

## Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae)

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### Abstract

The plankton larval duration for 100 species of Pacific and Atlantic damselfishes was estimated from daily growth increments on the otolith of juvenile fish collected at various localities between July 1987 and September 1988. For newly-settled fishes, larval duration was determined by counting the entire number of increments present on the otolith, while for older juveniles estimates were made by counting the number of increments between the center of the otolith and a mark corresponding to settlement. We document the development of otolith formation during the period when eggs are incubated on the reef and show that daily increments are only accreted after larvae hatch and enter the planktonic phase. The planktonic larval duration for damselfish is shorter and less variable, both between and within species, compared to other groups of reef fishes such as wrasses and surgeonfishes. Larval duration ranged from 12 to 39 d. Average duration between species ranged from 13.1 to 35.2 d. The time spent in the plankton was not significantly correlated with geographic distribution when evaluated among species, however, genera with confined regional distribution have a shorter mean larval life than do widely distributed genera. Size at settlement was positively correlated with time spent in the plankton among species, but a significant correlation between these variables was only evident within one of ten species. The low variance in planktonic larval duration within species indicates that most damselfish are unable to delay metamorphosis following competency. This inability to postpone settlement limits the potential for dispersal, especially when dispersal time between suitable habitats is greater than about 30 d.

### Introduction

Virtually all coral reef fishes have a planktonic larval phase (Sale 1980). The time spent in the plankton can be as short

as a few days in some species, but can last as long as several months in others (Brothers and McFarland 1981, Brothers et al. 1983). This planktonic phase exacts a high cost in terms of early mortality, since only a small fraction ( $\ll 1\%$ ) of the offspring produced survive to settle on the reef. Benefits to dispersal include avoiding intense local predation, eliminating inbreeding depression, and exploiting unpredictable, patchy habitats (Johannes 1978, Barlow 1981). The duration of the larval phase could play a major role in determining patterns of distribution and abundance of reef fish populations (Williams 1980, Doherty 1983, Shulman et al. 1983, Victor 1983, 1986a, Sale et al. 1984, Sweatman 1985, Doherty and Williams 1988), yet for most reef fishes little is known about this aspect of their life cycle.

With the discovery of daily incremental marks on the otoliths of many fishes (Pannella 1971, 1980, Brothers et al. 1976), and their validation in tropical reef fishes (Victor 1982, Schmitt 1984), it is possible to age larval fishes accurately and thus determine the time they have spent in the plankton prior to settlement. Adaptations to planktonic existence, such as delayed metamorphosis and reduced growth rate, have been revealed through analysis of daily increments in at least one species (Victor 1986b). Accurate determination of the age of individuals by the otolith method also permits calculation of life-history parameters essential for demographic analyses. For example, the intensity and timing of recruitment of larvae is influenced by both planktonic processes (e.g. Victor 1986a) and variation in reproductive effort (Robertson et al. 1988).

Knowledge of planktonic larval duration can have important implications for biogeographic studies. For example, if dispersal and colonizing ability increases with time spent in the plankton, differences in planktonic larval duration among species should correlate directly with species distribution and perhaps abundance. Species inhabiting outlying, geographically isolated locations in the Pacific have significantly longer larval durations than both congeners and conspecifics near the center of their distribution (Brothers and Thresher 1985, Victor 1986c).

Pomacentrids are represented worldwide by approximately 320 species (Allen 1975, and in press). They occur in many different habitats and are primarily either benthic-dwelling, territorial omnivores or schooling planktivores. The distributions of species vary – some are endemic to one, or a few islands, while others range widely throughout the Pacific and Indian Oceans. This paper examines the relationship between the time larvae spend in the plankton, their size at settlement, and the species geographic distribution.

### Materials and methods

We collected damselfishes in the western Pacific at Palau (Western Caroline Islands, Micronesia) in July 1987. Most collections were made on reefs in proximity to Ngel Channel and Malakal Harbor. Outer reef species were collected at Ngemelis Island and Denges Passage. Hawaiian damselfishes were collected at Kailua-Kana on the island of Hawaii in August 1987. In the eastern Pacific, collections were made at Taboguilla Island (Panamá), and Cocos Island (87° W; 7° N) in November 1987, the Galápagos Islands in January 1988, and Cabo San Lucas, Baja California in September 1988. Temperate eastern Pacific species were obtained at Santa Barbara, California in February 1988. Caribbean damselfishes were collected at Tague and Cane bays on St. Croix (US Virgin Islands) in October 1987 and June 1988.

With few exceptions, all fish collected were small juveniles (<30 mm standard length) that were either captured with an aquarium dipnet and the anaesthetic Quinaldine, or speared. The fish were preserved in 95% ethanol and the otoliths (sagittae and lapilli) were extracted later in the laboratory. Preparation of otoliths and description of increment characteristics are presented in detail elsewhere (Victor 1982, 1986a, b, c). Briefly, otoliths were mounted on microscope slides in immersion oil and examined using transmitted light at 400× and 1 000× magnification, with a polarizing filter placed between the light source and the slide. The lapilli were usually used, since their daily increments were often more discernable than those on the sagittae. Repeated counts were taken on each otolith until three consecutive counts were within  $\pm$  two increments. The mean of these three counts was rounded to the nearest whole number. Daily increments were evident in all species, but clarity and definition were variable between and within species. Differences in clarity were also commonly found between pairs of otoliths from the same individual. Subdaily increments (i.e., faint increments occurring between dark, well-defined increments) were found in some of the species we examined. Victor (1986c) described bifurcation of increments (the multiplying of increments at different focal planes) and the assumptions made in interpretation. In all cases, we followed Victor's criteria for interpreting which increments were daily. In general, the fewer, larger increments are considered to be accreted daily.

Damselfish eggs are deposited on reef substrate and undergo embryonic development for 3 to 6 d (Thresher 1984) before hatching into a yolkless larvae. We collected eggs from the nests of damselfish over several consecutive days in

St. Croix (US Virgin Islands). Pre- and just-hatched (during transport of eggs from the field to the laboratory) larvae were examined to determine the state of otolith development and insure that our increment counts did not include the time embryos spent undergoing development on the reef. For the Caribbean three-spot damselfish *Stegastes planifrons*, the sagitta and lapillus are formed at least two days prior to hatching, but daily increments are not accreted until after hatching. With a radius  $\leq$  to the width of a single increment, these early concretions form the nucleus of the growing otolith (Fig. 1). We assumed this pattern of otolith development is similar for all the species we examined. Our counts should reflect only the duration of the planktonic larval life.

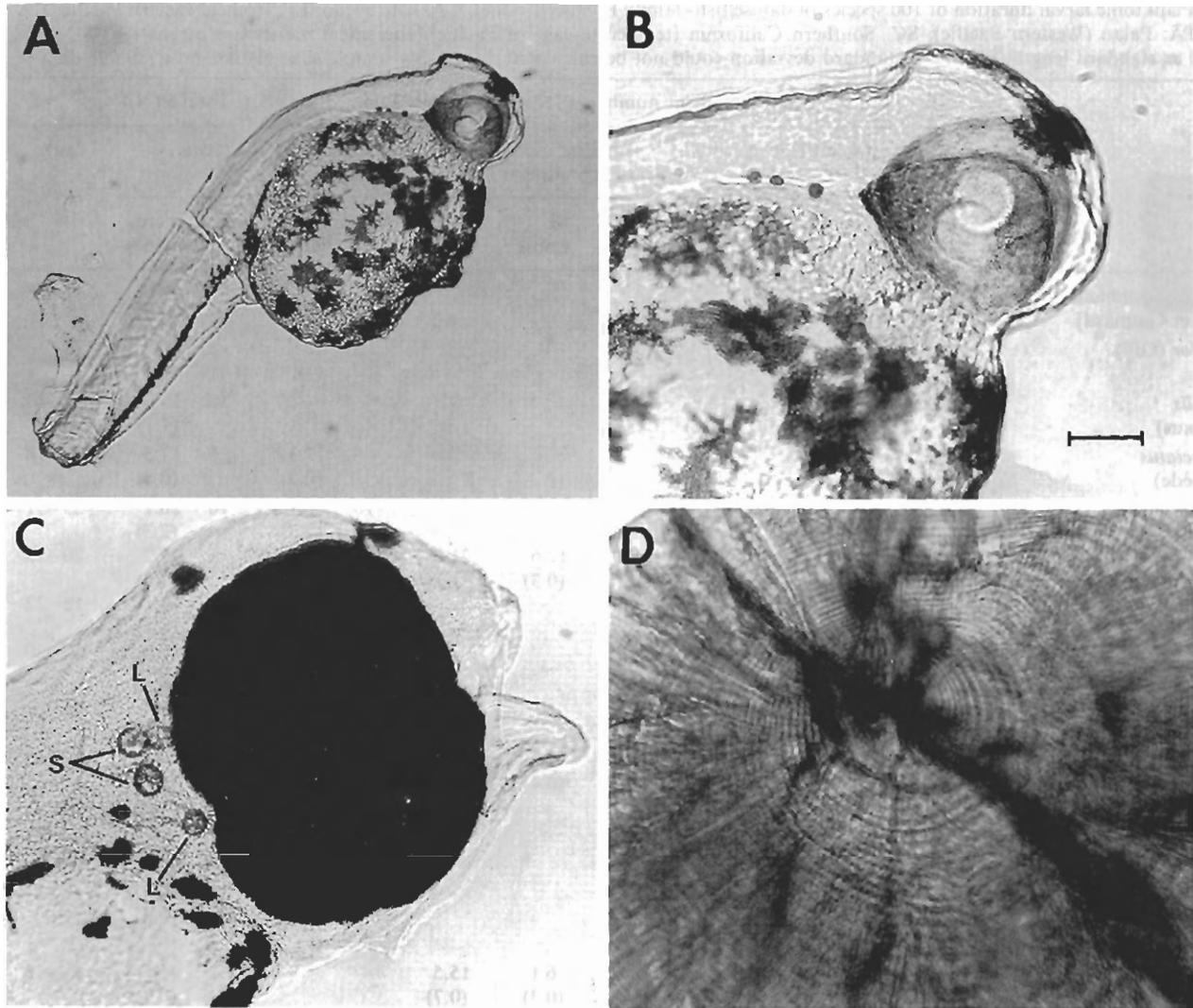
Estimates of planktonic larval duration can be derived from simple counts of daily increments in two ways. Either juveniles can be captured within 24 h after they recruit onto the reef from the plankton, in which case total increment-counts equal time in the plankton (except for those species that also have an egg-phase in the plankton), or from the presence of a reference mark (e.g. hiatus in increment formation or abrupt change in increment width) on the otolith that is associated with settlement onto the reef (Brothers and McFarland 1981, Victor 1982, 1983, 1986b, c, Brothers et al. 1983). We used both approaches in our survey.

In Palau and St. Croix, we constructed several small (1 m<sup>2</sup> in area) artificial reefs on sandy areas at least 2 m from adjacent reef substrate. These reefs consisted of a mixture of live and dead coral rubble. Because small reef fishes rarely venture over open sandy substrate, the juvenile damselfishes that colonized these patches were assumed to have come directly from the plankton. We collected newly settled recruits at 1 to 2 d intervals over the course of a 2 wk period centered around the new moon. For species that did not recruit to these patches, we collected the smallest individuals present on adjacent reefs. In many cases, these were probably recently metamorphosed recruits. We base this inference on a comparison of the size of newly settled individuals of closely related congeners that settled on artificial reefs, and the presence of larval pigmentation. For species that were larger than settlement size, we used a transition mark on the otolith and assumed that this mark represented the time of settlement.

The daily periodicity of otolith increments has been experimentally established for wrasses (Victor 1982), silversides and herring (Schmitt 1984), and the Caribbean bicolor damselfish (Robertson et al. 1988). Following an experimental protocol similar to that of Robertson et al., we verified daily increment formation for the Caribbean beaugregory *Stegastes leucostictus* (unpublished data). For the data reported here, we assume that (i) results from the work cited above apply to all damselfishes, and (ii) that the increments formed prior to settlement are also daily.

### Results

The planktonic larval duration for individual damselfishes ranged from 12 d for *Amblyglyphidodon curacao* and *Di-*



**Fig. 1.** *Stegastes planifrons*. Development of otoliths in pre- and post-hatching larvae of Caribbean damselfish. (A) Three-day old larvae (1.4 mm total length) teased free from egg capsule. (B) Magnification of (A) showing developing otoliths. (C) Otoliths in just-hatched, 5 d old larvae (1.6 mm total length); L: lapilli; S: sagittae. (D) Lapillus from 13.6 mm recruit magnified at same scale as (C), showing size of larval lapillus at hatching relative to that of recently settled larvae. Scale bar = 5  $\mu\text{m}$  (for B, C, and D)

*schistodus perspicillatus* to 39 d for *Stegastes flavilatus* (Table 1). Damselfish larvae appear to spend a relatively short period of time in the plankton (2 to 5 wk) compared to many other reef fish. Species with longer larval durations have significantly higher coefficients of variation (CV = standard deviation  $\div$  mean) [Spearman correlation;  $r = 0.39$ ,  $p < 0.01$ ,  $n = 50$  (based on species with sample size of  $\geq 10$  individuals)]. Intraspecific variability in the length of larval life is, however, generally low (Table 2). Among conspecifics, time spent in the plankton usually only varies from 3 to 6 d (Table 1).

Damselfish larval durations tend to be similar within genera, particularly among species within the same geographical area (Fig. 2). For example, genera confined to the western Pacific region have, on average, shorter larval durations while more widespread genera (such as *Chromis* and

*Stegastes*) exhibit both longer and more variable times in the plankton. Comparisons between geographic areas show that, despite the narrow range in larval duration, species in Hawaii and the eastern Pacific generally exhibit longer larval lives than their congeners from the western Pacific and Caribbean regions (Fig. 2). Even though the small sample sizes for our Hawaiian collections preclude rigorous analysis, this same pattern has been confirmed for wrasses (Victor 1986c), and the trend noted in several other families as well (Brothers and Thresher 1985).

Can the differences in size at settlement observed among species be accounted for by the amount of time larvae spend in the plankton? Analysis of 45 species show that mean size at settlement is positively correlated with mean larval duration (Fig. 3). Even though much of the variation (76%) remains unexplained, it appears, in general, that species with

**Table 1.** Planktonic larval duration of 100 species of damselfish (family Pomacentridae). CA: Caribbean; EP: tropical eastern Pacific; HA: Hawaii; PA: Palau (Western Pacific); SC: Southern California (temperate eastern Pacific). Increment values are means ( $\pm 1$  SD); size expressed as standard length (SL). (-): standard deviation could not be calculated due to low sample size; blanks: no available data

Species	Site	Pre-transition increment number, PIN (=days) based on:						Total PIN				
		artificial-reef recruits			smallest individuals of recruitment size			settlement mark		mean	range	
		n	SL (mm)	increments	n	SL (mm)	increments	n	increments			
<i>Abudefduf abdominalis</i> (Quoy et Gaimard)	HA							2	17.5 (0.7)	2	17.5 (0.7)	17-18
<i>A. concolor</i> (Gill)	EP							2	22 (-)	1	22 (-)	22
<i>A. saxatilis</i> (Linnaeus)	CA	10	11.2 (0.8)	18.2 (1.1)						10	18.2 (1.1)	17-20
<i>A. sexfasciatus</i> (Lacépède)	PA							6	17.3 (0.8)	6	17.3 (0.8)	16-18
<i>A. sordidus</i> Forsskal)	HA							10	26.1 (2.3)	10	26.1 (2.3)	23-31
<i>A. taurus</i> (Müller et Troschel)	CA				3	12.6 (0.3)	21.0 (1.7)	3	21.3 (1.2)	6	21.2 (1.3)	20-23
<i>A. troscheli</i> (Gill)	EP							11	18.1 (1.6)	11	18.1 (1.6)	16-22
<i>A. vaigiensis</i> (Quoy et Gaimard)	PA							3	18.3 (1.5)	3	18.3 (1.5)	17-20
<i>Amblyglyphidodon aureus</i> (Cuvier)	PA							5	16.0 (0)	5	16.0 (0)	16
<i>A. curacao</i> (Bloch)	PA	3	7.4 (0)	13.7 (1.1)	7	7.0 (0.4)	12.8 (0.4)			10	13.1 (0.7)	12-15
<i>A. leucogaster</i> (Bleeker)	PA							4	15.0 (0)	4	15.0 (0)	15
<i>A. ternatensis</i> (Bleeker)	PA	1	9.7 (-)	20.0 (-)				1	20.0 (-)	2	20.0 (-)	20
<i>Amphiprion chrysopterus</i> Cuvier	PA							1	17.0 (-)	1	17.0 (-)	17
<i>A. clarkii</i> (Bennett)	PA				2	6.1 (0.3)	15.5 (0.7)			2	15.5 (0.7)	15-16
<i>A. melanopus</i> Bleeker	PA				2	6.7 (0.1)	21.5 (0.7)	3	16.7 (1.5)	5	18.6 (2.9)	15-22
<i>A. perideraion</i> Bleeker	PA							2	18.0 (0)	2	18.0 (0)	18
<i>Cheiloprion labiatus</i> (Day)	PA				1	7.9 (-)	19.0 (-)	3	15.7 (5.8)	4	16.5 (1.7)	15-19
<i>Chromis agilis</i> Smith	HA							4	32.7 (2.2)	4	32.7 (2.2)	30-35
<i>C. alpha</i> Randall	PA							1	30.0 (-)	1	30.0 (-)	30
<i>C. alta</i> Greenfield and Woods	EP							5	18.7 (1.2)	5	18.7 (1.2)	18-20
<i>C. atrilobata</i> (Gill)	EP							2	33.0 (7.1)	2	33.0 (7.1)	28-38
<i>C. atripes</i> Fowler et Bean	PA				8	12.3 (0.7)	32.7 (5.5)	2	26.0 (1.4)	10	31.4 (5.6)	25-34
<i>C. caudalis</i> Randall	PA							2	27.0 (1.4)	2	27.0 (1.4)	26-28
<i>C. cyanea</i> (Poey)	CA				5	14.0 (0.5)	28.6 (3.2)	12	30.5 (2.7)	17	29.9 (2.9)	27-34
<i>C. delta</i> Randall	PA							3	24.0 (1.0)	3	24.0 (1.0)	23-25
<i>C. hanui</i> Randall et Swerdloff	HA							1	27.0 (-)	1	27.0 (-)	27
<i>C. insolata</i> (Cuvier)	CA							10	19.8 (1.1)	10	19.8 (1.1)	18-21

Table 1 (continued)

Species	Site	Pre-transition increment number, PIN (=days) based on:						Total PIN				
		artificial-reef recruits			smallest individuals of recruitment size			settlement mark		mean		range
		n	SL (mm)	increments	n	SL (mm)	increments	n	increments	n	increments	
<i>C. lepidolepis</i> Bleeker	PA				10	11.4 (0.4)	30.6 (3.0)			10	30.6 (3.0)	28-34
<i>C. lineata</i> Fowler et Bean	PA							2	37.0 (1.4)	2	37.0 (1.4)	36-38
<i>C. limbaughi</i> Greenfield and Woods	EP							5	24.2 (2.6)	5	24.2 (2.6)	20-27
<i>C. margaritifera</i> Fowler	PA	2	15.4 (0.4)	35.5 (0.7)	8	13.5 (0.5)	32.7 (2.1)			10	33.2 (2.1)	30-36
<i>C. multilineata</i> (Guichenot)	CA				1	14.4 (-)	26.0 (-)	11	25.7 (2.4)	12	25.8 (2.3)	24-30
<i>C. punctipinnis</i> (Cooper)	SC							14	35.2 (2.1)	14	35.2 (2.1)	32-38
<i>C. retrofasciata</i> Weber	PA							10	18.7 (2.2)	10	18.7 (2.2)	17-24
<i>C. ternatensis</i> (Bleeker)	PA				10	11.5	28.3 (2.6)			10	28.3 (2.6)	25-31
<i>C. vanderbilti</i> (Fowler)	HA							2	31.0	2	31.0	30-32
<i>C. viridis</i> (Cuvier)	PA	2	6.6 (0.4)	20.5 (2.1)	8	8.0 (0.4)	20.7 (2.1)			10	20.7 (1.9)	18-24
<i>C. weberi</i> Fowler et Bean	PA							5	31.2 (3.4)	5	31.2 (3.4)	26-34
<i>C. xanthura</i> (Bleeker)	PA							3	28.3 (5.0)	3	28.2 (5.0)	23-33
<i>Chrysiptera biocellata</i> (Quoy et Gaimard)	PA							10	18.2 (1.0)	10	18.2 (1.0)	17-20
<i>C. cyanea</i> (Quoy et Gaimard)	PA				10	10.2 (0.5)	15.4 (0.7)			10	15.4 (0.7)	14-16
<i>C. glauca</i> (Cuvier)	PA							10	17.5 (1.8)	10	17.5 (1.8)	15-20
<i>C. leucopoma</i> (Lesson)	PA							10	20.9 (1.5)	10	20.9 (1.5)	18-23
<i>C. oxycephala</i> (Bleeker)	PA	1	8.5 (-)	20 (-)	9	8.7 (0.9)	21.8 (1.7)			10	21.5 (1.6)	19-24
<i>C. rex</i> (Snyder)	PA				10	11.2 (0.8)	19.3 (2.2)			10	19.3 (2.2)	16-23
<i>C. traceyi</i> (Woods et Schultz)	PA							1	23.0 (-)	1	23.0 (-)	23
<i>Dascyllus albisella</i> Gill	HA							7	26.8 (1.6)	7	26.8 (1.6)	25-29
<i>D. aruanus</i> (Linnaeus)	PA				12	7.2 (0.2)	20.0 (2.4)			12	20.0 (2.4)	16-24
<i>D. melanurus</i> Bleeker	PA				2	6.4 (0.5)	21.5 (0.7)	2	21.0 (1.4)	4	21.2 (0.9)	20-22
<i>D. reticulatus</i> (Richardson)	PA				10	8.6 (0.5)	20.6 (1.2)			10	20.6 (1.2)	18-22
<i>D. trimaculatus</i> (Ruppell)	PA	2	11.1 (0.6)	23.5 (0.7)	2	10.1 (0.2)	28.5 (2.1)			4	26.0 (3.4)	23-30
<i>Dischistodus chrysopoecilus</i> (Schlegel et Miller)	PA	10	11.3 (0.4)	18.8 (2.1)	5	10.8 (0.2)	20.8 (1.0)			15	19.5 (2.0)	16-23
<i>D. melanotus</i> (Bleeker)	PA	1	9.6 (-)	13.0 (-)				2	14.0 (1.4)	3	13.7 (1.2)	13-15
<i>D. perspicillatus</i> (Cuvier)	PA	2	8.6 (0.2)	13.0 (0)	9	8.6 (0.4)	14.0 (1.0)			11	13.8 (1.0)	12-15
<i>D. pseudochrysopoecilus</i> (Allen et Robertson)	PA				6	9.4 (0.9)	14.3 (0.5)	5	14.2 (0.8)	11	14.3 (0.6)	13-15

(continued overleaf)

Table 1 (continued)

Species	Site	Pre-transition increment number, PIN (= days) based on:						Total PIN				
		artificial-reef recruits			smallest individuals of recruitment size			settlement mark		mean		range
		<i>n</i>	SL (mm)	increments	<i>n</i>	SL (mm)	increments	<i>n</i>	increments	<i>n</i>	increments	
<i>Hemiglyphidodon plagiometopon</i> Bleeker	PA				10	9.8 (1.2)	18.0 (1.4)			10	18.0 (1.4)	16–20
<i>Hypsypops rubicundus</i> (Girard)	SC							2	20.0 (2.8)	2	20.0 (2.8)	18–22
<i>Microspathodon chrysurus</i> (Cuvier et Valenciennes)	CA	1	11.5 (–)	27.0 (–)				9	22.5 (1.3)	10	23.0 (1.9)	21–27
<i>M. dorsalis</i> (Gill)	EP							1	34.0 (–)	1	34.0 (–)	34
<i>Neopomacentrus nemurus</i> (Bleeker)	PA	2	10.5 (0)	16 (0)	20	10.5 (0.6)	19.5 (2.1)			22	19.2 (2.2)	16–24
<i>Paraglyphidodon melas</i> (Cuvier)	PA				7	8.6 (0.3)	15.6 (1.3)	3	17.3 (0.6)	10	16.1 (1.4)	14–18
<i>P. nigroris</i> (Cuvier)	PA				4	9.0 (0.5)	22.3 (0.5)	6	21.3 (2.2)	10	21.7 (1.8)	19–24
<i>Plectroglyphidodon dickii</i> (Lienard)	PA							5	26.6 (1.5)	5	26.6 (1.5)	25–28
<i>P. imparipennis</i> (Vaillant et Sauvage)	HA							8	17.5 (1.6)	8	17.5 (1.6)	28–33
<i>P. lacrymatus</i> (Quoy et Gaimard)	PA							10	20.4 (1.7)	10	20.4 (1.7)	18–23
<i>P. sindonis</i> (Jordan et Evermann)	HA							1	30.0 (–)	1	30.0 (–)	30
<i>Pomacentrus alexanderae</i> Evermann et Seale	PA	1	10.7 (–)	19.0 (–)	9	10.6 (0.6)	17.5 (0.5)			10	17.7 (0.7)	17–19
<i>P. amboinensis</i> Bleeker	PA				10	11.2 (0.2)	17.8 (1.0)			10	17.8 (1.0)	16–19
<i>P. bankanensis</i> Bleeker	PA	1	12.9 (–)	20.0 (–)	6	14.3 (0.4)	18.3 (1.0)	3	19.3 (1.2)	10	18.8 (1.1)	17–20
<i>P. burroughi</i> Fowler	PA							6	16.8 (1.2)	6	16.8 (1.2)	15–18
<i>P. coelestis</i> Jordan et Starks	PA							8	18.9 (0.8)	8	18.9 (0.8)	18–20
<i>P. emarginatus</i> Cuvier	PA				10	12.6 (0.5)	18.4 (1.2)			10	18.4 (1.2)	17–20
<i>P. grammorhynchus</i> Fowler	PA							6	14.8 (0.8)	6	14.8 (0.8)	14–16
<i>P. lepidogenys</i> Fowler et Bean	PA							1	20.0 (–)	1	20.0 (–)	20
<i>P. moluccensis</i> Bleeker	PA	3	10.9 (0.2)	21.0 (1.0)	7	10.7 (0.4)	19.4 (1.7)	2	18.0 (0)	12	19.6 (1.7)	18–23
<i>P. pavo</i> (Bloch)	PA	1	14.1 (–)	27.0 (–)	9	14.1 (0.4)	21.9 (2.0)			10	22.4 (2.5)	20–27
<i>P. philippinus</i> Evermann et Seale	PA							1	16.0 (–)	1	16.0 (–)	16
<i>P. reidi</i> Fowler and Bean	PA							1	18.0 (–)	1	18.0 (–)	18
<i>P. rhodonotus</i> Bleeker	PA				10	12.5 (0.1)	15.8 (1.1)			10	15.8 (1.1)	14–17
<i>P. simsiang</i> Bleeker	PA				1	9.9 (–)	16.0 (–)	9	15.8 (1.0)	10	15.8 (0.9)	14–18
<i>P. taeniometopon</i> Allen	PA							3	15.7 (0.6)	3	15.7 (0.6)	15–16
<i>P. vaiuli</i> Jordan et Seale	PA				6	12.7 (0.4)	16.8 (0.8)			9	16.8 (0.8)	16–18
<i>Pomacentrus</i> sp. 1	PA				10	10.8 (0.8)	17.4 (0.7)			10	17.4 (0.7)	16–18

Table 1 (continued)

Species	Site	Pre-transition increment number, PIN (=days) based on:						Total PIN				
		artificial-reef recruits			smallest individuals of recruitment size			settlement mark		mean	range	
		n	SL (mm)	increments	n	SL (mm)	increments	n	increments	n	increments	
<i>Pomacentrus</i> sp. 2	PA							1	14.0 (-)	1	14.0 (-)	14
<i>Stegastes acapulcoensis</i> (Fowler)	EP							19	21.3 (1.7)	19	21.3 (1.7)	19-23
<i>S. arcifrons</i> (Heller et Snodgrass)	EP							14	25.3 (4.3)	14	25.3 (4.3)	20-33
<i>S. diencaeus</i> (Jordan et Rutter)	CA				5	11.2 (0.2)	22.2 (1.1)	5	20.4 (0.9)	10	21.3 (1.3)	19-24
<i>S. dorsopunicans</i> (Poey)	CA				3	11.6 (0.3)	21.6 (1.5)	7	21.0 (1.3)	10	21.2 (1.3)	20-23
<i>S. fasciolatus</i> (Ogilby)	HA							2	25.0 (1.4)	2	25.0 (1.4)	24-26
<i>S. flavilatus</i> (Gill)	EP							10	31.2 (6.1)	10	31.2 (6.1)	25-39
<i>S. leucurus beebei</i> (Nichols)	EP							10	31.2 (2.8)	10	31.2 (2.8)	27-36
<i>S. leucostictus</i> (Müller et Troschel)	CA	1	9.9 (-)	20.0 (-)	9	9.5 (0.4)	20.1 (0.8)			10	20.1 (0.7)	19-21
<i>S. lividus</i> (Bloch et Schneider)	PA							1	25.0 (-)	1	25.0 (-)	25
<i>S. nigricans</i> (Lacepede)	PA							1	24.0 (-)	1	24.0 (-)	24
<i>S. partitus</i> (Poey)	CA				4	12.8 (2.1)	28.5 (0.6)	10	28.9 (1.3)	14	28.8 (1.1)	27-31
<i>S. planifrons</i> (Cuvier et Valenciennes)	CA				2	13.6 (0.2)	21.0 (1.4)	10	21.5 (2.0)	12	21.4 (1.9)	17-25
<i>S. redemptus</i> (Heller et Snodgrass)	EP							5	23.0 (1.9)	5	23.0 (1.9)	20-25
<i>S. variabilis</i> (Castelnau)	CA				5	12.1 (0.1)	23.4 (0.9)	10	23.2 (1.2)	15	23.3 (1.1)	22-25
<i>Stegastes</i> sp. 1	CA							1	21.0 (-)	1	21.0 (-)	21
<i>Stegastes</i> sp. 2	PA							2	22.5 (0.7)	2	22.5 (0.7)	22-23

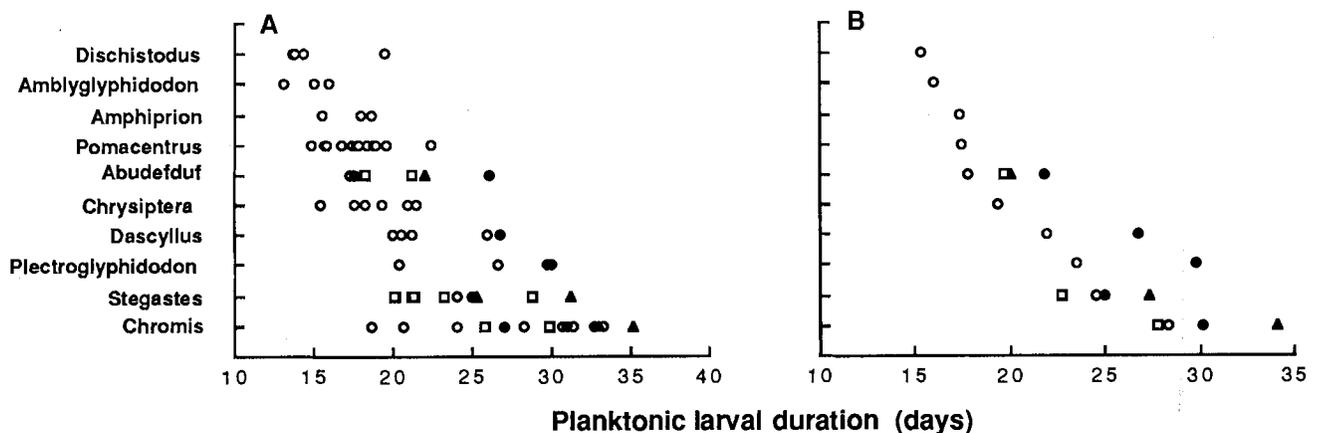


Fig. 2. Planktonic larval duration for damselfish species representing ten genera. (A) Mean values for individual species (see Table 1 for other statistics); (B) means for genera by region. ○: western Pacific species; ●: Hawaiian species; ▲: eastern Pacific species; □: Caribbean species

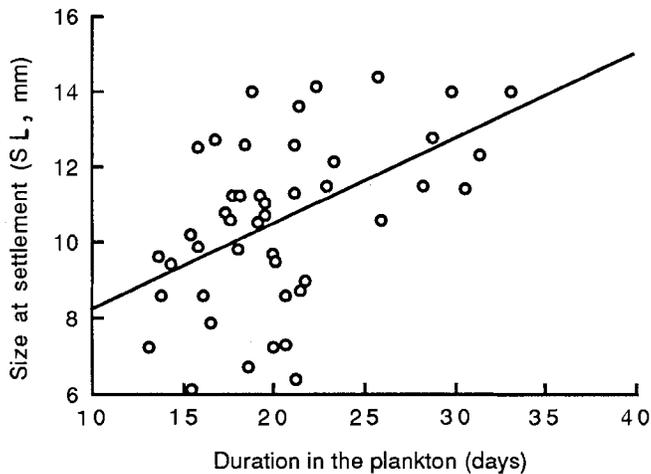


Fig. 3. Relationship between larval duration in the plankton and size (SL = standard length) at settlement. Data points represent means for individual species (see Table 1 for other statistics). Least-squares best-fit line is:  $y = 6.0 + 0.224x$  ( $F_{1,43} = 13.87$ ,  $p < 0.001$ ,  $r^2 = 0.24$ )

Table 2. Summary of ranges and coefficients of variation (CV, %) for planktonic larval duration of damselfish (family Pomacentridae) and wrasses (family Labridae). No. of species are based on species with a sample size of  $\geq 10$  individuals, damselfish data are summary statistics based on this study, and wrasse data are summary statistics based on Victor (1986c)

	Damselfish	Wrasses
No. of species	50	69
Larval life (d):		
Range of species means	13.7–35.2	19.2–103.9
Range of individuals	12–39	15–121
Mean CV ( $\pm 1$ SD)	$8.1 \pm 3.4$	$12.0 \pm 3.7$
Range of CV	3.5–19.6	6.2–22.7

longer-lived larvae (approximately  $> 25$  d) are larger than 10 mm in size at settlement and, conversely, smaller settlers spend less than average time in the plankton.

The relation between body length (size) and age at settlement for individual fish, however, indicates that size at settlement is not simply a direct function of time spent in the plankton (Table 3). Only two of ten species examined showed a significant positive correlation between size and age at settlement, while there was no correlation or a negative correlation in six others (albeit the sample sizes were perhaps too small to detect significant trends in some cases). In several instances (four of ten species), the variance in age (expressed as CV: Table 3) was up to three times larger than the variance in size at settlement. It is not known whether this phenomenon is due to differences in growth rate among individuals or an ability to reduce growth rate following competency while in the plankton.

## Discussion

### Planktonic larval durations

The range of larval duration found in this survey is concordant with previous reports for other damselfishes (Brothers et al. 1983, Brothers and Thresher 1985, Robertson et al. 1988). The most notable finding of this study is that damselfishes tend to spend a remarkably short and invariant period of time in the plankton in contrast to other reef fishes for which a comparable data base exists (e.g. wrasses; Victor 1986c, and present Table 2). We caution, however, that our data for individual species are based mainly on collections taken from a single locality over a short period of time. If additional variability exists, either temporally or between locations, then our values may be low. For example, we note a significant difference in larval duration between *Stegastes partitus* in St. Croix (mean = 28.8 d,  $n = 14$ ; present study)

Table 3. Summary statistics for length and age at settlement for ten species of damselfish. Values for length (SL) and age are means ( $\pm$ SD).  $r_{la}$ : Pearson product-moment correlation coefficient between length and age at settlement; CV: bias-corrected coefficient of variation (expressed as the proportion);  $t$ : Student's  $t$ -test statistic ( $*p < 0.05$ ,  $**p < 0.01$ );  $CV' = (1 + (\frac{1}{4}n)) \cdot CV$ ; test statistic calculated as  $CV'_1 - CV'_2 / \sigma_{cv_1} \sigma_{cv_2}$  (see Sokal and Braumann 1980 for description of statistical procedures)

Species	$n$	SL at settlement (mm)	Age at settlement (d)	$r_{la}$	CV length	CV age	$t$
<i>Abudefduf saxatilis</i>	10	11.2 (0.80)	18.2 (1.13)	0.06	0.075	0.064	0.31
<i>Amblyglyphidodon curacao</i>	10	7.1 (0.35)	13.1 (0.74)	0.46	0.050	0.058	0.32
<i>Dascyllus auranus</i>	12	7.2 (0.24)	20.0 (2.37)	0.01	0.035	0.021	1.05
<i>D. reticulatus</i>	10	8.6 (0.54)	20.6 (1.17)	-0.43	0.064	0.058	0.21
<i>Dischistodus chrysopoecilus</i>	15	11.1 (0.40)	19.5 (2.00)	-0.45	0.037	0.104	3.03**
<i>Neopomacentrus nemurus</i>	22	10.5 (0.53)	19.2 (2.22)	0.55**	0.051	0.118	3.15**
<i>Pomacentrus alexanderae</i>	10	10.6 (0.53)	17.7 (0.67)	0.00	0.051	0.039	0.52
<i>P. moluccensis</i>	12	10.7 (0.37)	19.9 (1.66)	0.60*	0.035	0.085	2.49*
<i>P. pavo</i>	10	14.2 (0.34)	22.4 (2.50)	-0.05	0.024	0.115	3.04**
<i>Stegastes leucostictus</i>	11	9.5 (0.42)	20.2 (0.75)	-0.46	0.045	0.038	0.40

and Panamá [mean = 36.5 d,  $n = 206$ , Student's  $t$ -test  $t_{[219]} = 23.3$ ,  $p < 0.001$ ; Robertson et al. (1988)]. Similarly, we found that *S. flavilatus* in Panamá had a much shorter larval life (mean = 27.0 d,  $n = 5$ ) than individuals in Ecuador (mean = 35.4,  $n = 5$ ,  $t_{[8]} = 5.54$ ,  $p < 0.001$ ). Victor (1986c) also reported significant differences in planktonic duration for conspecific wrasses occurring in Palau and Hawaii.

Given that the variance in larval duration is higher for wrasses than damselfishes, one might predict higher rates of regional and local endemism among damselfishes. This is the case; for example, four wrasse species, all with long and highly variable planktonic larval periods, have distributions which extend over the entire Pacific (Victor 1986c). The damselfish fauna of the eastern and western Pacific, however, are mutually exclusive (with the possible exception of the taxonomically uncertain species *Abudefduf troschelii*), and are dominated by different genera (e.g. *Stegastes* in the eastern Pacific and *Pomacentrus* in the western Pacific; Allen in press).

In the tropical eastern Pacific, offshore island groups such as Galápagos, Cocos and the Revillagigedos support several endemic species of damselfishes (Allen and Woods 1980), while nearly all the wrasse species in this region are widely distributed (Thomson et al. 1979, see Bussing 1983 for the single exception). This pattern indicates a higher potential for dispersal in wrasses with a longer, more variable time in the plankton.

Ichthyoplankton surveys also indicate that damselfish larvae (in contrast to wrasses, parrotfishes, butterflyfishes, and others) are restricted to nearshore waters (Leis and Miller 1976, Leis 1982, Leis and Goldman 1984, Richards 1984). Victor (1987), however, found larval *Stegastes* spp. in the eastern Pacific several hundred kilometers offshore. These larvae ranged in age from 23 to 38 d and, based on the nearest source of these larvae, appear to be capable of travelling up to  $18 \text{ km d}^{-1}$ . Whether this observed potential for dispersal is representative of damselfish in general, or simply the result of a chance oceanographic event, is unclear.

It is perhaps not surprising that size at settlement is positively correlated with duration in the plankton in interspecific comparisons, but the large variation in size at settlement, particularly among species spending fewer than 25 d in the plankton, warrants some explanation. We considered two possible influences on, or associations with, variation in planktonic duration. First, higher productivity might be expected to shorten time of larval development. In this case, species inhabiting productive regions should have shorter planktonic durations. Second, species inhabiting isolated islands might require prolonged larval lives to reach appropriate habitats, yet settle at a size comparable to species with a contiguous distribution. We found no evidence in our survey supporting either scenario. Larval durations for damselfishes in the highly productive eastern Pacific are among the longest. And, there is no consistent pattern evident for insular species.

Chambers and Leggett (1987) found significantly higher variation in age at settlement compared to size at settlement in 15 of 18 populations of laboratory-reared winter

flounder. Their analyses showed that slower growing larvae develop at a slower rate, remain as larvae longer, and subsequently metamorphosis at a larger size. This increase in size at settlement due to slower development, however, was proportionally less than the concomitant increase in time (age) to settlement. They concluded that the differences in variance between age and size at settlement largely reflects different rates of growth among individuals in the population, rather than a delay in metamorphosis following competency. Compared to wrasses, which are known to postpone settlement for up to several weeks by reducing their growth rate following competency (Victor 1986b), the relatively low variance in age at settlement for damselfishes (present Table 3, and Robertson et al. 1988), indicates a limited capacity to extend larval life past competency. Inability to delay metamorphosis for those species with a short-lived planktonic larval life of  $\leq 1$  mo would decrease the potential for dispersal and may account for the restricted range in distribution evident in many species of pomacentrids.

#### Larval duration and biogeographical distribution

Explaining biogeographical patterns of species distributions would be simple if larval durations in the plankton were directly correlated with geographic distribution. For damselfishes, there is a rough positive correlation between duration of larval life and geographic distribution at the generic, rather than the species level (Fig. 2). Five of the six genera with species having shorter than average planktonic larval lives are all confined to the Indo-Pacific province. In the genus having the shortest time in the plankton (*Dischistodus*, with an overall mean of 15.3 d), three of the four species we examined are, in fact, among those with the most restricted distributions. The reason for this is probably complex, since extant distributions reflect both historical events and processes acting in the present (e.g. ecological suitability of habitats, species tolerances to physical stress, oceanographic conditions coupled with timing of reproduction which may limit dispersal, and others). *Abudefduf* is the only exception to this pattern. In this cosmopolitan genus, species found within geographic regions are wide-ranging yet have shorter than average larval lives. This anomaly may be explained by the fact that many, if not all, species of *Abudefduf* are reported to be capable of metamorphosing into juveniles while drifting beneath floating debris (e.g. Gooding and Magnuson 1967). This rafting behavior is, however, presumably exceptional among damselfishes.

If any correlation exists between larval duration and geographic distribution, it should be evident among species with extreme distributions. Analysis of such cases, however, reveals no relationship at the species level (Table 4). Length of planktonic larval life is independent of geographic distribution. Similar results have been reported for a diverse sample of Indo-West Pacific taxa (Brothers and Thresher 1985, Thresher and Brothers 1985). Many reef fishes found in the western Pacific and Caribbean provinces have widespread distributions yet short larval lives. Given the close proximity

**Table 4.** Mean planktonic larval duration for species with restricted and widespread distributions in western, central and eastern Pacific Ocean. Range of distribution based on Allen (1975): FIJ, Fiji; GI, Gilbert Islands; GBR, Great Barrier Reef; HA, Hawaii; IO, Indian Ocean; JA, Japan; LI, Line Islands; MA, Marshall Islands; MX-EC, continental shores from Mexico to Ecuador; NH, New Hebrides; OSI, offshore islands (Galápagos, Cocos, Malpelo); PA, Palau; PNG, Papua New Guinea; PIT Pitcairn Islands; SI, Society Islands; SO, Solomon Islands; TU, Tuamotu Islands

Species	Range of distribution	Larval duration (d)	
		wide-spread spp.	restricted spp.
Western/Central Pacific			
<i>Chromis bicolor</i>	IO, PA, GBR, TU, LI	33.2	
<i>C. caudalis</i>	PA, SO		27.0
<i>C. lepidolepis</i>	PA, GBR, FIJ, LI	30.6	
<i>C. lineata</i>	PA, PNG, SO		37.0
<i>C. margaritifera</i>	PA, MA, GBR, TU, LI	33.2	
<i>C. viridis</i>	IO, PA, GBR, TU, LI	20.7	
<i>C. weberi</i>	IO, PA, GBR, LI, PIT, FIJ	31.2	
<i>Chrysiptera</i>			
<i>biocellata</i>	PA, GBR, FIJ, LI	18.2	
<i>C. glauca</i>	PA, GBR, PIT, LI	17.5	
<i>C. leucopoma</i>	IO, PA, GBR, SI, LI	20.9	
<i>C. oxycephala</i>	PA, PNG		21.5
<i>C. traceyi</i>	PA, MA		23.0
<i>Dascyllus</i>			
<i>albisella</i>	HA		26.8
<i>D. aruanus</i>	PA, PNG, GBR, FIJ, LI	20.0	
<i>D. melanurus</i>	PA, PNG, GBR		21.2
<i>D. trimaculatus</i>	PA, GBR, FIJ, PIT, LI	26.0	
<i>Pomacentrus</i>			
<i>burroughi</i>	PA, PNG		16.8
<i>P. coelestis</i>	PA, JA, GBR, TU, LI	18.9	
<i>P. emarginatus</i>	PA, PNG		18.4
<i>P. pavo</i>	PA, GBR, TU, LI	22.4	
<i>P. simsiang</i>	PA, PNG, NH		19.6
<i>P. vaiuli</i>	PA, GBR, MA, GI	16.8	
Eastern Pacific			
<i>Chromis</i>			
<i>atrilobata</i>	MX-EC, OSI	33.0	
<i>Microspathodon</i>			
<i>dorsalis</i>	MX-EC, OSI	34.0	
<i>Stegastes</i>			
<i>acapulcoensis</i>	MX-EC		21.3
<i>S. arcifrons</i>	OSI		25.3
<i>S. flavilatus</i>	MX-EC		31.2
<i>S. leucorus</i>			
<i>beebei</i>	OSI		31.2
Means		25.1 (6.7)	24.6 (5.9)
		(n = 15)	(n = 13)
Significance		p > 0.9, Wilcoxon two-sample test	

of many islands, which can function as stepping stones to promote dispersal, this observation is not unexpected. What does require explanation is the converse – why do some species with long planktonic durations have a restricted range, as seen in insular and mainland endemic species of *Stegastes* in the eastern Pacific? Possible explanations in-

clude strict habitat requirements, larval behavior that reduces transport, or localized oceanographic conditions that promote the retention of larvae near their source of origin (Bakun 1986, Lobel and Robinson 1986, Sammarco and Andrews 1988). Unfortunately, there is no direct evidence to indicate which, if any, of these processes influence species distributions.

The relationship between planktonic larval duration and geographic distribution among damselfishes remains unclear. Gene flow among populations could increase with the length of larval life. While most population genetic studies conducted on tropical reef fishes support panmixis (Bell et al. 1982, Shaklee et al. 1982, Shaklee 1984, Rosenblatt and Waples 1986, E. Bermingham personal communication), Waples (1987) has shown that the extent of gene flow can be directly related to dispersal capabilities in some shorefish species. Even when species appear to have high dispersal capabilities, there is some evidence from marine invertebrates that genetic differentiation among populations of conspecifics is best explained by restricted gene flow, rather than by local selection (Burton and Feldman 1981, Burton 1983). A full understanding of the relationship between length of larval life, dispersal ability, and gene flow must await detailed population genetic studies.

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