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Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae)

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Abstract

The planktonic larval durations of a preliminary sample of one hundred species of wrasses from both the Pacific and Atlantic Oceans were estimated with the use of the daily otolith-increment aging-technique. Larval durations were determined by counting the number of daily increments between the center of the otolith and the mark corresponding to settlement. The duration of the planktonic larval phase of wrasses appears to be extremely variable between species, ranging from 15 d in *Diproctacanthus xanthurus* to 121 d in a specimen of *Thalassoma ballieui*. Larval durations within species were also variable, especially in species with relatively long durations. Congeners tended to have similar larval durations and similar otolith-increment characteristics. Hawaiian and Eastern Pacific species had longer larval durations than their Caribbean or Western Pacific congeners. Similarly, Hawaiian populations had significantly longer larval durations than their Western Pacific conspecifics. The implications of these findings for biogeographical studies are discussed.

Introduction

Coral-reef fishes, diverse in most other respects, are notably consistent in having a planktonic larval stage. Virtually all of the thousands of species native to coral reefs have larvae which spend some time adrift in the plankton (Sale, 1980). This phase of their life history can play an important, perhaps crucial, role in determining the distribution, abundance, and dynamics of reef-fish populations (Williams, 1980; Doherty, 1983; Victor, 1983 a, 1984, and in press). There is, nevertheless, very little known about even the most basic aspects of the larval life of coral-reef fishes (Sale, 1980). The distance over which these larvae are able to disperse, presumably a function of the duration of the larval phase, is a particularly important quantity for both ecological and biogeographical studies. Both Sale (1980) and Anderson *et al.* (1981) have agreed that the scale on which community ecological studies of reef assemblages should be performed depends directly on the larval dispersal distance. In addition, it is possible that varying dispersal abilities could account for many of the complex patterns characteristic of coral-reef fish biogeography.

Estimates of the duration of the larval life of reef fishes are difficult to derive without an accurate aging technique. Randall (1961) estimated the planktonic larval duration of a surgeonfish in Hawaii by measuring the difference in timing between the seasonal onset of spawning and the subsequent influx of settlers. This method depends on the presence of distinct seasonal cycles of spawning and settlement and requires that incoming larvae originate from the local population. The discovery of daily incremental marks on the otoliths of many fishes has greatly simplified the process (Panella, 1971; Brothers *et al.*, 1976). It is possible to use this technique to make extremely precise and accurate measurements of the age of individual fishes. There are two methods by which one can derive an estimate of the planktonic larval duration using the daily otolith-increment technique. One method is to capture larval recruits as they settle onto the reef and count the number of daily increments on their otoliths (Brothers *et al.*, 1983; Victor, 1983 b). Alternatively, if there is a mark on the otolith that can be demonstrated to be associated with settlement, one can then estimate the planktonic larval duration for any settled individual by counting the number of daily increments between the center of the otolith and the settlement mark (Brothers and McFarland, 1981; Victor, 1982, 1983 b).

The wrasse family (Labridae) is, at present, unique among coral-reef fishes in that there is direct experimental evidence demonstrating the existence of both daily increments and a distinct mark on their otoliths corresponding to settlement (Victor, 1982, 1983 b). This family is, furthermore, one of the most speciose of reef-fish families

(with about 400 species, second only to the gobies), and is unparalleled in diversity of both form and habit (Nelson, 1976). Wrasses also exhibit a great variety of distributional patterns, with some species endemic to single islands and others found throughout the Indian and Pacific Oceans. For these reasons, this family is particularly suitable for a detailed and comprehensive study of planktonic larval durations. In the present study, I document the duration of the planktonic larval stage for a hundred species of wrasses from both the Pacific and Atlantic Oceans using the daily otolith-increment aging-technique. I also examine some of the problems inherent in otolith-aging of coral-reef fish larvae and discuss the implications of these preliminary findings for biogeographical studies of coral-reef fishes.

Materials and methods

The wrasses from the Caribbean Sea were collected in January and February of 1983 from Aguadargana Reef in the San Blas Islands of Panamá in the southern Caribbean Sea. The large number of bluehead wrasses, *Thalassoma bifasciatum,* were obtained between 1980 and 1984 from various reefs at the western edge of the San Blas Islands. The wrasses from the western Pacific were collected during July and August of 1983 from Palau in the Caroline Islands. Most specimens were captured on Augulpelu reef on the east coast of Palau near Koror, while the remainder were collected in the Ngel Channel and in Malakal Harbor. The Hawaiian wrasses were collected from the Wainae coast of Oahu and the Kona coast of Hawaii in May 1984. The wrasses from the eastern tropical Pacific were collected around the island of Pacheca, the northermost of the Perlas Islands in the Gulf of Panamá in November 1982 and in November 1984. The eastern Pacific temperate wrasses were obtained from Southern California in July 1985. The north Atlantic wrasses were collected along the Massachusetts coast in May 1985.

Most of the samples consisted of juvenile wrasses which I subdued with the anaesthetic Quinaldine and then captured with an aquarium dipnet. Larger individuals were shot with various sized spears. Those fish small enough to be conveniently preserved in the field were immediately put into 95% ethanol (formalin dissolves otoliths), while the otoliths were removed directly from the larger fishes. Two of the three pairs of otoliths (the sagittae and the lapilli) were used in this study. The largest pair, the sagittae, often exhibited clear increments and thus were usually selected for examination. In many cases, the lapilli, the mid-sized pair, proved to have clearer increments than the sagittae. In those species with very narrow otolith increments, however, the sagittae were always used since increments on the lapilli often become too narrow to detect. The otoliths were obtained by first removing the top of the cranium and then extracting the otoliths with a pair of fine forceps from their pockets in the floor and sides of the braincase. They were then cleaned, dried, and placed into a drop of immersion oil. Most otoliths were easily countable without further preparation, but some of the larger and less clear needed to be ground before their daily increment sequence could be counted. Grinding was performed by hand on a glass plate with Carborundum 600 grit in immersion oil.

The otoliths were examined under a compound microscope using transmitted light at magnifications of 400 to 1 000×. A rotatable polarizing filter placed between the light source and the slide was used to accentuate the marks on the otolith. Increment sequences were clearer on otoliths that had remained in oil for more than a few weeks or months. Each daily increment consists of a light line followed by a narrower dark line. The light line corresponds to a mostly crystalline growth zone, while the dark line consists of a zone comprised mainly of a protein matrix (Watabe *et al.*, 1982). The settlement mark was identified as a band with increments that were wide and very faint (Victor, 1982, 1983 b). The dark lines within this band are often not apparent and the settlement mark then looks like a band without increments at all. The settlement mark is usually quite conspicuous because increments at the end of the larval sequence often have highly contrasting light and dark lines making up each increment.

The number of daily increments between the center of the otolith and the settlement mark was counted and recorded for each individual captured. Otolith increments have been experimentally demonstrated to be daily for two species of tropical wrasse juveniles (Victor, 1982, 1983 b). These studies also demonstrated that a distinct settlement mark is produced on the otoliths of these species when the planktonic larva first settles onto the reef. Direct experimental evidence for the production of daily increments on the otoliths of planktonic larvae in the field (as opposed to settled juveniles) has not yet been obtained for any fish. It is therefore assumed in this study that (1) the increments observed on larval otoliths are also daily, and (2) the daily increments and settlement marks demonstrated in the two species of wrasses are common to all wrasses. Wrasse otoliths appear within a day or two of fertilization in tropical waters (Victor, unpublished data). I therefore added two days to the number of pre-settlement increments to arrive at an estimate of the entire planktonic larval duration.

Results

Otolith increments

Incremental marks were found on all the otoliths examined. In many of the species examined, there was only one array of increments and the counting was therefore straightforward. However, on the otoliths of many other species there appeared to be more than one type of repeating incremental mark. The different arrays of increments were usually apparent at slightly different focal planes. These arrays appeared to be an integral part of the crystal structure of the otolith rather than any optical artifact. The presence of different superimposed sequences of in-

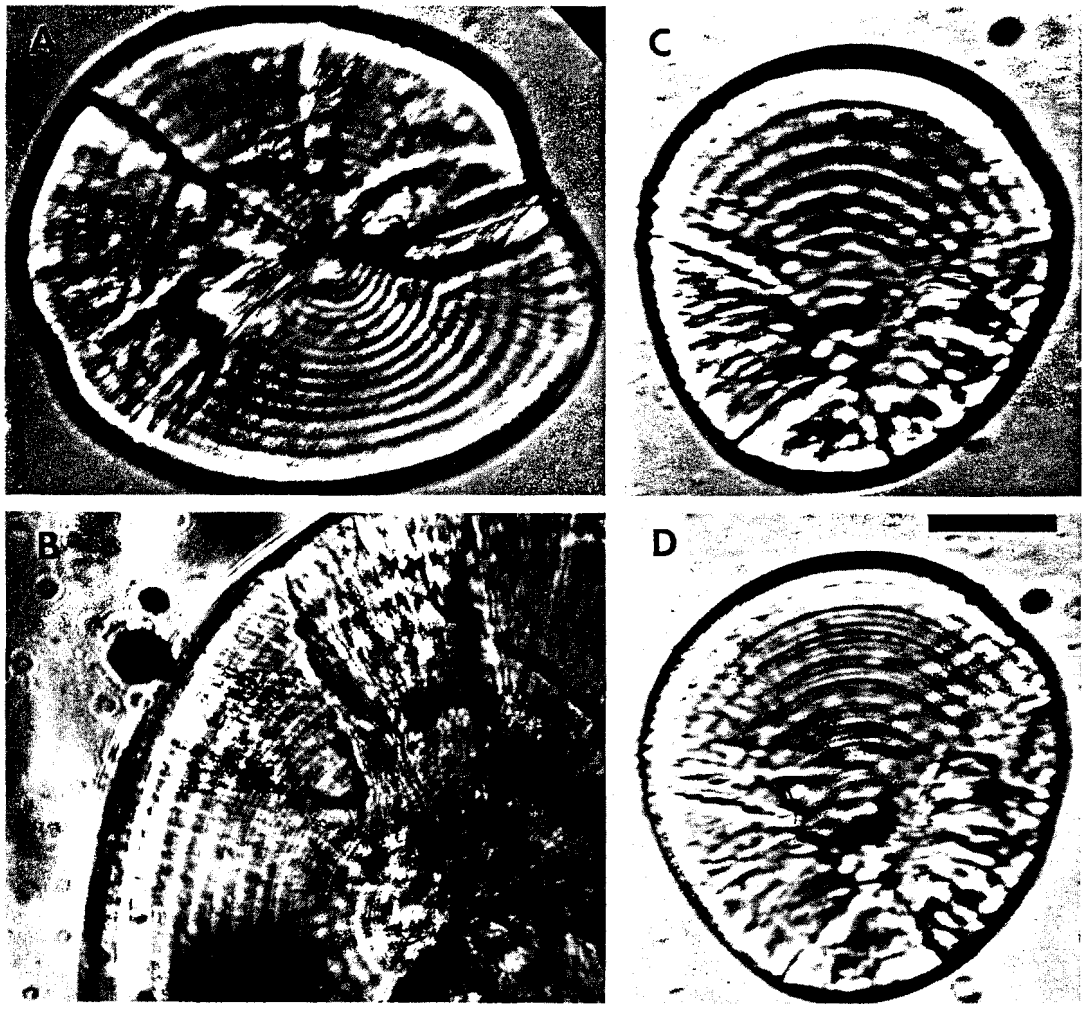

Fig. 1. *Halichoeres bivittatus.* (A) Sagitta of 11.4 mm standard length (SL) larva; (B) detail of same otolith at a different focal plane showing additional arrays of "sub-increments"; (C) lapillus of same larva with a single array of increments, and (D) at a different focal plane showing an additional array of "sub-increments". Scale bar = 58 μm for (A), 40 μm for (B), and 48 μm for (C) and (D)

crements on the same otolith is not unusual, both Panella (1980) and Brothers and McFarland (1981) mention the widespread existence of "subdaily" otolith increments. Despite this appellation there are, at present, no objective criteria for separating daily from subdaily increments on the otoliths of larval fishes.

In those species with more than one set of increments I used two criteria for deciding which array of increments was to be considered daily. The first criterion was based on the presumption that the largest repeating cycle of increment formation was daily. In other words, if, as the focus under the microscope was slowly changed, each increment gradually split into two, resulting in an array with exactly twice as many increments, I concluded that the fewer and larger increments were daily (this bifurcation phenomenon is a common feature of fish otoliths I have examined, division of increments into three or more increments is also common, Fig. 1). The basis for this presumption rests on the fact that otolith increments are thought to be the product of temperature, light, feeding, or activity cycles (or some combination thereof) influencing the metabolism of the fish (Panella, 1980). While there is some evidence of subdaily cycles of feeding and activity in fishes, for example vertical migration in planktonic larval fishes (Ahlstrom, 1959), there are, to my knowledge, no reports of supradaily cycles occurring on a two-, three-, or four-day cycle (the most common numbers of "sub-increments" within each of the increments in the higher-order array). Furthermore, the higher-order array (with fewer increments) was usually visible over more quadrants of the otolith and at wider planes of focus than the finer array of "sub-increments", which tended to appear on smaller sections of the otolith and at a single plane of focus. These "sub-increments" were typically found on otoliths with relatively wide higher-order increments. It may be, as Panella (1980) suggests, that these fine increments occur on all fish otoliths but are only detectable on fast-growing otoliths.

The second criterion, used when incremental marks of all kinds were unclear, was based on a principle of conformity. I presumed that since the basic appearance of sequences of increments is very similar between individuals

Table 1. Planktonic larval duration of 100 species of wrasses (family Labridae). CA: Caribbean; EP: tropical eastern Pacific; HA: Hawaii; NA: North Atlantic; PA: Palau (Western Pacific); SC: Southern California (temperate eastern Pacific)

Species	Site	*n*	Larval duration (d)			
			mean	SD	min	max
Anampses chrysocephalus	HA	4	29.5	1.7	28	31
A. cuvier[a]	HA	2	44.5	10.6	37	52
A. twistii	PA	4	28.8	6.5	23	38
Bodianus axillaris[d, g]	PA	4	23.5	4.4	18	28
B. bilunulatus[a]	HA	10	66.8	9.3	52	78
B. diplotaenia[d, g]	EP	10	39.5	4.1	32	48
B. mesothorax[c, d, g]	PA	3	30.3	4.0	26	34
B. rufus[a, g]	CA	10	41.6	6.5	32	51
Cheilinus bimaculatus	HA	3	54.3	4.9	51	60
C. bimaculatus[b]	PA	10	46.7	3.9	41	52
C. chlorourus	PA	8	27.1	1.7	25	30
C. digrammus	PA	10	26.1	4.3	21	36
C. fasciatus	PA	7	25.7	1.4	24	27
C. trilobatus	PA	8	29.6	3.2	26	36
C. undulatus	PA	3	34.3	5.5	29	40
C. unifasciatus[g]	HA	10	36.2	3.3	31	42
Cheilio inermis[b]	PA	10	56.1	8.9	43	73
Choerodon anchorago[g]	PA	10	19.3	1.8	17	23
Cirrhilabrus cyanopleura[d]	PA	10	21.1	1.6	19	24
Clepticus parrae[a, g]	CA	10	38.5	4.7	35	49
Coris flavovittata	HA	2	53.0	1.4	52	54
C. gaimard[a]	HA	10	44.9	3.2	42	53
C. gaimard[a]	PA	9	41.1	5.0	36	52
C. variegata[d, f]	PA	10	22.0	2.1	19	25
C. venusta[a]	HA	10	46.1	4.2	40	50
Cymolutes lecluse[b, g]	HA	10	75.9	10.2	60	91
C. praetextatus[b, g]	PA	1	71.0	–	–	–
Diproctacanthus xanthurus[c, d, f, g]	PA	10	17.3	1.4	15	20
Doratonotus megalepis[d, g]	CA	10	21.9	1.5	20	24
Epibulus insidiator	PA	10	30.4	4.6	25	38
Gomphosus varius	HA	3	65.3	5.8	62	72
G. varius[a]	PA	9	51.8	6.4	42	60
Halichoeres argus[c, d]	PA	10	25.0	2.0	22	27
H. biocellatus[c, d]	PA	10	24.8	2.8	20	28
H. bivittatus[d]	CA	10	24.1	1.5	22	26
H. chierchiae[a]	EP	10	31.3	3.7	25	38
H. chloropterus[c, d, g]	PA	10	21.1	1.7	19	25
H. chrysus[c, d]	PA	10	26.1	1.9	23	29
H. dispilus[a]	EP	10	41.1	5.5	33	50
H. garnoti	CA	10	25.9	2.0	23	30
H. hortulanus[a, d]	PA	10	32.5	3.4	28	37
H. maculipinna	CA	10	25.8	2.6	22	29
H. margaritaceus[d]	PA	10	21.7	2.3	18	26
H. marginatus[d]	PA	10	22.2	1.8	20	25
H. melanurus[d]	PA	10	22.1	1.6	20	24
H. nebulosus[c, d]	PA	10	23.9	1.9	20	26
H. nicholsi[a]	EP	10	32.4	3.5	26	38
H. ornatissimus[a]	HA	10	39.5	6.5	33	56
H. pictus[d]	CA	10	24.9	2.2	22	28
H. poeyi[d]	CA	10	24.1	1.6	22	27
H. prosopeion[c, d, e]	PA	10	21.2	2.3	19	26
H. radiatus[d]	CA	10	24.9	2.6	22	31
H. richmondi[d]	PA	4	20.8	1.0	20	22
H. scapularis[d, f]	PA	10	24.4	1.9	21	28
H. semicinctus	SC	7	29.9	3.6	24	36
H. trimaculatus[a, d]	PA	10	26.8	4.0	21	32
Hemigymnus fasciatus[c, d, e, f, g]	PA	10	25.8	4.4	19	34
H. melapterus[c, d, e, f, g]	PA	10	23.9	3.3	20	29
Labrichthys unilineatus[d]	PA	10	19.2	2.0	17	24
Labroides bicolor[d]	PA	4	24.5	1.3	23	26
L. dimidiatus[c, d]	PA	10	20.3	1.9	18	24
L. pectoralis[a, d]	PA	10	26.8	4.2	22	31
L. phthirophagus	HA	10	32.1	3.5	27	38

Table 1 (continued)

Species	Site	*n*	Larval duration (d)			
			mean	SD	min	max
Labropsis micronesica[d, f, g]	PA	1	22.0	–	–	–
L. xanthonota[d, e, f, g]	PA	2	30.5	3.5	28	33
Lachnolaimus maximus[c, d, f, g]	CA	10	25.8	2.7	21	30
Macropharyngodon geoffroy[a]	HA	9	32.3	5.1	25	43
M. meleagris[a, d]	PA	10	25.0	4.8	20	36
M. negrosensis	PA	1	25.0	–	–	–
Novaculichthys taeniourus	HA	2	73.5	0.7	73	74
N. taeniourus[a]	PA	10	55.0	8.4	46	71
N. macrolepidotus[a]	PA	2	70.5	9.2	64	77
Oxyjulis californica[g]	SC	7	39.4	2.6	36	43
Pseudocheilinus evanidus[a]	HA	10	49.4	9.5	38	72
P. evanidus[c, d]	PA	10	35.6	4.2	31	42
P. hexataenia[a, d]	PA	10	35.0	6.8	26	46
P. octotaenia[a]	HA	10	47.7	5.1	38	55
P. octotaenia[d]	PA	4	35.5	2.1	33	38
P. tetrataenia[a]	HA	3	49.3	6.7	42	55
Pseudojulis melanotis[d, g]	EP	6	35.7	3.1	31	40
P. notospilus	EP	5	37.6	2.7	35	42
Pseudojuloides cerasinus	HA	10	42.4	5.0	35	52
Pteragogus cryptus	PA	3	20.6	1.5	19	22
P. flagellifera	PA	1	23.0	–	–	–
P. guttatus	PA	2	20.5	2.1	19	22
Semicossyphus pulcher[g]	SC	10	37.4	5.1	34	52
Stethojulis balteata	HA	10	42.1	4.4	35	48
S. bandanensis[d]	PA	10	26.4	3.6	22	32
S. strigiventer[d, g]	PA	10	23.4	2.2	20	28
Tautoga onitis[g]	NA	5	25.4	3.4	22	30
Tautogolabrus adspersus[g]	NA	5	28.4	2.5	25	32
Thalassoma amblycephalum[a]	PA	10	72.4	9.8	53	90
T. ballieui[a]	HA	10	84.0	19.1	65	121
T. bifasciatum[a]	CA	1 172	49.3	5.5	38	78
T. duperrey[a]	HA	10	89.2	11.3	75	114
T. hardwicke[a]	PA	10	47.0	8.0	39	63
T. janseni[a]	PA	10	63.3	12.1	50	85
T. lucasanum[a]	EP	10	74.3	10.6	62	94
T. lunare[a]	PA	10	46.8	6.3	39	55
T. lutescens hybrid?[h]	HA	1	78.0	–	–	–
T. quinquevittatum[a]	PA	10	56.4	7.9	46	68
T. trilobatum[a]	HA	10	78.3	12.3	60	99
Xyrichtys martinicensis[b, f, g]	CA	10	78.3	12.7	59	98
X. novacula[b]	CA	10	50.5	7.8	38	62
X. pavoninus	EP	1	57.0	–	–	–
X. pavoninus[b, g]	HA	2	72.5	6.4	68	77
X. splendens[b]	CA	8	103.9	8.9	85	114

[a] Occasional individuals with numerous additional narrow increments within larval period
[b] Increments at edge of larval period becoming increasingly narrow
[c] "Bifurcation" arrays prominent within larval period
[d] Finer "sub-increment" arrays prominent within larval period
[e] Difficult to distinguish which of multiple arrays to consider daily
[f] Increments within larval period occasionally unclear
[g] Settlement mark unclear
[h] Probable *T. lutescens* × *T. duperrey* hybrid

of a species characterized by clear increments, then, for species with less obvious otolith increments, one could use conclusions based on the clearest otoliths to help decide what to count as daily increments for those individuals with less distinct increments. It should be emphasized that this method was applied only in the small minority of cases in which increments were particularly unclear (see Table 1). In each of these cases, some of the specimens, especially newly-recruited juveniles, had clear otolith increments.

I made use of a similar conformity principle when one portion of an otolith had unclear increments or had more than one type of incremental mark and the higher-order array, usually considered daily, was sufficiently indistinct to cast doubt on its validity. In these difficult cases (accounting for only a small number of the species examined),

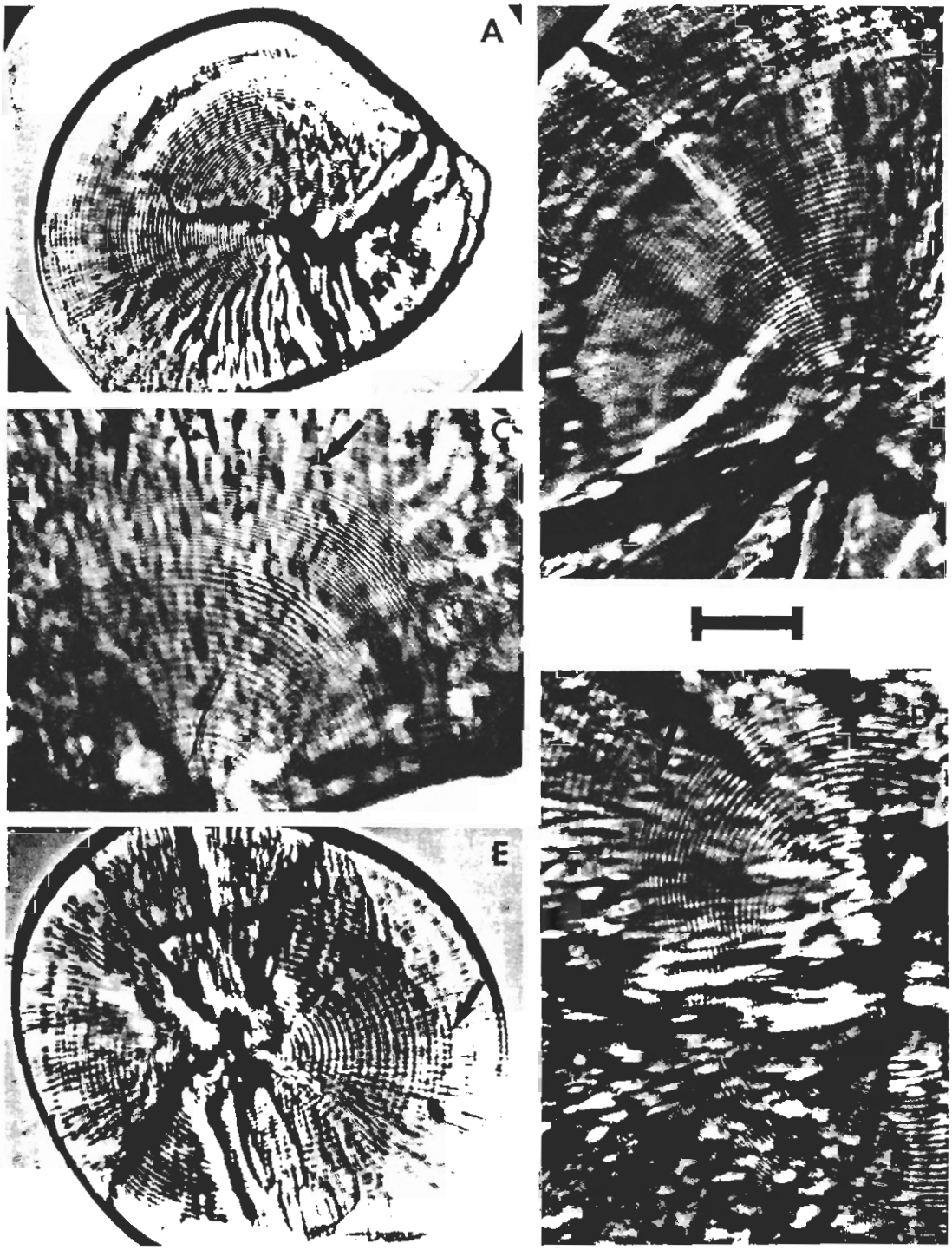

Fig. 2. (A) Lapillus of a 16.1 mm SL *Bodianus bilunulatus* from Hawaii, arrow indicates settlement transition; (B) sagitta of a 19.3 mm SL *Thalassoma trilobatum* from Hawaii; (C) sagitta of a 46.0 mm SL *Pseudocheilinus evanidus* from Hawaii, showing reduction in width of increments characteristic of individuals with particularly longer larval durations than their conspecifics; (D) sagitta of a 44.5 mm SL *Coris gaimard* from Hawaii; (E) sagitta of a newly-settled 12.1 mm SL *Halichoeres ornatissimus* from Hawaii. Scale bar = 80 μm for (A), 64 μm for (B), 66 μm for (C), 60 μm for (D), and 88 μm for (E)

I decided to count as daily those increments within the indistinct portion of the sequence that most resembled the adjacent clearer increments. This method was based on the observation that abrupt changes in the width and character of increments rarely occurred within increment sequences (other than in one easily identifiable situation discussed below).

The appearance of the otolith increments and the settlement mark seemed to be a conservative phylogenetic character. Congeners generally had similar and often distinctive-looking patterns of increments. The basic features that varied were the thickness of increments, the contrast between the dark line and the light line that make up each

increment, the shape of the incremental rings (whether circular, oval, or variously irregular), and the clarity and width of the settlement mark. For example, *Thalassoma* species' otolith increments were narrow and very distinctive, having relatively less contrast between the dark and light lines of each increment and an absence of any additional finer arrays of increments (Fig. 2 B). The increments of *Gomphosus varius,* a near relative, were indistinguishable from *Thalassoma* otolith increments. The otolith increments of *Pseudocheilinus* species had a lot of contrast and a very abrupt settlement mark. *Bodianus* species' otoliths typically had clear increments (Fig. 2 A) and, in most of the species, a very indistinct settlement mark. Geographic influences occasionally blurred these distinctions. For example, the numerous *Halichoeres* species from both the Caribbean and the western Pacific had particularly wide increments (Fig. 1), while the few *Halichoeres* species from Hawaii and the eastern Pacific had narrower increments more typical of other labrid genera (Fig. 2 E). *Coris* species' otoliths typically had very clear increments and settlement marks (Fig. 2 D), with the exception of *C. variegata* which had both unclear increments and an indistinct settlement mark.

Occasional individuals of many labrid species had an abrupt reduction in the width of the increments near the end of the planktonic larval period (Fig. 2 C, see Table 1). This transition always occurred after a typical sequence of increments. In most cases, the initial sequence of typical increments matched in both number and appearance the total sequence of larval increments for most other individuals in the sample. On some individuals, the number of narrow increments almost exceeded the number of typical increments before the transition. A related feature was characteristic of most of the individuals of the razorfish genus *Xyrichtys* and of two other wrasse genera, *Cheilio inermis* and *Cymolutes* spp. (see footnotes to Table 1). In these fishes, the increments at the end of the planktonic larval period become progressively finer until they fade into the settlement mark, making it difficult to decide the upper limit on the number of these increments. In comparison, the increments after the settlement mark are extremely wide. Since there are no abrupt changes in the appearance of these increments, and no alternative arrays of wider increments, these very fine increments were counted as daily.

Planktonic larval durations

The planktonic larval durations of the labrid fishes examined ranged from 15 d in *Diproctacanthus xanthurus* to 121 d in a specimen of *Thalassoma ballieui* (Table 1). Despite the small sample sizes, pronounced intraspecific variability in larval duration was more the rule than the exception, with most species having a difference of weeks between the shortest and longest durations in the sample. Species with longer durations tend to exhibit proportionally higher variance than those with shorter durations. In many species, even some with relatively short larval lives, one or two specimens out of the sample had distinctly longer durations. These individuals often had larval durations almost twice as long as their conspecifics with shorter larval lives.

Larval durations tend to be similar between species in a genus, especially from the same geographical area. *Thalassoma* species and the razorfishes (*Novaculichthys* spp., *Cymolutes* spp., and *Xyrichtys* spp.) always have long larval durations, typically over two months. Larval lives of medium length, about six weeks, are characteristic of the genus *Pseudocheilinus* and the genus *Coris* (one exception is *C. variegata,* which has a short larval duration). The

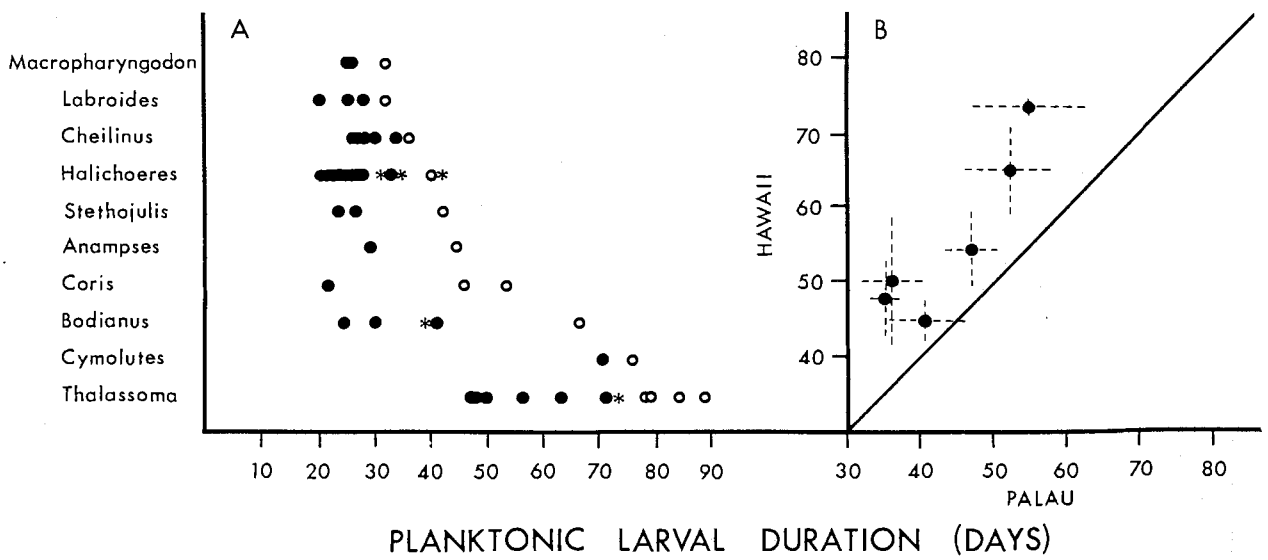

Fig. 3. (A) Mean planktonic larval durations of ten genera of wrasses (other statistics included in Table 1) ●: Caribbean and Western Pacific species; *: Eastern Pacific species; ○: Hawaiian species; species collected both in Hawaii and at other sites are not included. (B) Comparison of planktonic larval durations of Western Pacific and Hawaiian populations for the six species collected at both sites ($\bar{x} \pm SD$) (Table 1); continuous line represents equal larval durations at the two sites

genera *Cheilinus, Halichoeres, Macropharyngodon, Pteragogus,* and a number of other labrid genera have short larval lives, usually less than one month. Two notable exceptions to this pattern are *Cheilinus bimaculatus* and the Hawaiian and eastern Pacific *Halichoeres* species, which have distinctly longer larval lives.

Labrid species native to Hawaii and the eastern Pacific have longer larval lives than their Caribbean or western Pacific congeners (Fig. 3 A). This marked geographic effect is clearly evident within species as well. An analysis of variance indicated that the Hawaiian populations of six wide-ranging wrasse species have consistently and significantly longer larval durations than their conspecifics from the western Pacific ($p < 0.0001$, Fig. 3 B).

Discussion

Planktonic larval durations

The range of planktonic larval durations exhibited by labrid fishes encompasses the entire range of larval durations previously reported for reef fishes (Sale, 1980; Brothers *et al.,* 1983). Perhaps the most notable feature of labrid larval durations is the variability within many species. This flexibility may be a product of a life history dominated by the wide dispersal of pelagic propagules and an extremely patchy availability of habitat. In this situation it would be advantageous to avoid a rigorously programmed schedule for metamorphosis, since it would be unlikely that a planktonic larva would be near a reef at any specific time. The observation that species with longer larval durations have proportionally greater variance in larval duration supports this hypothesis, since these species would be more likely to have dispersed far from their source and therefore would need longer waiting periods before encountering a reef. Indeed, labrid larvae in Hawaii (all of whom have long larval lives), are found well offshore, in contrast to some other reef fishes whose larvae are concentrated in nearshore waters (Leis and Miller, 1976). Leis (1983) found *Thalassoma* spp. larvae (a genus characterized by long larval durations) in the East Pacific Barrier, many hundreds of kilometers from the nearest coral reefs. Species with very short larval lives may be able to complete their development in nearshore waters and thus tend to settle without much delay. This explanation is somewhat akin to the model proposed for marine invertebrate larvae by Jackson and Strathmann (1981).

Geographical variation in larval duration seems to influence all labrid groups similarly. Both the short-duration *Halichoeres* genus and the long-duration *Thalassoma* genus have longer larval lives in the eastern Pacific and their longest larval lives in Hawaii. Larval duration does not appear to respond inversely to the degree of isolation of a species (as might be expected if planktonic larvae were at risk of being washed away from their native habitat), since Hawaiian endemics, who would be most prone to such losses, have, nevertheless, especially long larval lives. Increased productivity in the ocean does not seem to reduce the larval duration either. Labrids from the highly productive eastern Pacific region tend to have distinctly longer larval durations than their Caribbean or western Pacific counterparts. It is probable that the geographical variation in larval duration is a product of physical factors operating in the plankton. Whether these factors are local phenomena or basic regional differences (such as water temperature) remains to be answered. It should be emphasized that nothing can be inferred about larval growth rates from data on lengths of larval life until the size at settlement for each species is known. Species with longer larval lives need not be growing slower; if they settle at significantly larger sizes it is certainly possible that their rates of growth may be even higher than those species with short larval lives.

The finding that distinctive suites of larval otolith-increment characteristics are unique to certain genera, or even species, of wrasses should greatly facilitate the identification of larvae. It is, at present, difficult to identify many wild-caught reef-fish larvae, especially those taxa that share meristic characters. Brothers (1984) has discussed several larval otolith features that distinguish certain families of reef fishes. It is likely that most planktonic reef-fish larvae will eventually be identifiable, at least to genus, on the basis of internal otolith characters. For studies such as these, larvae should be fixed and preserved in ethanol rather than formalin, since formalin will dissolve or render opaque the otoliths of fishes.

The presence of multiple arrays of incremental marks on the otoliths of some larval fishes makes it difficult to conclude with certainty that otolith increment counts directly reflect the duration of the larval stage. My observations of the otolith increments of many tropical larval fishes indicate that wrasses have some of the clearest otolith increments and settlement marks found among reef-fish larvae. The otoliths of many other reef-fish families have multiple arrays of increments that are sufficiently prominent to confound any observer and often display no consistent mark that could correspond to settlement. Schmitt (1984) has demonstrated that daily increments are laid down on the otoliths of some tropical fish larvae in captivity. Although the plankton is by nature a particularly difficult place to perform experiments, it is clearly necessary to demonstrate experimentally the meaning of the incremental marks on the otoliths of larval fishes in the field.

Larval dispersal and biogeography

The most intriguing application of information on the duration of the larval stage of coral-reef fishes is to the biogeography of this uncommonly diverse assemblage. It is, however, important to consider the complexities of this question before simply trying to correlate average larval life with range. The finding that some species with short larval lives have wide ranges while the species with the longest recorded larval duration for any tropical fish

(*Thalassoma ballieui*) is endemic to Hawaii, should indicate that there are no simple answers.

One important point is that the mean or modal larval duration for a species is irrelevant to biogeographical questions. Distant areas are colonized by those individuals that have remained planktonic for extended periods. The importance of this fact is underscored by the observation that occasional individuals of certain species have spent almost twice as long in the plankton as many of their counterparts. Since my samples were relatively small (usually ten), these individuals could account for a significant fraction of the population. Clearly, the maximum larval duration evident within one's samples would be the better estimate of the capability of a species for long-distance dispersal. A corollary of this principle is that very small samples will usually miss these individuals and thus provide only an estimate of the mean larval duration.

Another, perhaps even more important, factor is geographical variation in larval duration. Since members of the same species in different places can have different larval durations, one cannot infer the dispersal ability of a species from a collection from a single site. For example, if one was to compare the larval durations of a wide-ranging species collected in Hawaii with a species endemic to the western Pacific, one would find that the wide-ranging species had a significantly longer larval period (probably fulfilling one's expectations). However, it may well be that the western Pacific populations of the wide-ranging species have a larval duration no different to the endemic, since fishes captured in Hawaii consistently have longer larval durations. Even if dispersal ability is determining the range of a species, that range will be a product of many independent colonization events in different regions, for which the critical data are the larval durations of the probable source population and the degree of isolation of the target area.

These results dictate a more refined protocol for studies testing the role of larval dispersal ability in the biogeography of reef fishes. It is necessary to first identify the likely source populations of an area under study (by major current flows or by inference from diversity clines), and then collect large samples of specimens in order to determine the capability of each species for long-distance larval dispersal. In this way, it should be possible to discover whether the many diverse patterns of reef-fish distributions are simply a product of their dispersal abilities or a response to other unrelated factors, such as habitat suitability, competitive interactions, or even purely chance events.

There are some indications from this preliminary data base that dispersal ability might be important in determining species ranges. Almost all of the labrid taxa from Palau with very short larval lives (*Labrichthys unilineatus, Chaerodon anchorago, Diproctacanthus xanthurus,* some *Halichoeres* species, and *Pteragogus* species) have relatively restricted ranges. On the other hand, most of the Palauan wrasses with long larval lives have very extensive ranges and many are found in Hawaii as well (e.g. *Cheilinus bimaculatus, Cheilio inermis, Coris gaimard, Gomphosus varius, Novaculichthys taeniourus,* and *Thalassoma quinquevittatum*). Furthermore, the three Indo-Pacific labrids whose ranges extend as far as the eastern Pacific shoreline all have particularly long larval lives (*Novaculichthys taeniourus, Thalassoma lutescens,* and *Xyrichtys pavoninus*). The majority of labrid species, however, lie between these extremes and display a great variety of distributional patterns, many of which have not yet been thoroughly documented. Progress on an explanation for these patterns must await more detailed information on the ranges of species and the duration of their larval lives.

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