<i>Bodianus</i>	1	XII, 10	III, 12	9.9	43	is	is	is
<i>Stegastes</i>	8	XII, 14	II, 12	4.8–7.6	23–35	0.19	0.19	



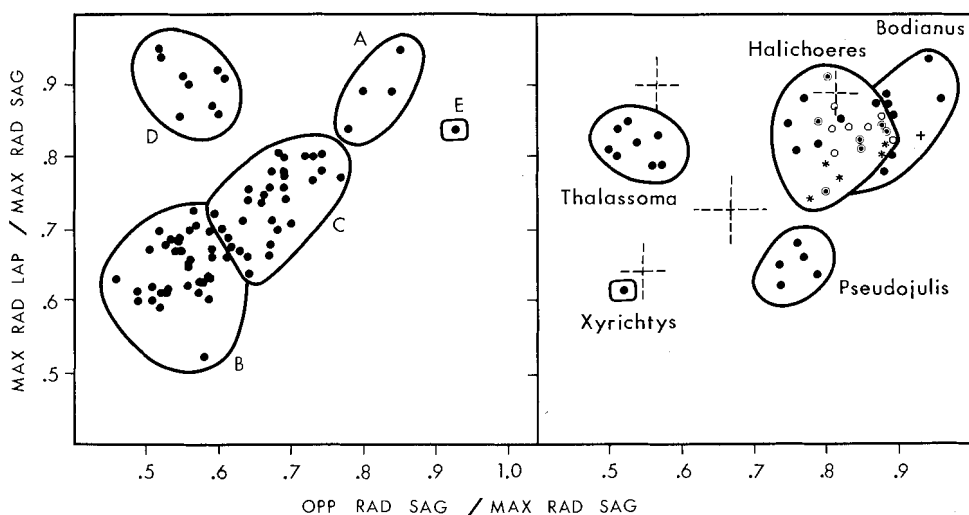
**Fig. 2.** *Stegastes* sp. Planktonic larvae from eastern Pacific Ocean: upper right, 5.0 mm SL; lower, 7.7 mm SL

phology and melanophore patterns. A fin-ray count of D-XII,14 A-II,12 was sufficient to identify the damselfish larvae to the genus *Stegastes*. Identification to species was not possible, since many species of this genus from this area are identifiable only by color pattern (Thomson *et al.*, 1979). Since only three of the five types of labrid larvae had unique fin-ray counts, morphological characters of the otoliths were also used for identification (Brothers, 1984). There were distinct differences in otolith morphology between all five labrid types, primarily in the relative size of the lapillus and the roundness of the sagitta. When the

ratio of the maximum radius of the lapillus to the maximum radius of the sagitta was plotted against the ratio of the opposite of maximum radius of the sagitta to the maximum radius of the sagitta (a measure of roundness), the values for the five types occupied non-overlapping regions (Fig. 3).

When the same ratios were plotted for the larval portion of the otoliths from settled juveniles of eight common species known to belong to these five genera of eastern Pacific labrids, a similar distribution was found (Fig. 3). The regions of the graph occupied by different genera exhibited little overlap. In contrast, the values for congeners (the four species of the genus *Halichoeres*) overlapped almost completely. This apparent divergence of otolith morphology at the generic level provides an additional set of characters for separating and identifying unknown larval taxa.

Several lines of evidence support the assignment of each of five larval types to that genus which shares the same relative position on the otolith morphology graph: (1) the fin ray counts of each larval type directly match those of its putative genus (from Thomson *et al.*, 1979), (2) there are only two other genera of tropical eastern Pacific wrasses (the genera *Semicossyphus* and *Decodon*: Thomson *et al.*, 1979), neither of which share fin-ray counts with any of the larval types studied, and (3) the maximum radius of



**Fig. 3.** Relationship between relative size of lapillus (ordinate, maximum radius of lapillus ÷ maximum radius of sagitta) and roundness of sagitta (abscissa, opposite of maximum radius of sagitta ÷ maximum radius of sagitta); at right, for larval otolith in 8 species known to belong to these five genera (captured on reefs in Panamá). Dashed crosses in right-hand graph show mean ± one standard deviation of ratios in left-hand graph, except for E (*Bodianus*), which was represented by one individual only

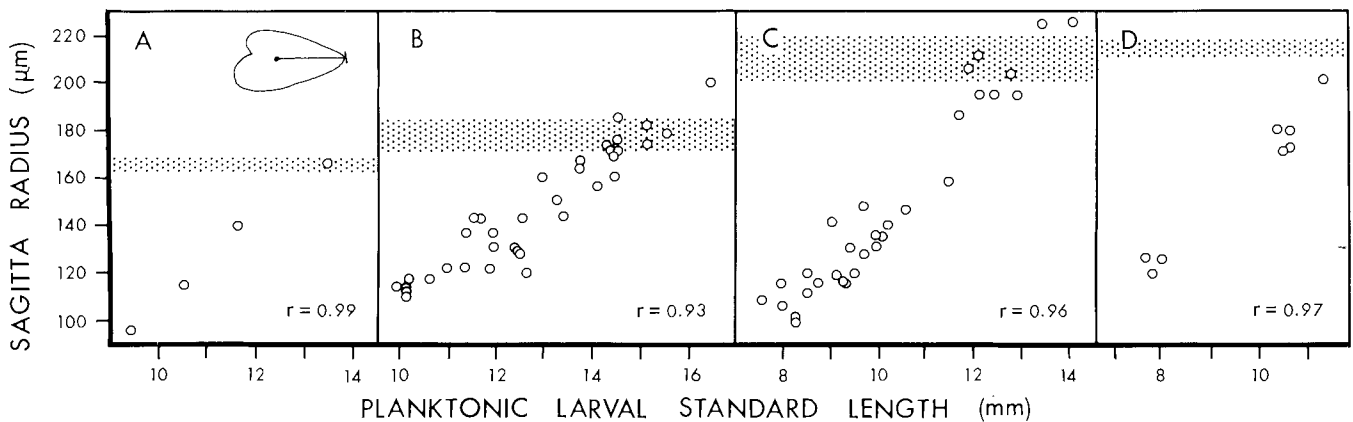


Fig. 4. Change in maximum radius of sagitta (A, upper right) with length of larvae for four types of labrid larvae from eastern Pacific Ocean (A, *Halichoeres* sp.; B, *Xyrichtys* sp.; C, *Pseudojulis* sp.; D, *Thalassoma* sp.) Shaded regions represent mean  $\pm$  one standard error of maximum radius of sagitta at settlement for the corresponding four genera of labrids captured on reefs in Panamá

the sagitta at the settlement transition for each genus (measured on the otoliths of settled juveniles) generally matches the maximum radius of the sagitta attained by the corresponding larval type studied (Fig. 4).

The morphological measurements of the larval otoliths taken from settled juveniles did not, however, match exactly those of the planktonic larvae (especially for the putative *Pseudojulis* sp.). In general, the relative size of the larval lapillus tended to be less when back-calculated from settled individuals (Fig. 3). These differences are probably a result of allometric growth in otoliths. The back-calculated ratios were from the otolith ring corresponding to larvae just prior to settlement, which were probably larger on average than the sample collected from the plankton (which included many small individuals). There was a significant decrease in the relative size of the lapillus with increasing larval length (linear regressions of the ratio of the lapillus radius to the sagitta radius on standard length of larvae, slope = 0.01, 0.02, 0.01,  $0.02 < p < 0.08$ , 0.05, 0.03, 0.0001; for the genera *Thalassoma*, *Halichoeres*, *Xyrichtys*, and *Pseudojulis*, respectively). In addition, potential species-level differences, geographical effects (perhaps in growth rates), and small sample sizes could also account for the less than exact correspondence.

#### Larval descriptions

All of the labrid larval types were elongate and laterally compressed (Fig. 1). Labrid larvae are characterized by a small mouth, few melanophores, a broad caudal peduncle, and no head or body spination. Larvae which appeared to represent a species of the genus *Halichoeres* had blunt heads and large, almost round, eyes with a series of melanophores on the membranes between some fin rays in both the dorsal and anal fins (Fig. 1A). Smaller larvae were similar, although less likely to have melanophores. Larvae of *Xyrichtys* sp. were more elongate and had no melanophores at all (Fig. 1B). Their most notable character was a narrow eye with a pronounced extension of choroid tissue anteriorly below the pupil.

Larvae that appeared to belong to the genus *Pseudojulis* were unusual in having a very pointed snout with a relatively large mouth and narrow eyes (Fig. 1C). There were conspicuous melanophores at the tip of both the lower and upper jaws as well as on the fringes of the rear of the dorsal and anal fins, continuing onto the caudal rays. Smaller individuals were less likely to have melanophores on the rear fins. Larvae of the genus *Thalassoma* lacked melanophores entirely and had a wider body than the other types (Fig. 1D). Smaller larvae also had relatively wide bodies but narrower eyes. The larva of the genus *Bodianus* had a very blunt head with particularly large round eyes and some melanophores on the body below the base of the dorsal fin and above the base of the anal fin (Fig. 1E). The pomacentrid larvae were all of one type, characterized by a deep body (with scales in the larger specimens; labrid larvae are unscaled), a serrated preopercle, and a complex melanophore pattern, including heavy pigment over the brain case (Fig. 2). Smaller individuals had no scales, fewer melanophores, and a large internal melanophore on the upper rear body.

Identification to the species level was not possible, since congeners share fin counts and probably otolith morphometrics as well. It is likely that *Thalassoma lucasanum* are represented, since they are far more common than their only other congener recorded from the area, *T. lutescens* (Thomson *et al.*, 1979). The razorfish is likely to be *Xyrichtys pavoninus*, although this species is said to extend south only to Panamá (Thomson *et al.*, 1979). *Pseudojulis* sp. probably represents *P. melanotis*; however, the distributions of species of the genus *Pseudojulis* are not well described (Thomson *et al.*, 1979). I have considered *P. notospilus* to be a member of the genus *Halichoeres*, according to J. Randall, personal communication).

#### Larval age and growth

The relationship between otolith length (the maximum radius of the sagitta) and larval standard length was linear

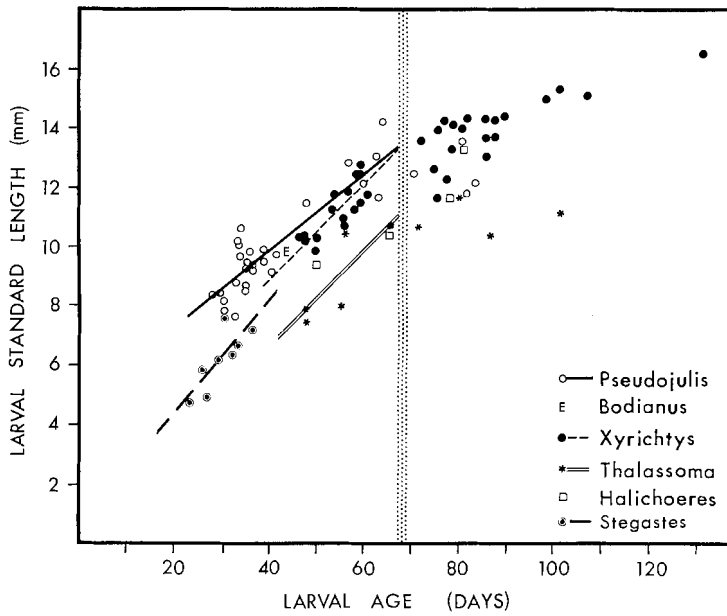


Fig. 5. Growth of labrid and pomacentrid larvae in eastern Pacific Ocean. Lines represent regression of length on age for individuals younger than 67 d. Vertical stippling indicates age at which rate of growth decreased

and close for four of the labrid larval types (correlation coefficients greater than 0.93). The exact form of the relationship differed between larval types, with larvae of *Thalassoma* sp. having particularly long otoliths relative to their standard length (Fig. 4D).

The rate of growth of larvae less than about 70 d old, as estimated by the change in length with age of larvae captured in plankton tows, tended to be linear and similar between larval types (from 0.13 to 0.19 mm d<sup>-1</sup>, excluding *Halichoeres* sp. and *Bodianus* sp., for which there were insufficient samples; Fig. 5 and Table 1). After about 70 d in the plankton there was a distinct reduction in the growth rate, although limited sample sizes of these older larvae preclude good estimates for all but the larvae of *Xyrichtys* sp., whose estimated growth rate was down to 0.06 mm d<sup>-1</sup> (Fig. 5; Table 1).

Despite the similarity of the growth rates of larvae caught in the plankton tows, the growth rates of the various larval types prior to the age at which they first appeared in the samples were probably quite different. Estimates of these growth rates depend on the size at hatching, which is unknown for these fishes. If, however, it is assumed that the genera in this study are all about the same size at hatching [i.e., about the 1.1 mm SL (standard length) recorded for *Thalassoma bifasciatum* from the Caribbean Sea (Victor, 1986c)], then the extrapolated early larval growth-rates vary from 0.15 to 0.28 mm d<sup>-1</sup> (Table 1). These growth rates were calculated simply by dividing the change in size from hatching to the smallest size appearing in the sample by the change in age since hatching of the smallest larvae [estimated as the total count of daily otolith increments, assuming that otolith growth begins around the time of hatching, as it does in *T. bifasciatum* (Victor, 1986c)].

The distribution of ages of larvae differed greatly between genera. The pomacentrid larvae were all less than 36 d old, while three of the labrid larval types were never

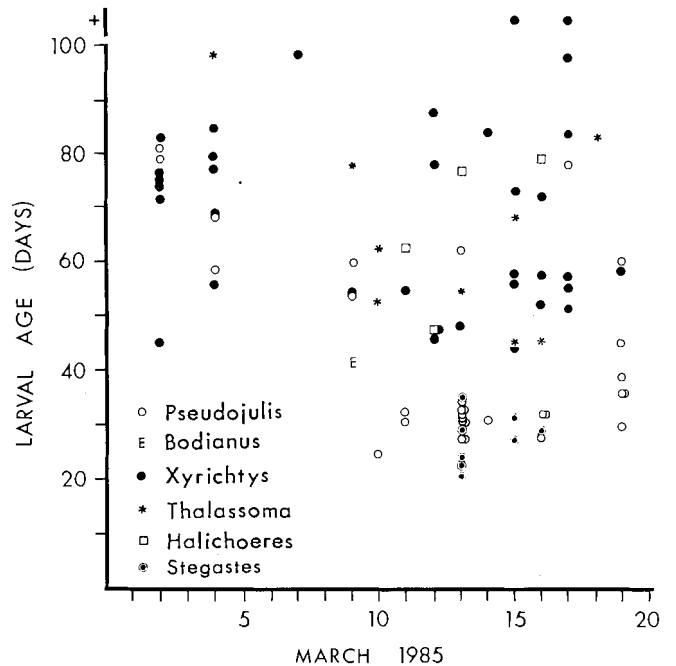


Fig. 6. Age distribution of labrid and pomacentrid larvae collected from plankton each night during March 1985 in eastern Pacific Ocean. Dates with no data indicate nights on which plankton tows were not performed

found to be younger than 46 d, despite the fact that these three types were numerous and accounted for more than half of the collection. Very few larvae over 90 d old were captured, although the largest larva of *Xyrichtys* sp. reached 131 d. There was no evidence that the plankton tows were sampling a progressively older cohort over the duration of the sampling period. Larvae of a wide range of ages were captured on most of the sampling days and the youngest larvae of some types appeared almost continuously through the sampling period (Fig. 6).

## Discussion

### Larval identification

The otoliths of fishes vary a great deal in gross morphology and have long been used in taxonomic studies (Brothers, 1984). There can, however, be pronounced ontogenetic changes in the shape of otoliths, making inter-age comparisons useless. The presence of daily increments can help to circumvent this problem. Since otoliths grow only at the edges, the shape of the otolith at all previous ages is preserved unmodified within the otolith and is delineated by the incremental marks. As a result, the otoliths of unidentified larvae can be directly compared with the corresponding larval otoliths embedded within the otoliths of settled juveniles or adults of known taxa. In this study, this method was used to help identify genera of larvae that share meristic characters. Attributes of the daily otolith increments themselves can also be very useful for identifying larval fishes. Many characteristics of the increments (such as width, contrast, and shape) can vary between families and genera of fishes (Brothers, 1984; Victor, 1986b) and can thus be used as a distinguishing character in larval identifications.

Despite the prominence of labrid and pomacentrid fishes in coral-reef fish assemblages, their larvae have not been well described (Richards and Leis, 1984). No descriptions are available for any eastern Pacific types, and the later developmental stages of the genera *Pseudojulis* or *Stegastes* have never been described. Some Indo-Pacific and Caribbean larvae of the genera *Xyrichtys* and *Thalassoma* have been illustrated by Leis (1983), Leis and Rennis (1983), and Richards and Leis (1984).

Larvae of *Thalassoma bifasciatum* from the Caribbean also have a wide body, but have some melanophores on the dorsal fin (Richards, 1984; Richards and Leis, 1984) that are not present in either the eastern Pacific type or the Indo-Pacific type (Leis, 1983). Larvae of *Xyrichtys* sp. from the Caribbean are also reported to have no melanophores and a narrow eye with a ventral extension of choroid tissue (Richards, 1984; Richards and Leis, 1984). Larvae of an Indo-Pacific *Xyrichtys* sp. share all of these attributes, but have a gap between the first two dorsal spines and the rest of the dorsal fin (Leis and Rennis, 1983) which is not shared by the Caribbean or eastern Pacific types. Larvae of *Halichoeres maculipinna* from the Caribbean are reported to have melanophores on only the last three dorsal and anal rays (Richards, 1984), although larvae of the Caribbean *H. bivittatus* have the same pattern of melanophores on the dorsal and anal fin as the eastern Pacific type described here (Victor, unpublished data). The melanophore pattern of the larva of the eastern Pacific *Bodianus* sp. is similar to that reported for a Caribbean *Bodianus* sp. by Richards (1984). The larvae of some *Stegastes* species from the Caribbean (*S. variabilis*, in particular) have almost identical melanophore patterns to the eastern Pacific type (Victor, unpublished data). In general, it appears that congeneric reef-fish larvae of these two families from different

oceans are very similar and share most of their basic characters.

### Larval growth

The growth rates of eastern Pacific labrid and pomacentrid larvae are at the lower end of the range of growth rates reported for marine fish larvae in the field, typically from 0.1 to 0.55 mm d<sup>-1</sup> (Methot and Kramer, 1979; Boehlert, 1981; Bailey, 1982; Laroche *et al.*, 1982; Lough *et al.*, 1982; Victor, 1986c). The only other data on the growth rates of coral-reef fish larvae in the plankton are from *Thalassoma bifasciatum* of the Caribbean, derived by analyses of the widths of daily otolith increments (Victor, 1986c). Larvae of *T. bifasciatum* of a comparable stage of development to the labrid larvae in this study were estimated to grow 0.26 mm d<sup>-1</sup>, almost twice as fast as the 0.16 mm d<sup>-1</sup> of the eastern Pacific *Thalassoma* sp. recorded here. Whether this reflects a general pattern of regional differences in larval growth rates is unknown, although it has been reported that eastern Pacific labrids have distinctly longer larval durations than their Caribbean and eastern Pacific conspecifics or congeners (Victor, 1986b). These longer larval durations could be an indicator of consistently lower growth rates in the plankton in this region (assuming the size at settlement is similar between regions).

Larvae of *Thalassoma bifasciatum* experience an abrupt reduction in growth rate after attaining competency (defined as reaching settlement size: Victor, 1986c). Their growth rate during this period of delayed metamorphosis was estimated to be 0.08 mm d<sup>-1</sup>, very similar to the reduced growth rate of larvae of *Xyrichtys* sp. after about 70 d in the plankton (0.06 mm d<sup>-1</sup>). As might be expected from their higher pre-competent growth rate, larvae of *T. bifasciatum* reach this inflection point in growth earlier, after only about 42 d (Victor, 1986c). The reduced growth rates of eastern Pacific labrid larvae probably also reflect the onset of competency.

### Larval dispersal

The presence of some young reef-fish larvae in the oceanic plankton hundreds of kilometers from the nearest reefs indicates that reef-fish larvae are capable of rapid long-distance dispersal. The pomacentrid larvae were the youngest captured, starting at about 23 d old (Table 1). Since pomacentrids lay demersal eggs and their larvae only enter the plankton after hatching (Thomson *et al.*, 1979), this age reflects a planktonic larval life of about 21 d (the youngest labrid larvae had been in the plankton for 27 d). The collection site is 370 km east of the Galápagos and about 600 km south of Malpelo Island and Cocos Island. The continental coastline is from 600 to 1 000 km to the north and east. Assuming direct transport from the nearest point-source, the Galápagos, the estimated maximum dispersal speed was 18 km d<sup>-1</sup> (or 22 cm s<sup>-1</sup>; it is important to note

that this is a minimum estimate of the maximum speed, analogous to estimating the maximum running speed of humans by the fastest runner in a school team).

This estimate of the maximum rate of dispersal is certainly an underestimate, since the islands are relatively small point-sources and it is possible, if not likely, that the larvae captured in this study originated on the Central American coastline, twice as far from the collection site as the Galápagos. Furthermore, the calculation assumes direct transport, and it is probable that the currents carrying larvae do not travel in a straight line. It was not possible to consider the role of current speeds and direction in the calculation, because larvae were collected over a range of depths which included several current flows traveling in different directions and at very different speeds. Since larvae are capable of vertical migration as well, it is highly improbable that any meaningful inferences can be drawn from simple measures of surface-current characteristics.

It is difficult to reconcile these findings with Leis' conclusions that very few shorefish larvae move far from shore in the eastern Pacific (Leis, 1983). The extensive EASTROPAC plankton surveys found extremely few shorefish larvae more than 500 km from shore and none more than 800 km from shore (Leis, personal communication). The DOMES survey captured only four shorefish larvae 600 to 1 200 km from shore, and all four were labrid larvae (Leis, 1983). My results indicate that reef fish should be able to disperse well beyond these limits, since some of my larvae had traveled at least 400 km in less than one month and many kinds of reef fishes have larval lives of two or more months. It may be that insufficient sampling effort has been concentrated on waters far offshore.

While the actual mechanism has yet to be elucidated, it appears that cohorts of reef-fish larvae are thoroughly mixed in the plankton. Conspecifics settling on the same day and in the same place have a wide variety of larval durations, indicating that cohorts of individuals spawned over a number of weeks can be present simultaneously in the same parcel of water (Victor, 1984). The present study further demonstrates that different taxa of reef-fish larvae spawned over a period of months can occur in the same water mass at the same time. Although the sampling period was short relative to the spread of ages of larvae caught each day, it appears that the population of larvae being sampled was not becoming progressively older. Young larvae appeared at the collection site throughout the sampling period, indicating that there was probably a continuous delivery of reef-fish larvae into the area.

Some eastern Pacific labrid larvae collected in the present study, especially of *Xyrichtys* sp. and *Thalassoma*, had greatly extended larval lives. These probably represent a maximum, since these genera are known to have the longest larval lives among the wrasses and, furthermore, populations in this region generally have distinctly longer larval durations than those in other parts of the world (Victor, 1986b). The oldest larva of *Xyrichtys* sp. in this collection (131 d old) constitutes the longest documented larval dura-

tion for any reef fish (the next longest, a *Thalassoma balieui* caught on a reef in Hawaii, had been in the plankton for 121 d; Victor, 1986b). Some of the individuals captured in the plankton in this study are older than the longest durations recorded for small samples of settled individuals of their species from Panamá (Victor, 1986b), suggesting that they are beyond the usual range of ages at which some populations of their species manage to find reefs on which to settle. The presence of large numbers of presumably competent reef-fish larvae so far from the nearest reefs indicates that offshore transport and entrapment may be a significant source of loss during the larval phase of reef fishes.

In contrast to the labrid larvae, the pomacentrid larvae did not remain in the plankton longer than about a month. This finding is in agreement with reports that pomacentrids have relatively short larval lives (3 to 5 wk) with no capability of extending larval life beyond 45 d (Brothers *et al.*, 1983; Robertson *et al.*, personal communication). One might expect that these larvae would then be found in coastal waters and not be found far offshore where the ability to extend larval life would be very advantageous. Indeed, Richards (1984) reported that very few pomacentrid larvae were captured in oceanic surveys in the Caribbean Sea, despite the fact that pomacentrids are extremely common on Caribbean reefs (many labrid larvae were captured in the surveys). Since the present study demonstrates that eastern Pacific pomacentrid are capable of dispersing far from reefs, the fact that they do not attain ages much beyond a month indicates that mortality in the plankton must be more severe for them than for those fishes that often remain in the plankton for several months. This may reflect a behavioral strategy adapted to maximize successful return of larvae that remain nearshore to the detriment of individuals transported far offshore. In general, it appears that many species of larvae of similar sizes and presumably similar origins can occupy the same water mass, yet still display very different age distributions. These differences in the larval durations of reef fish species may well be a product of different rates of mortality conferred by specific behavioral strategies in the plankton.

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#### Literature cited

- Bailey, K. M.: The early life history of the Pacific hake, *Merluccius productus*. Fish. Bull. U.S. 80, 589-598 (1982)
- Boehlert, G. W.: The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish Bull. U.S. 79, 789-794 (1981)

- Brothers, E. B.: Otolith studies. *In: Ontogeny and systematics of fishes*, pp 50–57. Ed. by H. G. Moser. Lawrence, Kansas: Allen Press 1984
- Brothers, E. B. and W. N. McFarland: Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 178, 369–374 (1981)
- Brothers, E. B. and R. E. Thresher: Pelagic duration, dispersal, and the distribution of Indo-Pacific coral reef fishes. *In: The ecology of coral reefs*, pp 53–69. Ed. by M. L. Reaka. Washington, D.C.: U.S. Department of Commerce 1985
- Brothers, E. B., D. McB. Williams and P. F. Sale: Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. *Mar. Biol.* 76, 319–324 (1983)
- Doherty, P. J.: Some effects of density on the juveniles of two species of tropical territorial damselfishes. *J. exp. mar. Biol. Ecol.* 65, 249–261 (1982)
- Doherty, P. J.: Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64, 176–190 (1983)
- Doherty, P. J., D. McB. Williams and P. F. Sale: The adaptive significance of dispersal in larval reef fishes. *Envir. Biol. Fish.* 12, 81–90 (1984)
- Johannes, R. E.: Reproductive strategies of coastal marine fishes in the tropics. *Envir. Biol. Fish.* 3, 65–84 (1978)
- Laroche, J. L., S. L. Richardson and A. A. Rosenberg: Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. *Fish. Bull. U.S.* 80, 93–104 (1982)
- Leis, J. M.: Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (86 taxa) in Hawaii. *Mar. Biol.* 72, 89–97 (1982a)
- Leis, J. M.: Distribution of fish larvae around Lizard Island, Great Barrier Reef: coral lagoon as refuge? *Proc. 4th int. Symp. coral Reefs* 2, 471–477 (1982b). (Ed. by E. D. Gomez *et al.* Quezon City, Philippines: Marine Sciences Center, University of the Philippines)
- Leis, J. M.: Coral reef fish larvae (Labridae) in the East Pacific barrier. *Copeia* 1983 (3), 826–828 (1983)
- Leis, J. M. and B. Goldman: A preliminary distributional study of fish larvae near a ribbon coral reef in the Great Barrier Reef. *Coral Reefs* 2, 197–203 (1984)
- Leis, J. M. and J. M. Miller: Offshore distributional patterns of Hawaiian fish larvae. *Mar. Biol.* 36, 359–367 (1976)
- Leis, J. M. and D. S. Rennis: The larvae of Indo-Pacific coral reef fishes, 269 pp. Honolulu: University of Hawaii Press 1983
- Lobel, P. S. and A. R. Robinson: Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Res.* 33, 483–500 (1986)
- Lough, R. G., M. Pennington, G. E. Bolz and A. A. Rosenberg: Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments. *Fish. Bull. U.S.* 80, 187–199 (1982)
- Methot, R. D. and D. Kramer: Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. *Fish. Bull. U.S.* 77, 413–423 (1979)
- Richards, W. J.: Kinds and abundances of fish larvae in the Caribbean Sea and adjacent areas. NOAA natn. mar. Fish. Serv. tech. Rep. U.S. Dep. Commerce 776, 1–54 (1984)
- Richards, W. J. and J. M. Leis: Labroidae: development and relationships. *In: Ontogeny and systematics of fishes*, pp 542–547. Ed. by H. G. Moser. Lawrence, Kansas: Allen Press 1984
- Sale, P. F.: The ecology of fishes on coral reefs. *Oceanogr. mar. Biol. A. Rev.* 18, 367–421 (1980)
- Thomson, D. A., L. T. Findley and A. N. Kerstitch: Reef fishes of the Sea of Cortez, 302 pp. New York: John Wiley & Sons 1979
- Thresher, R. E. and E. B. Brothers: Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). *Evolution*, Lawrence, Kansas 39, 878–887 (1985)
- Victor, B. C.: Daily otolith increments and recruitment in two coral reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Mar. Biol.* 71, 203–208 (1982)
- Victor, B. C.: Recruitment and population dynamics of a coral reef fish. *Science*, N.Y. 219, 419–420 (1983a)
- Victor, B. C.: Settlement and larval metamorphosis produce distinct marks on the otoliths of the slippery dick, *Halichoeres bivittatus*. *In: The ecology of deep and shallow coral reefs*, pp 47–51. Ed. by M. L. Reaka. Washington D.C.: U.S. Department of Commerce 1983b
- Victor, B. C.: Coral reef fish larvae: patch size estimation and mixing in the plankton. *Limnol. Oceanogr.* 29, 1116–1119 (1984)
- Victor, B. C.: Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* 56, 145–160 (1986a)
- Victor, B. C.: Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Mar. Biol.* 90, 317–326 (1986b)
- Victor, B. C.: Delayed metamorphosis with reduced larval growth in a coral reef fish, *Thalassoma bifasciatum*. *Can. J. Fish. aquat. Sciences* 43, 1208–1213 (1986c)
- Wellington, G. M. and B. C. Victor: El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68, 15–19 (1985)
- Williams, D. McB.: Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. mar. Sci.* 30, 159–170 (1980)
- Williams, D. McB., E. Wolanski and J. C. Andrews: Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* 3, 229–236 (1984)

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