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Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia

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Abstract

The length of larval life in some coral reef fishes was estimated from the number of growth increments in the otoliths of newly settled fishes. We examined 210 individuals comprising 38 species and 5 unidentified taxa, and belonging to 12 families. During 2 successive austral summers (1976–1977 and 1978–1979), specimens were collected from the lagoon at One Tree Reef, Great Barrier Reef, Australia. By assuming that growth increments in otoliths are laid down on a regular daily cycle commencing near the time of hatching, we calculated typical ages ranging from 3 to 6 wk with a minimum of just over 2 wk and a maximum of 12 wk. The otoliths also contain distinctive microstructural features which can serve as approximate temporal markers for the change from the postlarval to juvenile life stage.

Introduction

Most coral reef fishes have a pelagic larval phase (Breder and Rosen, 1966; Leis and Miller, 1976; Sale, 1980). After a period as short as a day or perhaps as long as a year, larvae descend to the reef, ending the pelagic phase, and become relatively site-attached juveniles (the term "recruitment" in the present paper refers to this event). Extensive dispersal is possible during the larval phase (Williams *et al.*, unpublished data) and mortality suffered during larval life is probably a major determinant of the abundance of adult reef fishes (Johannes, 1980; Doherty, 1982). Despite the importance of the pelagic larval life in the dynamics of populations of reef fishes, our understanding of larval ecology is very limited. Knowledge of the duration of the larval phase is a basic requirement for any studies of larval ecology. Estimates of this length of time are presently available for only a few species (references in Johannes, 1980; see also: Brothers and McFarland, 1981; Victor, 1982; Brothers and Thresher, unpublished data).

The relatively recent observation of daily growth increments in the otoliths of tropical fishes, apparently laid down from a very early stage in development, provides a powerful tool for estimating the duration of larval life (e.g. Brothers *et al.*, 1976; Pannella, 1980; Brothers and McFarland, 1981). In the present paper, we examine the duration of larval life in a wide range of species of coral reef fishes, as determined from the number of daily growth increments in the otoliths of newly recruited fishes.

Materials and methods

All fishes were collected from the lagoon of One Tree Reef on the Great Barrier Reef (23°30′S; 152°06′E). Those examined here are a subsample of two separate collections made during periods of maximum recruitment during the summers of 1976–1977 and 1978–1979. In the first instance, all fish present on 16 small, isolated, colonies of the coral *Seriatopora histrix* and 16 similar colonies of *Acropora formosa* were collected daily from 12 January to 14 February 1977). These collections were made as part of a separate study of spatial and temporal patterns of recruitment of reef fishes (Williams and Sale, 1981). For the second series of specimens, similar daily collections of all juveniles present on a series of patch reefs were made in February 1979. Recruitment was particularly heavy at the start of this period (Williams, in press), and between 30 January and 4 February some pomacentrids were not collected when first sighted, but left *in situ* for up to 6 d. Low density of recruits of these species makes it very likely that a fish collected at a given site was the same fish observed at recruitment up to 6 d earlier.

Fishes were anesthetized with quinaldine and collected in fine-mesh hand-nets. On at least 10 occasions coral colonies were re-sampled within 12 h. This confirmed that over 95% of fishes were collected in the first sampling. The vast majority of fishes comprised new recruits, recogniz-

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able by a combination of their size, behavior and degree of pigmentation. If we had any doubt that a particular individual had not recruited from the plankton during the 24 h prior to collection, we discarded it from the sample of fish to be aged.

Samples were fixed and preserved in 70% ethanol. After identification, the fish were measured (nearest 0.1 mm, standard length) and the otoliths were removed (sagittae and lapilli). Handling and preparation of the otoliths followed the procedures described in Brothers *et al.* (1976) and Brothers and McFarland (1981). The polarized light source and video-microscope system employed was critical in enhancing image quality. Both sagittae and lapilli were examined at 1 536× or 2 790× and counts were compared (the highest counts were used where there was a difference between otolith types). Lapilli were generally more easily read and gave consistent results for most species. However, sagittae were preferred for certain groups, such as gobies, labrids, and scarids.

In many specimens transitions or breakpoints in microstructure could be resolved near the otolith margin (e.g. Brothers and McFarland, 1981; Victor, 1982; Brothers and Thresher, unpublished data). Different criteria were used for different species and otoliths; for example, in labrid and scarid sagittae the transition was marked by the abrupt appearance of wider and fainter growth increments, whereas in pomacentrid lapilli the transition was marked by narrower increments. Transitions were often difficult to define, and could only be resolved when they were at least 3 or 4 increments away from the margin. If transitions were at or very close to the margin, their subtle nature would generally cause them to remain unnoticed. Questionable transitions were not tallied, and only total counts were recorded.

Results

Otoliths of 210 newly-settled individuals comprising 38 species and 5 unidentified taxa, and belonging to 12 families were examined. We assumed that growth increments on otoliths are laid down on a regular daily cycle commencing near the time of hatching. Typical ages ranged from 3 to 6 wk, with a minimum of just over 2 wk and a maximum of about 12 wk (Table 1).

Ages within families tended to be relatively consistent, but there were some notable exceptions. The mean age of 11 species of pomacentrid ranged only from 21 to 24 d (*Pomacentrus australis* was an apparent exception: see "Discussion") and the mean age of 4 species of apogonid ranged from 18 to 23 d. Newly settled juveniles of the labrid *Thalassoma lunare,* however (mean of 55 d), were twice the age of the other labrids examined (means of 25 to 30 d), and the 3 species of chaetodontids ranged in mean age from 26 to 39 d. For those taxa where data are available, there was no significant difference in mean age between the two austral summers of collection.

The ages of individuals within a given species differed by as little as a day or two in some species but up to 22 d in others. The data are too limited, however, to make any general statements about the potential ranges of duration of larval life in these fishes.

Otoliths of some fishes had distinct transitions in increment spacing and optical density. Ages determined from pre-transition counts were generally 4 or 5 d shorter than ages based on total counts (Table 1). However, in some species, pre-transition counts were markedly lower than mean total counts: the difference was 6 d for *Thalassoma lunare,* 7 d for *Halichoeres hoeveni,* 6 or 7 d in the scarids, 10 d in *Naso* sp., 12 d in *Petroscirtes mitratus,* 14 d in *Paragobiodon melanosoma,* and 50 d in *Pomacentrus australis.*

In the pomacentrids, at least, the transition is not clearly associated with the time of permanent recruitment and metamorphosis (gaining of juvenile colouration). Particularly high recruitment of several species of pomacentrids occurred from 29 January to 3 February 1979 (Williams, in press). Dates of settlement were recorded for 63 individuals recruiting during this 5 d period, but the fish were not collected until February 4, 1979. If the

Table 1. Length of larval life (in days) as indicated by total count of otolith increments and count of increments prior to the first transition in otolith growth, with mean total length of individuals. Mean counts and lengths are shown ± standard error. *N* = number of individuals examined. SL = standard length

Species	Otolith increments						Mean fish SL
	Total counts			Pre-transition counts[a]			
	N	range (d)	mean (d)	*N*	range (d)	mean (d)	(mm)
Apogonidae							
Apogon cyanosoma[a]	5	18–19	18.2±0.2	0	–	–	10.3±0.1
A. doederlieni[b]	5	16–27	22.6±1.9	0	–	–	11.9±0.4
Cheilodipterus quinquelineata[b]	29	17–29	23.1±0.5	0	–	–	10.5±0.2
Unidentified apogonid	2	19, 19	19	0	–	–	8.7±0.3
Blenniidae							
Petroscirtes fallax	1	–	21[c]	0	–	–	
P. mitratus	2	24–25	24.5	2	12, 12	12	8.0±0.3

(continued overleaf)

Table 1 (continued)

Species	Otolith increments						Mean fish SL
	Total counts			Pre-transition counts[a]			
	N	range (d)	mean (d)	*N*	range (d)	mean (d)	(mm)
Acanthuridae							
Naso sp.	1	–	84	1	–	74	30.6
Chaetodontidae							
Chaetodon plebius	1	–	39	0	–	–	9.9
C. rainfordi	1	–	35	0	–	–	11.0
Chelmon rostratus	2	25–26	25.5±0.4	0	–	–	14.7±1.5
Gobiidae							
Amblygobius rainfordi	4	40–41	40.3±0.3	0	–	–	14.4±0.2
Gobiodon sp. a[b]	1	–	22[c]	0	–	–	5.0
Gobiodon sp. b[b]	4	27[c]–38[c]	29.8	0	–	–	5.5
Gobiodon sp. c	1	–	40[c]	0	–	–	7.2
Paragobiodon echinocephalus	1	–	36	0	–	–	4.8
P. lacunicola	1	–	31	0	–	–	5.2
P. melanosoma	3	39–47	42.3±2.4	1	–	28	6.3±0.5
Unidentified gobiids	2	31–41	36 ±5.0	0	–	–	9.4±0.7
Labridae							
Cirrhilabrus temminki	2	26–30	28.0–2.0	1	–	24	7.8±0.3
Coris variegata[b]	1	–	28	0	–	–	6.2
Coris variegata	2	28–33	30.5±2.5	1	–	26	9.1±0.4
Halichoeres hoeveni	2	27–28	27.5±0.5	1	–	21	9.3±1.1
Labroides dimidiatus	2	26, 26	26	2	22–23	22.5	10.2±0.5
Stethojulis ? sp.	1	–	26	1	–	23	6.8
Thalassoma lunare	3	53–56	54.7±0.9	3	47–50	48.5	11.0±0.2
Unidentified labrids	4	21–29	25.3±1.7	2	21–23	22	6.5±0.6
Lethrinidae							
Lethrinus nebulosus	1	–	37	0	–	–	19.1
Lutjanidae							
Unidentified lutjanids	2	25, 25	25	0	–	–	16.3±0.1
Monacanthidae							
Monacanthus chinensis[b]	1	–	20	0	–	–	16.2
Paraluteres prionurus[b]	1	–	28	0	–	–	11.9
Nemipteridae							
Scolopsis dubiosus[b]	3	15–24	19.0±1.5	0	–	–	14.7±0.3
Pomacentridae							
Abudefduf saxatilis	1	–	23	0	–	–	10.4
Chromis sp.	3	20–26	23.7±1.8	1	–	19	8.3±0.4
Dischistodus pseudochrysopoecilus	1	–	23	0	–	–	10.0
Dascyllus aruanus[b]	5	20–28	24.4±1.6	2	20, 20	20	7.0±0.2
Dascyllus aruanus	1	–	22	0	–	–	7.5
Glyphidodontops rollandi	6	23–24	23.3±0.5	3	19–20	19.7	10.9±0.5
G. talboti	1	–	22	0	–	–	9.9
Neopomacentrus azysron[b]	1	–	24	0	–	–	13.9
Pomacentrus sp.[b]	5	22–25	23.0±0.9	0	–	–	13.6±0.7
Pomacentrus sp.	15	23–24	22.9±0.2	0	–	–	14.2±0.2
P. amboinensis[b]	8	17–26	21.0±1.1	0	–	–	12.0±0.3
P. amboinensis	16	23–24	23.4±0.1	8	19–20	19.7	12.5±0.1
P. australis	6	63–85	75.0±4.5	4	23–26	25	22.8±0.8
P. popei	14	22–26	23.5±1.3	10	18–20	19.1	11.9±0.2
P. wardi	12	23–25	24.3±0.2	8	19–20	19.9	14.3±0.2
Scaridae							
Unidentified scarids	20	34–53	41.3±1.7	19	30–45	36.8	7.8±0.1
Unidentified scarids	4	42–58	48±3.8	4	34–50	41	8.4±0.1

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[a] Pre-transition counts shown only for individuals which showed a transition

[b] Species collected in 1976–1977, all others collected in 1978–1979

[c] Otolith edge slightly eroded due to poor preservation

otolith transition were directly associated with the time of settlement, there should be a significant positive correlation between the number of days from settlement to collection and the number of post-transition growth rings. However, while many of these individuals showed a transition when their otoliths were examined, some did not. No *Pomacentrus* species (Allen, 1975, p. 214) showed any evidence of a transition even 4 d after settlement and 12 *P. popei, P. amboinensis* and *P. wardi* also as old as 4 d post-settlement showed no evidence of a transition. When those fish lacking a transition are excluded from the analysis, there is still no significant correlation between the time since settlement and the number of rings post-transition for the 3 species pooled ($N=27$, $r^2=0.08$), or tested separately.

Discussion

The accuracy of our estimated lengths of larval life are dependent on the extent to which daily growth increments reflect the age of the fish and on the assumption that the fish collected are indeed only newly settled.

Daily growth increments are evidently present in the otoliths of all bony fishes, at least during the early life history (Brothers, 1982). Formation of increments may begin from as early as the pre-hatching "embryonic" phase, or as late as yolk absorption, depending upon the species. The time of initiation of daily increments is not known in the species studied. A few tropical pomacentrids with egg sizes and incubation periods similar to the species studied here initiate lapillar increment formation at hatching or one to two days following (Brothers, unpublished data). There may be some ill-defined increments produced before a "hatching" mark, however these are distinctive and were not tallied in our study. Pomacentrids and other demersal spawning species such as apogonids, blenniids and gobiids, some of which may brood for up to 10 d, are expected to start increment formation within a few days around hatching (species with particularly long pre-hatching development periods may start before hatching). Thus our counts could over- or underestimate the length of larval life for these fishes, depending upon the exact timing of growth-increment initiation. Given our current knowledge of the development patterns of these fishes (Thresher, in press) we feel that when errors exist, they are unlikely to exceed 5 d. For fishes with pelagic eggs (the remainder of the species examined), distinct growth increments first form at hatching or just thereafter. Our counts must underestimate the duration of their pelagic life by at least 2 d, and perhaps as much as 5 or 6 d.

Direct validation of the correct identification of daily growth increments was not carried out for the species in the present study, but the similarity of our results to independent estimates of length of larval life in certain species gives us confidence in our identification. By comparing time of the spawning and the recruitment season, Randall (1961) estimated a larval life of about 8 wk in the acanthurid *Acanthurus triostegus.* Our count of otolith increments in the only acanthurid collected (*Naso* sp.) suggest an age of about 11 or 12 wk. Pre-transition counts in a variety of acanthurid species all indicate presumed larval lives of 6 to 12 wk (Brothers, unpublished data). Several authors have indicated larval durations of several weeks for pomacentrids, as did our counts (Allen, 1975; May, 1967, cited in Johannes, 1980; Russell, 1971). Direct comparison of the age of laboratory-reared Atlantic pomacanthids and pomacentrids with otolith ages confirms the daily periodicity of growth increments in at least 3 species (Brothers, unpublished data). Further evidence in support of our assumption of daily increment formation in reef fishes is given in Brothers and McFarland (1981), Victor (1982), and Brothers and Thresher (unpublished data).

The ecological significance of the breakpoint or transition in otolith growth is not entirely clear. Similar transitions in otoliths of other species have been attributed to changes in growth associated with changes in the fish's environment and/or life history, such as the time of recruitment (Brothers 1981; Brothers and McFarland, 1981). Our data for pomacentrids, however, show no obvious direct correlation between the otolith breakpoint and time of recruitment. This may result mostly from the difficulty of discriminating a transition when it is near the otolith margin. Depending on the species, such transitions were (1) conspicuous for all individuals, (2) conspicuous for only about half the individuals, or (3) absent entirely.

The otolith breakpoint, when it does occur, could coincide with the end of a truly pelagic existence and arrival in the reef environment, or with an associated change in food availability rather than time of settlement. If so, this otolith transition may only be generally associated with settlement. Larval ponmacentrids have been observed to descend to the surface of a patch reef, "explore" a few small holes and then swim back up into the water column (Williams, 1980). Variable post-transitional counts in newly settled fish may represent varying periods of habitat selection among individuals. We cannot exclude the unlikely possibility of a temporary hiatus in increment formation around the time of settlement. Rather it appears that in some species the otolith transition may be more of an indication of the morphological changes which precede or accompany settlement, rather than a direct result of the ecological shift. The data here and in other studies (Victor, 1982; Brothers, unpublished data) indicate that the timing of the otolith transition relative to settlement is somewhat variable among species and perhaps among individuals.

The large size of "recruited" individuals of *Pomacentrus australis* examined in this study is an enigma. Recruitment of large numbers of these fish occurred throughout "One Tree Lagoon" at the same time as the particularly heavy settlement of other pomacentrids (29 January to 3 February 1979). Although *P. australis* generally settles at a size similar to other pomacentrids and is just as site-attached (Williams, 1979), all the "recruited" specimens of this fish in our study were as large as normal *P. australis* at 10 wk (consistent with the total count of 63 to 85 increments) and generally had suffered considerable fin and scale abrasion. The simplest explanation is that they had recruited earlier to a habitat other than the lagoon and their arrival within the lagoon was a post-recruitment migration. However, the sudden appearance of a large number of individuals (the greatest recruitment in 4 yr) at the same time as other species settled is a remarkable coincidence and such an extensive postsettlement migration of a pomacentrid would be unusual. Extensive movements of small juvenile *Acanthochromis polyacanthus* are known, and they probably occur in *Pomacentrus coelestus* as well (Thresher, personal communication). Robertson (1982) has also described off-reef emigration in a labrid, *Epibulus insidiator.* An alternative explanation for our observation on *P. australis* is that these fish are pelagic for approximately 75 d, and thus the otolith breakpoint is associated with neither time of settlement nor arrival in the reef environment. Another, least likely, explanation is that the larvae were in the reef environment for 50 d or so before settling.

The most surprising of our results is perhaps the relatively short larval life in the few chaetodontids examined and the relatively long duration in the gobiids. Chaetodontids, like acanthurids, have a highly specialized larval form (the tholichthys and acronurus respectively; see Thresher, in press), thought to be associated with a pelagic life of long duration (Leis and Miller, 1976; Ralston, 1975 cited in Johannes, 1980). The 25 to 26 d larval life of *Chelmon rostratus* is certainly not exceptionally long, although it agrees with pre-transition counts for two adult *C. rostratus* (26 and 28). However, estimates of 39 and 35 d, respectively, for *Chaetodon plebius* and *C. rainfordi* are moderately low and similar to those of the unspecialized scarid larvae. Pre-transition counts for 15 other Indo-Pacific butterfly fishes ranged from about 25 to over 80 d (Brothers and Thresher, unpublished data).

The *Gobiodon* spp. and *Paragobiodon* spp. examined by us are very small fish, presumably with a low fecundity relative to the other species considered and, given the small, apparently unspecialized pre-juveniles, one might expect a correspondingly short larval life. Instead, our estimates are in the order of 30 to 40 d. It is possible that the fish are so small at settlement that we missed them and those collected were not recently settled. However, we believe this possibility is unlikely, since the specimens collected were relatively small (Table 1), and relatively large numbers were caught (Williams and Sale, 1981). Data on gobiids from the western Atlantic (Brothers, unpublished data) indicate that some have a larval life duration as long or longer than these Pacific species, while certain species have apparent durations less than 3 wk. In general, there is a fair amount of intraspecific variability as well.

The exceptionally long larval life of *Thalassoma* spp. compared to other labrids is worthy of further study. *T. lunare* is not exceptional in the genus, with similar lengths of larval life estimated for *T. hardwicki* from the Philippines and *T. bifasciatum* from the Caribbean (Victor, 1982; Brothers, unpublished data). Brothers and Thresher (in preparation) have compiled comparative data for a wide variety of western Pacific and western Atlantic labrids, pomacentrids, apogonids, and pomacanthids. Based on the still rather limited data available, it is clear that coral-reef fishes show a diversity of patterns with regard to the duration of the larval stage. Some distinctions may be made at the family, genus, or species level, however there is certainly considerable variability within taxa. At the species level, some forms appear to have a relatively fixed duration, while others are much more plastic. The significance of these differences are not understood.

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