

LARVAL BROODING IN THE MARINE DAMSELFISH *ACANTHOCHROMIS POLYACANTHUS* (POMACENTRIDAE) IS CORRELATED WITH HIGHLY DIVERGENT MORPHOLOGY, ONTOGENY AND LIFE-HISTORY TRAITS

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ABSTRACT

The unusual life-history mode of the coral-reef damselfish *Acanthochromis polyacanthus* is rare in the marine environment and especially remarkable because it lacks a dispersive pelagic larval stage. Other highly divergent morphological, ontogenetic, behavioral, and life-history traits in this species provide comparative evidence for hypotheses about the requirements for survival of very young fish on the reef. The following correlates observed in *Acanthochromis* diverge significantly from the norm within the pomacentrid family and are concurrent with non-pelagic larvae: very large eggs (for a tropical damselfish); extended egg-stage duration; a mid-day hatching time; slow early embryonic development; much delayed skeletal ossification; large and well-developed hatchlings with fully formed caudal fins; no scales at hatch/settlement; a distinctly high and variable number of vertebrae; very extended and intense biparental care; unusual parent-juvenile interactions such as glancing; and selection of mates of extremely similar size and color. Furthermore, differences among disparate Great Barrier Reef populations of *Acanthochromis* in major life history traits, such as egg-clutch size, age at maturity, size at fledging, and mode of post-brooding dispersal, are suggested by the available data.

One of the conspicuous characteristics uniting the large majority of marine organisms is a life-history strategy involving high fecundity and a dispersive pelagic larval stage. The life history of the brooding damselfish, *Acanthochromis polyacanthus*, is therefore remarkable because it lacks a dispersive pelagic larval stage and instead broods its young on the coral reef for months. This qualitative difference in life history, along with other features of the species, makes *A. polyacanthus* a unique and valuable study system. The species gives the rare opportunity to obtain comparative evidence for the plethora of untested adaptive hypotheses about coral-reef fish life histories (Barlow, 1981; Shapiro et al, 1988; Hixon, 1991; Robertson, 1991). Furthermore, because its early life stages are non-dispersive and site-attached, several studies have used *Acanthochromis* (a monospecific genus) as a model species for ecological research on local-scale coral-reef fish dynamics (Thresher 1983, 1985a,b; Connell 1996). Despite this reasonably high profile, its abundance in numerous habitats, its widespread distribution along the Indo-Australian Archipelago, and the relative accessibility of all life stages, surprisingly little information is available about its ontogeny and about important segments of its life cycle. This is particularly remiss in this species, since its early stages are potentially informative about the requirements of early life on the reef as opposed to the open ocean. Furthermore, since many morphological and behavioral characteristics show a range of variability within the large (>300 spp.) pomacentrid family (Allen, 1975; Leis and Rennis, 1983; Thresher, 1984; Kavanagh et al., in press), these data are potentially useful in systematic analyses.

Over the past two decades, several studies have focused on aspects of the reproductive behavior of *Acanthochromis*, site-specific demography at One Tree Island on the south-

ern Great Barrier Reef, Australia, and population genetics along the Great Barrier Reef. Information about the life history of the species can be extracted from these studies, and these are briefly summarized below.

Acanthochromis is sexually monomorphic and appears to form monogamous long-term pairs (Robertson, 1973; Allen, 1975). However, if one of the pair dies or is removed, another nearby ripe adult takes its place almost immediately (Nakazono, 1993). *Acanthochromis* nests in caves in the reef (Thresher, 1985) and has biparental care of eggs and juveniles (Robertson, 1973). The eggs are relatively large (4.5 mm; Thresher, 1984). Robertson (1973) was the first to report on the unusual brooding behavior shown by *Acanthochromis*, where juveniles remain with the parents for several months, until they are 30–40 mm SL (Nakazono, 1993). Parents defend the school of juveniles from small predators (Allen, 1975). Juveniles show an unusual glancing behavior, where they swim up, touch, and ingest mucus from the sides of the parents frequently during brooding (Robertson, 1973; Kavanagh, 1998). Brood abandonment has been found to occur under several conditions. When one parent was removed in experiments at One Tree Island, the remaining parent found another partner quickly and drove off or preyed upon the old brood (Nakazono, 1993). In this same population, Thresher (1985) observed that *Acanthochromis* parents occasionally drive off their young (1–2 wk old) broods early in the season, and he suggested that this enabled a second brood to be produced. By a size frequency analysis, Thresher (1985) estimated age at maturity of One Tree Island *Acanthochromis* as approximately 2–3 yrs. Although regional differences in genetic population structure and in color patterns have been found among populations throughout its geographic distribution (Doherty et al., 1994), color pattern is typically consistent within a population. It appears that there is often strong sexual selection for mates of a similar color pattern, however in some interesting hybrid zones, these distinct color morphs come in contact and interbreed successfully in narrow zones of overlap (Planes and Doherty, 1997a,b).

Despite these varied studies, many aspects of the biology of *Acanthochromis* are still unreported. In this paper, I provide an age-specific morphological description of the unusual embryonic stage and present new morphological and behavioral data on all life stages to give a more complete natural history. These correlated traits will add some insight into what characteristics allow early life stages of reef fishes to survive on the reef rather than in open ocean waters. I divide up my observations into five categories of the life cycle: (1) eggs and embryos, (2) hatching and hatchlings, (3) brooded juveniles and parental care, (4) post-brooding dispersal and subadults, and (5) sexual maturity and reproduction.

METHODS

A. polyacanthus were observed periodically between December 1992 to December 1995 on Lizard Island, a mid-shelf continental island on the central Great Barrier Reef (GBR), Australia. Most data on feeding, parental care, and parent/juvenile interactions were collected by observing numerous *Acanthochromis* pairs and broods over 30-min periods at sites in the lagoon and exposed reefs of Lizard Island. Observations were also made on occasional trips to other areas of the GBR: Orpheus Island, Magnetic Island, and Davies Reef (central GBR), and Hyde Reef and Heron Island (southern GBR). Data on reproductive behavior, parental care, juvenile and subadult behaviors, and dispersal were recorded over approximately 250 h of observations. The temperature in the field during

this time varied seasonally from approximately 25–29°C. Size of adult pairs was estimated visually by a single observer (KK) after extensive *in situ* calibration whereby the size of an individual was estimated, then the individual was captured and measured. With one exception (18.8%), error in estimating the size of adult *Acanthochromis* was never greater than 10% (Kavanagh, 1997).

In addition to field observations, *Acanthochromis* pairs from Magnetic Island and Lizard Island were brought back to the James Cook University Aquarium facilities and kept in large (100–1000 L) aquaria where eggnecks, embryos, hatching behavior, and juveniles could be observed. Mean length-at-age (notochord length for preflexion embryos and standard length for older specimens) was determined for embryos and juveniles from 14 broods reared in the outdoor aquarium facilities at approximately 26–28°C. Standard morphometrics, including eye diameter, vertical gape, head length (snout to gill slit), total length, standard length, length from the tip of the snout to the anterior origin of the anal fin, depth at the anterior origin of the first dorsal fin, and depth at the caudal peduncle were taken from a sample of field-caught juveniles over the full range of sizes present. Egg size was measured as length along the longitudinal axis. Ages are presented as either days after fertilization (DAF) or days after hatch (DAH). Hatching time-of-day was determined by observing egg masses at approximately 2–3 h intervals throughout the day for hatching, then estimating the percent of egg mass already hatched by the evening, and examining the same egg masses again in the morning and throughout the next day until all the eggs had hatched.

A morphological description of the embryonic and juvenile stages is based on observations of known-age, captive-bred broods from Magnetic Island. Specimens were preserved in 10% formalin and examined using a dissecting microscope. Developmental series of embryos and juveniles were cleared and stained following methods of Potthoff (1984) to observe skeletal development and obtain meristic information.

RESULTS

EGGS AND EMBRYOS.—In clutches of captive-bred pairs, the eggs were attached individually to the substrate, upside down on the exposed undersurface. Each clutch produced by individual pairs collected from Lizard Island, Magnetic Island, or Heron Island consisted of a roughly circular patch of approximately 250–550 eggs. Some of these pairs were able to produce new clutches of eggs within days after removal of a newly-hatched brood. The eggs were 3.7–4.3 mm in length and 1.4–1.5 mm in width. Although egg sizes differed among females ($n = 5$), no consistent differences among females from different sites were apparent (Fig. 1). There was no detectable relationship between female size and clutch size (Fig. 2).

Initially (3 DAF), the embryo formed on the end of the egg closer to the substrate, with the head forming facing the substrate. At 5 DAF, the head of the embryo migrated to the outer edge of the egg, with the tip of the tail just touching the substrate end of the egg (Fig. 3A). The embryo stayed in this orientation (head-out) until hatching, although some variability was observed (<5%) wherein late-stage embryos were oriented head-down.

Acanthochromis embryos have a large head with a blunt snout (Fig. 3B). At 6 DAF, no mandible was present, but by 11 DAF, the jaw was fully formed. Under a dissecting scope, the otoliths were visible at 5 DAF and the heart and gills could be observed to be functioning at 5–6 DAF. The eye first showed pigment at 6–7 DAF. The dorsal and anal fin pterygiophores appeared at approximately 8 DAF, and developed from the middle of the fin outwards. Two predorsal bones developed in embryos at about 14 DAF. Notochord flexion was completed during embryonic development, at approximately 10 DAF (Fig. 3B). Pectoral fin buds were the first fins to develop and formed early in the embryonic

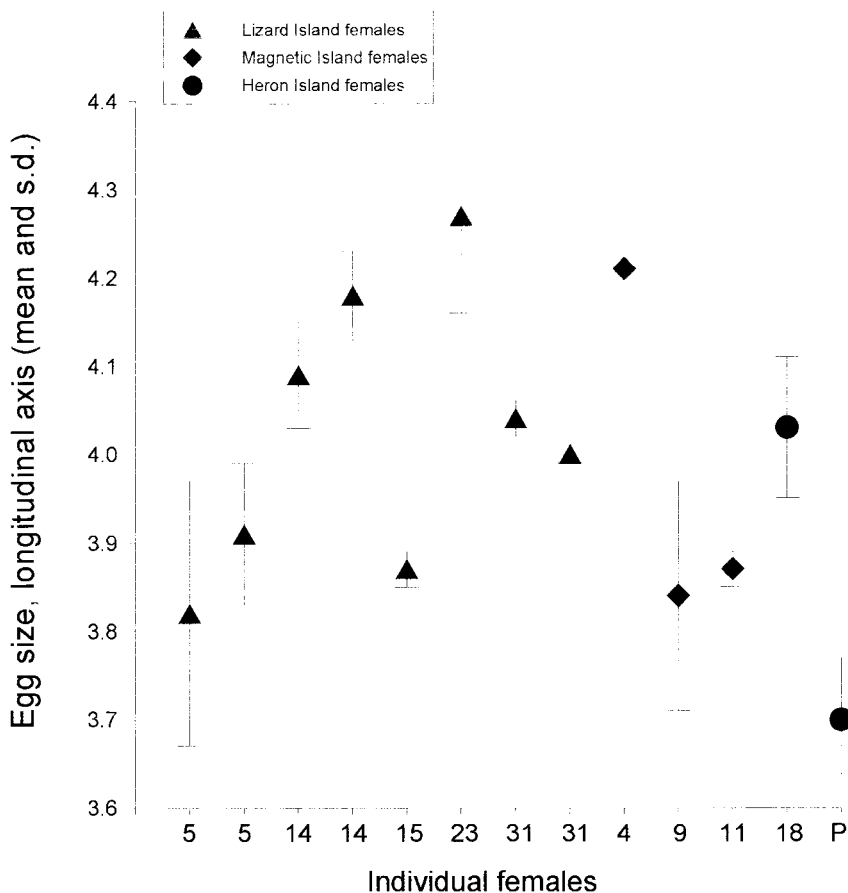


Figure 1. Mean egg diameters (longitudinal axis) of *Acanthochromis polyacanthus* females from Lizard Island, Magnetic Island, and Heron Island (Great Barrier Reef). X-axis indicates female ID number.

stage (6 DAF). In cleared and stained specimens, the first features to ossify were the cleithrum and the pharyngeal teeth, which ossified about 1 d before hatching.

The first pigmentation (3 DAF) consisted of evenly spaced small melanophores over the entire surface of the yolk, with a small concentration around the animal pole (end near substrate). As the embryo migrated toward the outer edge of the egg (by 5 DAF), the concentration of pigment moved with it. On the 5-d old embryo, melanophores were large and concentrated on the fore and hind brain, becoming lighter until about halfway down the notochord. A series of ventral midline melanophores, two dorsal, and one lateral were the only body pigmentation. The yolk sac has dense pigment, sometimes darker at the head end. The midline of the hindbrain was free of pigment. Shortly afterwards, pigment concentrated on the dorsal side of the notochord and a line of lateral melanophores developed. The dorsal pigment eventually (11 DAF) formed two lines. At this time, the mandible, branchiostegal and gular regions developed pigment, and the ventral melanophores were lost.

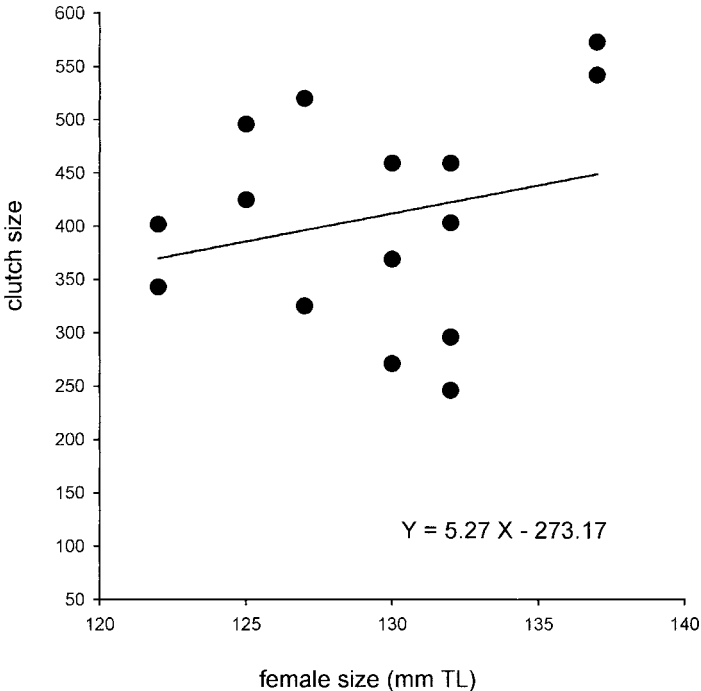


Figure 2. Clutch sizes for individual *Acanthochromis polyacanthus* females.

Egg stage duration in clutches held at 27–28°C was 15–17 d. Length-at-age for young *Acanthochromis* is given in Fig. 4. Growth in length appears to slow considerably from 11–17 DAF, corresponding with the latter part of the embryonic stage until hatch.

HATCHING AND HATCHLINGS.—Five broods were observed closely over their hatch day(s) to observe hatching. The hatchlings left the egg after a “cap” opened up on the non-adhesive end of the egg. Hatching occurred during the early daylight to midday hours, not before 08:00 or after about 14:00 and over many hours for a single clutch. If all the eggs had not hatched by mid-afternoon, hatching did not continue overnight, but waited till the following day.

After hatching the young emerged from the nest cave, began swimming immediately and stayed in a close group guarded by the parents. Feeding began within 24 h of hatching, determined by behavioral observation and confirmed by examining gut contents, although yolk was present in dissected juveniles aged 2 or 3 d.

At hatching, the dorsal and anal-fin rays began to extend distally, and spines were just forming (Fig. 5A). Full dorsal and anal fin counts are present within a day or two of hatching. The caudal fin was well-formed at hatching. Caudal-fin rays were truncate at hatching but gradually developed a fork over the next few days. All pectoral rays were present at hatching. Pelvic buds were not visible during the embryo stage, but began developing just after hatching (17 DAF). The cleithrum, pharyngeal teeth, maxilla, premaxilla, and parasphenoid are the only skeletal elements ossified at hatching.

JUVENILES AND PARENTAL CARE.—Juveniles remained in an aggregated group, defended by the parents, for up to 4 mo after hatching at Lizard Island. Bottom feeding was ob-

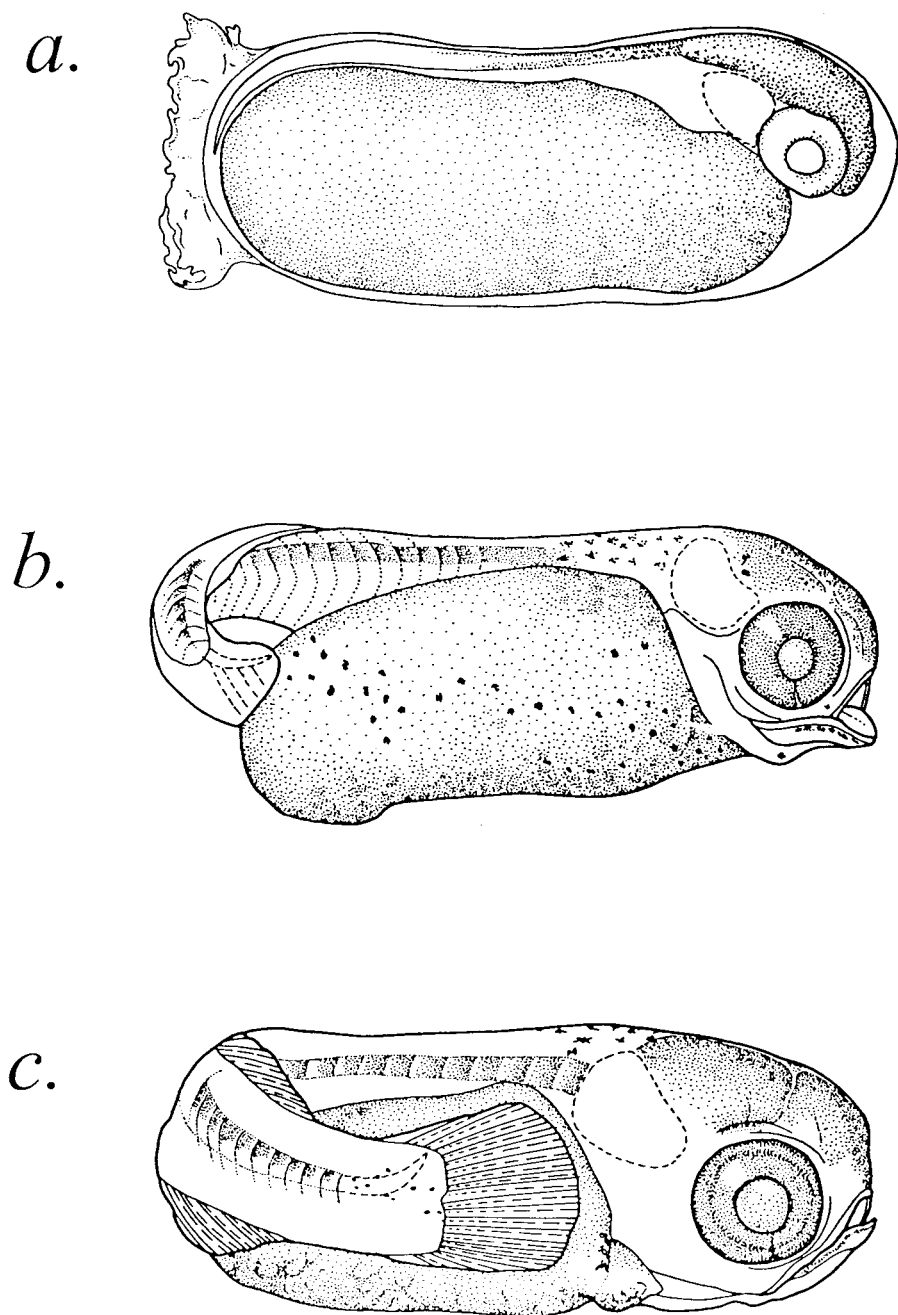


Figure 3. Stages in the embryonic development of *Acanthochromis polyacanthus* spawned from Magnetic Island pairs held in captivity. a) 6 d after fertilization (9 d before hatch); egg length 3.9 mm; approximate notochord length 3.6 mm. b) 9 d after fertilization, 6 d before hatch; notochord length is approximately 3.9 mm. c) 12 d after fertilization, 3 d before hatch; standard length is approximately 5.4 mm.

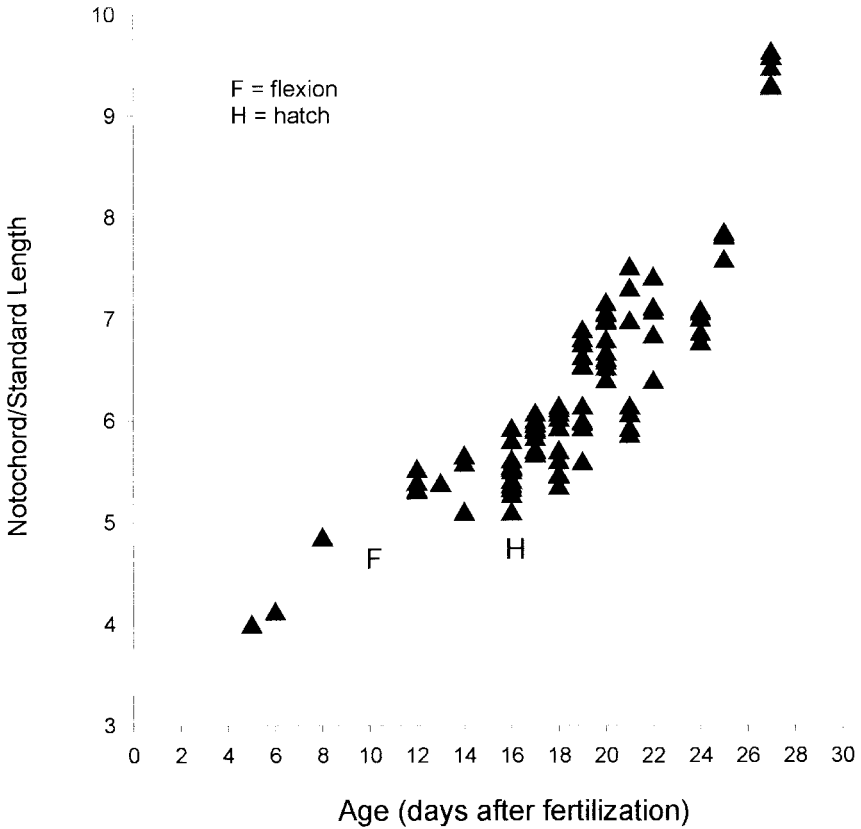


Figure 4. Length-at-age for embryonic and juvenile *Acanthochromis polyacanthus* reared in captivity. Age is in days after fertilization. Hatching occurs at 15–17 d; growth appears to slow before hatch.

served in all stages of development, including very young (Stage 2, see below) juveniles. Gut examination of a few of these juvenile fish confirmed that algae and small benthic invertebrates were actually ingested.

Cleared and stained *Acanthochromis* specimens had 29 or 30 vertebrae: 13–14 precaudal and 16–17 caudal (Plate 1). Ctenoid scales were formed between 12 and 17 DAH (28–35 DAF). The ossification of the fins was not complete until about 32 DAF.

At 4 DAH, melanophores increased on the dorsal midline and decreased on the ventral gut region. Shortly thereafter, a stripe formed through the eye and a few more melanophores appeared laterally. A yellow spot appeared on the caudal peduncle at this time, or, in some populations (e.g., Davies Reef), a yellow pigment stripe along the side was seen (5 DAH). Melanophores then increased on dorsal and lateral surfaces, and some formed over the anal fin (Fig. 5B,C). Pigment appeared on the pectoral fins, premaxilla, and around the mouth about 10 DAH, and a concentration of pigment appeared around the anus (Fig. 5D).

FIELD STAGING OF BROODED JUVENILES.—Juveniles grew from 5 mm to approximately 50 mm SL before fledging from the nest area. During this lengthy period, they undergo gross changes in shape, pigmentation, and behavior which are useful for field staging of brooded juveniles. The following staging criteria are based on field observations of Lizard Island



Plate 1. Hatchling *Acanthochromis polyacanthus*, cleared with trypsin and stained with Alcian Blue (cartilage) and Alizarin Red (ossified bone).

(central GBR, Australia) juveniles. Stage 1 juveniles are newly-hatched, and stay in a tightly aggregated ball close to the coral reef. They do not have any yellow pigment, and their caudal fin is truncate (Fig. 5A). By Stage 2, juveniles have a yellow lateral stripe or a large spot on the caudal peduncle (Fig. 5B). By Stage 3, they significantly increase in body depth and are typically in a much looser aggregation (Fig. 5C). Stage 4 juveniles have lost the yellow pigment, and developed black edges on their dorsal, anal, and caudal fins (Fig. 5D). Stage 5 juveniles have the coloration of the adult (e.g., black with white posterior body and tail), but are still brooded (Fig. 5E). Average sizes and ages for each of these stages, along with these criteria, are given in Table 1. Morphometrics of each stage are given in Table 2.

POST-BROODING DISPERSAL AND THE SUBADULT STAGE.—Dispersal behavior of juveniles was deduced from repeated observations of late-stage broods over several days. Stage 4 or 5 juveniles were seen to gradually spread out from the nesting site, by associating with coral heads increasingly farther away. Sometimes parents were observed to drive the juveniles from the immediate nesting area (1–3 m). In areas with high wave energy, juveniles often joined large groups of other planktivores feeding in the current off the reef. No major dispersal events (entire brood leaves in less than 1–3 d) were recorded from the

Table 1. Characteristics used for categorizing broods.

Stage of brood	Defining characteristics	Approx. age ¹	Size range, approx. (SL) ²
1	Newly-hatched. Tight ball of tiny larvae. No yellow pigment yet.	1–10 d	5–11 mm
2	Yellow stripes or spots along side. Still elongated body.	10–25 d	11–25 mm
3	Body depth increases significantly. Still has yellow pigment.	25–45 d	25–35 mm
4	No yellow pigment. Black edges to posterior part of dorsal and anal fin, and on dorsal and ventral edges of caudal fin. Generally light gray color.	45–75 d	35–45 mm
5	Adult coloration (white tail and posterior body), but still brooded	75–90 d	45–55 mm

¹ Based on observations of captive-bred juveniles reared at 27–30° C.

² Based on field-caught specimens and captive-bred juveniles.

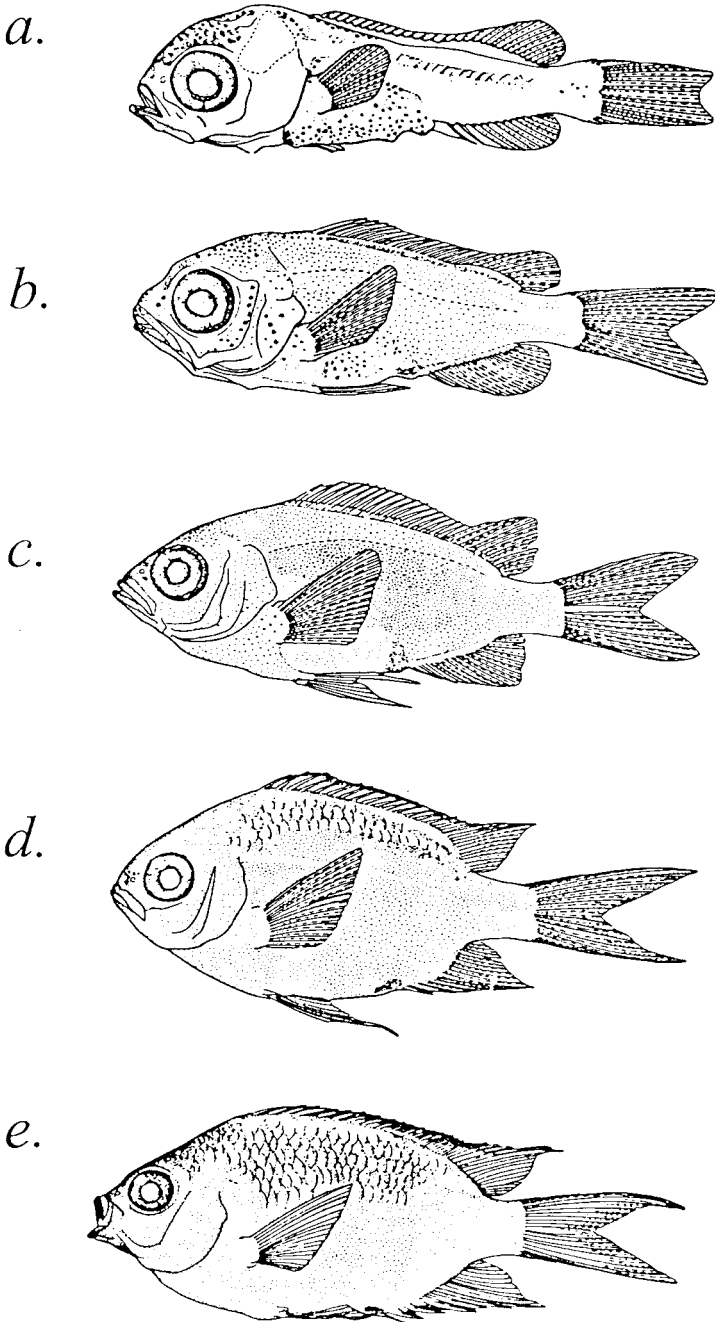


Figure 5. Stages in the development of juvenile *Acanthochromis polyacanthus*. Newly-hatched (Stage 1) spawned from Magnetic Island pairs held in captivity. Others are collected from wild populations at Lizard Island, Great Barrier Reef. Lengths, from top to bottom, are a) Stage 1 (newly-hatched): 5.7 mm SL; b) Stage 2: 12.0 mm SL; c) Stage 3: 19.5 mm SL; d) Stage 4: 29 mm SL; e) Stage 5: 47 mm SL.

Table 2. Morphometrics of juvenile and adult *Acanthochromis polyacanthus*. SL: Standard length; TL is total length; ED is eye diameter; Gape is vertical gape of mouth; HL is head length; Depth1 is depth at 1st dorsal fin; SAO is snout to anal origin; Depth2 is depth at the caudal peduncle. Proportion of SL is in parentheses. Stages refer to Table 1.

	SL	TL	ED	Gape	HL	Depth1	SAO	Depth2
Hatchlings/	4.2-4.9	5.6-6	0.75-0.77 (0.18-0.16)	0.55-0.77 (0.13-0.16)	1.6-1.9 (0.38)	1.6-1.8 (0.38-0.36)	3.2-3.4 (0.76-0.69)	0.68-0.72 (0.16-0.15)
Stage 1			1.0-1.5	2	4.3-4.6	3.8-4.9	5.0-9.1	1.1-1.9
Stage 2	11.7-13.7	14.6-18.0	(0.09-0.11)	(0.17-0.15)	(0.37-0.34)	(0.32-0.36)	(0.43-0.66)	(0.9-0.14)
Stage 3	21.6-25.0	30.0-32.9	2.9-3.1 (0.13-0.12)	3.9-4.6 (0.18)	7.6-8.4 (0.35-0.34)	9.1-10.0 (0.40-0.42)	15.3-16.0 (0.64-0.71)	2.9-3.1 (0.13-0.12)
Stage 4	32.3-35.5	45.6-45.9	4.1-4.3 (0.13-0.12)	5 (0.15-0.14)	10.0-10.3 (0.31-0.29)	14.6-15.0 (0.42-0.45)	22.0-22.9 (0.65-0.68)	4.5-4.9 (0.13-0.14)
Stage 5	39.3-41.0	45.0-46.1	4.5-4.7 (0.11)	4.5-5.0 (0.13-0.11)	12.8-13.0 (0.33-0.32)	19.0-17.4 (0.42-0.48)	27.0-32.5 (0.69-0.79)	5.6-6.6 (0.14-0.16)
Adult	77.4-110.0	108.0-153.0	8.6-9.4 (0.11-0.09)	7.7-10.0 (0.10-0.09)	22.2-30.0 (0.29-0.27)	41.3-56.6 (0.53-0.51)	57.9-81.5 (0.75-0.74)	11.6-16.7 (0.15)

repeated observations of over 50 late-stage broods. No territoriality was observed until pairs were established. Aggregations of subadult and unpaired adult *Acanthochromis* were commonly seen feeding in currents off the crest or wandering, individually or in smaller groups, over reef flats.

SEXUAL MATURITY AND REPRODUCTION.—Size at maturity, approximately 65 mm SL, was determined from estimates of size of the smallest paired adult seen with a brood. Eighty percent of brooding adults observed were between 80 and 110 mm SL (Fig. 6). Age at maturity was approximately 9 mo, determined from juveniles (from Magnetic Island parents) hatched and reared in captivity until they paired and spawned.

In the populations observed, male and female of a pair rarely differed in length even though a large range of sizes of fish were present in the area (Kavanagh, 1997). Of 205 pairs from Lizard Island in which size was estimated, only five mates were estimated to be of detectably different length. Of those pairs that differed, the mean difference in size between mates was 7 mm, or about 5% of total length (range 1–9%; $n = 5$).

Courtship of *Acanthochromis* was observed in this study several times. The courtship pattern was similar to that described for *Chromis* spp. (Thresher, 1984), with the (presumed) male swimming on his side with median fins erect towards the (presumed) female, circling then leading the female towards a nest site repeatedly. Sometimes the male would swim slowly with an exaggerated wiggle.

One set of observations was particularly interesting, as it recorded the end of the care of one brood, reformation of the pair, and the defense of the new nesting site. Initially, I observed a pair with a late-stage (stage 5, Table 1) brood interacting as a family group

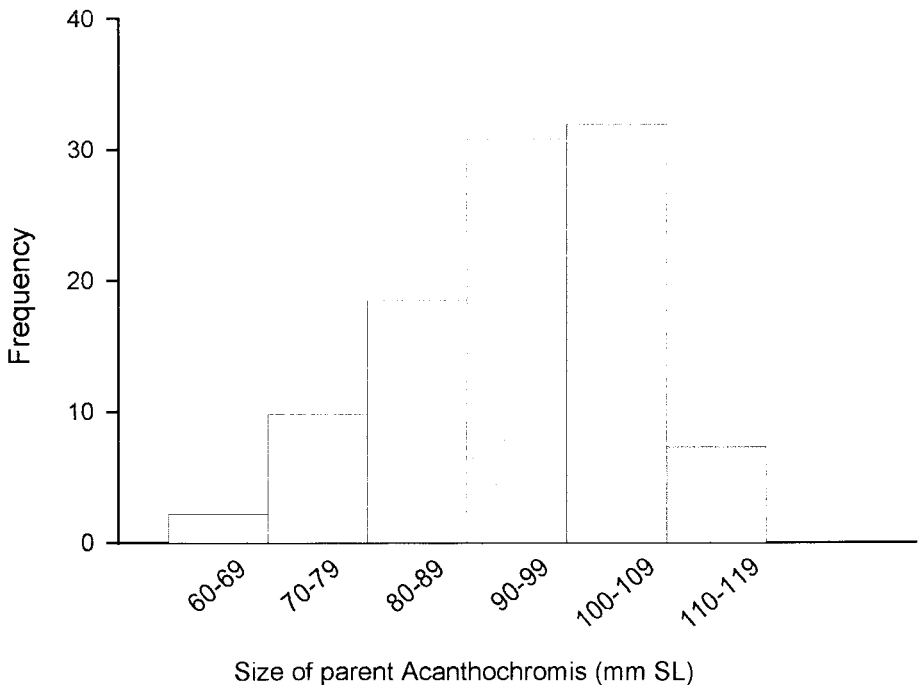


Figure 6. Frequency histogram of estimated standard lengths of 205 *Acanthochromis* adults guarding broods in the Lizard Island, Great Barrier Reef population.

Table 3: Selected traits of *Acanthochromis polyacanthus* and other damselfishes. Traits indicating ages at particular developmental stages are taken from young reared at $\sim 28^{\circ}$ C.

Trait	Other Pomacentrids	Acanthochromis
Egg size (L \times W)	0.7–2.5 mm \times 0.4–1.0 mm	3.7–4.6 mm \times 1.4–1.5 mm
Hatchling length	1.9–4.0 mm	5.0–5.9 mm
Vertebral count	11+15 = 26	13–14 + 16–17 = 29–30
Age at first eye pigment	2–3 d	6 d
Age at flexion	10 d	10 d
Egg stage duration	2–8 d	15–17 d
Age at full skeletal ossification	~ 20 d (presettlement)	~ 32 d
Hatching time of day	sunset	midday
Care of eggs	males only	biparental
Care of free-swimming young	none	biparental; lasts several weeks to months

(parents defending brood; juveniles glancing off parents). The individual parents were identifiable by spots or rips in their fins. When they were observed 2 d later (day 3), the male was vigorously chasing its own juveniles away from the immediate nest area (about 1 m) and very defensively avoiding being glanced. The female continued to interact with the juveniles, tending them and allowing them to glance. The male also chased intruders of any species away from the nesting site, and was observed courting three females in the area, sometimes leading two at a time back towards the nest cave. They were never seen to enter the nest cave in over an hour of observation. When observations on this family group resumed the next afternoon (day 4), the male was paired up with his original mate (female parent of the stage 5 brood), and both were chasing away intruders from the nest area. This time, both were seen to chase away juveniles of their previous brood. Over the next few days, the renewed pair was seen to aggressively defend the nesting cave and refuse any interaction with their own juveniles. They spent minutes at a time inside the cave. It was observed that the majority of the stage 5 juveniles of this pair remained in the area, within 10 m, for at least the next week (when observations ceased.) Over 2 h of observation on 3 d, a total of 93 aggressive chases and 14 courtship swims were recorded for the pair.

BEHAVIOR-INDUCED COLOR CHANGES AND A NEW COLOR MORPH.—In both field and laboratory conditions, I observed color patterns of both “all-black” (black with a small white or gray edge to the tail) and black-and-white color morphs (Randall et al, 1990) change under certain conditions. At night, *Acanthochromis* adults and juveniles sheltered in coral rubble and developed a vertical white bar against an all-black background, or, in Lizard Island (black-and-white morph) fish, they were seen to acquire a reversed coloration pattern (white with black posterior body and tail) as they began their day/night transition. Under stress, various color changes in shades of black, grey, and white were observed, including these nocturnal patterns. In addition, field observations indicated that black-and-white fish (Lizard Island) changed the intensity of their black color on different days, from a dull grey to a deeper black. However, the essential daytime color of the fish in a population (e.g., all-black or a black-and-white pattern) was always consistent and easily distinguishable.

As reported in numerous papers, diurnal adult color patterns differ between isolated reefs (Planes and Doherty, 1996a,b; Doherty et al., 1994; Randall et al., 1990; Allen,

1975). While all previous color morphs reported have included pigmentation produced only by melanophores (black, gray, or white), this study found a new color morph in which the pelvic fins, pectoral fin base, and ventral area of the body are bright yellow. This color morph was found on Magnetic Island, an inshore reef near Townsville, Australia. The color of the Magnetic Island fishes were otherwise similar to that referred to by Doherty et al (1994) as the most common morph of the central Great Barrier Reef (black with white posterior body and tail).

DISCUSSION

EGGS, EMBRYOS, AND HATCHLINGS.—Despite the much larger eggs, the egg-clutch sizes of *Acanthochromis* overlap with those of the related anemonefishes, which typically have about 100–1000 eggs per clutch (pers. observ.; Fautin and Allen, 1992). Clutch sizes of the captive *Acanthochromis* pairs in this study (central GBR) were up to 2–5 times greater than reported in the literature for Heron Island (southern GBR) pairs (Robertson, 1973). It cannot be assessed from available data whether this large difference is related to female size or is a fixed life-history difference for these geographically-disparate and genetically-distinct populations. At over 4 mm, the eggs of *Acanthochromis* are the largest of any damselfish, and one of the largest of any tropical reef-fish (Leis and Rennis, 1983; Kavanagh et al., in press). There is no evidence of regional variation in egg sizes of separated *Acanthochromis* populations (Fig. 1).

The time of day at which hatching occurs in demersal eggs of reef fishes (and the time of spawning for broadcast spawners) are suggested to be adapted to minimize predation on the new hatchlings as they disperse away from the immediate reef environment (Shapiro et al., 1988; Robertson, 1991). Most damselfish eggs hatch very precisely at sunset (Doherty, 1980; Thresher, 1984), as a rapid response to darkened conditions (pers. observ.). Other demersal and broadcast spawners also appear to time the release of eggs or larvae into the sea with the day/night changeover period, suggesting this behavior may be adaptive (Robertson, 1991). The hatching time of *Acanthochromis*, in contrast, does not coincide with sunset, but instead they hatch preferentially in morning and midday. As new hatchlings are dependent on their diurnally-active parents for survival (Nakazono, 1993), this unique diurnal hatching time might also be seen as advantageous for the first hours of life on the reef for the non-pelagic young.

Differentiation of the jaw and internal organs is relatively delayed in *Acanthochromis* compared with other pomacentrids (e.g., *Chromis atripectoralis* feeds at 4 DAF while a 6 DAF *Acanthochromis* does not have a jaw yet). Eye development also begins late, with pigment developing in the embryo several days later than confamilial species (however, the rate of retinal development is comparatively very rapid over the next 2 wks; unpubl. data). The size at which scales form in other pomacentrids is variable, but they are usually evident before settlement (Leis and Rennis, 1983; Kavanagh et al., in press). The timing of scale formation in *Acanthochromis* is near the age at which most pomacentrids settle (~30 DAF), but much later than when *Acanthochromis* juveniles “settle” (hatch) on the reef (~16 DAF) suggesting scales are not critical to benthic survival.

The timing of notochord flexion in *Acanthochromis* is well within the range of many other pomacentrids (~10 DAF; unpubl. data). As in other pomacentrids, dorsal and anal fins in *Acanthochromis* begin to form just after flexion, with rays developing first. How-

ever, the ossification of the fins and skeleton is much delayed in this species, for weeks longer than other pomacentrids. Since other pomacentrids have ossified skeletons as pelagic larvae well before settlement (Potthoff et al, 1987; unpubl. data), the uniquely delayed ossification of *Acanthochromis*' skeleton suggests that an ossified skeleton is more important to pelagic than benthic early life. Typical pomacentrids can and often must swim large distances as larvae to find appropriate settlement habitat, and an ossified skeleton would clearly be advantageous for more efficient swimming. Delaying ossification in *Acanthochromis* until hatching is surely required because of the necessity of flexibility during the long embryonic period, but *Acanthochromis* apparently does not require a fully ossified skeleton even for a week or more after hatching.

The most remarkable feature of the skeleton of *Acanthochromis* is the high and variable number of vertebrae (Table 4). All other pomacentrid species are reported to have 26 vertebrae, or, rarely, 25 (Leis and Rennis, 1983). *Acanthochromis* has increased this number by 4–5, with the increase in vertebrae concentrated in the precaudal region. Because dorsal-spine pterygiophores tend to interdigitate with the neural spines of the vertebrae, the large number of dorsal spines (17), from which *Acanthochromis* derives its name, is probably coincident with the high precaudal vertebral count. The uniquely high number of precaudal vertebrae may provide a functional advantage. One possibility is that the enlargement of the precaudal area effectively translates to an increase in the body cavity. This larger body cavity would allow *Acanthochromis* to hold a greater number of its relatively huge eggs. In reptiles, studies of allometrically increasing number of presacral vertebrae and/or body cavity area have been correlated with life-history traits and interpreted as a means of maintaining a minimum critical clutch size among divergent populations (Griffith, 1990; Forsman and Shine, 1995).

DISPERSAL.—In this study, post-brooding dispersal (fledging) of *Acanthochromis* juveniles occurred at an exceptionally large size, about 40–50 mm SL, in broods observed on Lizard Island. Previous reports of dispersal sizes from One Tree Island (southern GBR) pairs indicate a smaller size at fledging, approximately 25–40 mm SL (Nakazono, 1993; Robertson, 1973). If this striking difference is demonstrated to be consistent among these separated populations, it would suggest a life-history response to the different environmental conditions in the southern GBR reefs. For example southern GBR reefs experience cooler winter temperatures (ENCORE, Great Barrier Reef Marine Park Authority, 1996) and have fewer predators (Caley, 1995). Thus, one might predict that earlier fledging might be advantageous in southern reefs, because it would allow a second brood to be produced in the more restricted (cooler winter temperatures) spawning season. Comparative regional studies of these populations, in addition to ageing field-caught juveniles, would be useful for further testing these hypotheses.

Another contrasting observation regarding fledging in *Acanthochromis* is the mode of dispersal. No large dispersal events, or multiple-brood fledgings, were recorded in the repeated observations of late-stage broods in this study. Studies from One Tree Island on the southern GBR suggest that the common mode of dispersal in those populations is for large groups of juvenile *Acanthochromis* to aggregate and disperse from an area (Thresher, 1985; Nakazono, 1993). Nearly all of the observations made on Lizard Island were on contiguous reef habitat rather than the isolated patch-reefs of Thresher's studies (1985), and this alone may account for the different conclusions. Studies in progress on isolated patch-reefs in the central GBR (Trunk Reef) indicate that large groups of juveniles from these *Acanthochromis* populations will in fact move between patch-reefs over distances

on the order of 50–100 m (A. Lewis, James Cook University, pers. comm.). These habitat differences in the mechanism of juvenile dispersal may have implications for population and community dynamics.

The distributional range of *Acanthochromis* stretches across several deep oceanic regions, for example between the Solomons Islands and Vanuatu, suggesting that the restricted juvenile dispersal and lack of a pelagic larval stage does not prevent the species from colonizing new geographic regions across potentially difficult dispersal barriers. On the other hand, despite obvious west to east corridors across the reefs of Southeast Asia, the occurrence of this species stops abruptly at approximately the famous “Wallace’s line.” The western limit of *Acanthochromis*’ distribution embraces Komodo Island, the west coast of Sulawesi, and NE Kalimantan between about latitude 1 and 4° (G. Allen, pers. comm.).

ADULT STAGE AND REPRODUCTION.—Captive-bred *Acanthochromis* from Magnetic Island stock matured at a much younger age (9 mo) than previously reported in the southern GBR population (2–3 yrs; Thresher, 1985). Although different methods were used in the southern GBR studies (size frequency analysis), if verified, such a substantial life-history difference could have significant impacts on population dynamics and ecology of the separated groups. The size-at-maturity for *Acanthochromis* needs to be confirmed by analysis of gonad maturation, as the estimate used in this study may actually reflect the ability of an individual to hold a brooding territory rather than definitive sexual maturity.

Previous studies report positive assortative mating by color pattern in *Acanthochromis* (Planes and Doherty, 1997a). The data in this study suggest that sexual selection is not only for the same color pattern but for similar-sized mates as well—pairs of *Acanthochromis* were remarkably similar in size even when a large size range existed in the local population of potential mates. Courtship observations lead one to question the previous conclusions of long-term monogamy in *Acanthochromis*. If the observations of “extramarital” courtship in this study are taken with those of Nakazono (1993), which demonstrated that if one adult in a pair is removed, a new ripe partner is found almost immediately, these suggest that *Acanthochromis* is easily willing to reform pairs and monogamy may only last for the duration of a brooding period or a season.

SUMMARY

The study of unusual or extreme forms in nature has explanatory power in evolutionary hypotheses by fortuitously demonstrating the successful suite of character states accompanying a relatively radical departure from the norm. Repeated correlations of divergent traits in independent lineages suggest dependence and increase predictive power. This and other studies found that *Acanthochromis* is decidedly an outlier when compared with other pomacentrids in various traits, while in other traits, it is well within the typical range. The following correlates observed in *Acanthochromis* diverge significantly from the norm within the pomacentrid family and are concurrent with non-pelagic larvae: very large eggs (for a tropical damselfish); extended egg-stage duration; a mid-day hatching time; slow early development; much delayed skeletal ossification; large and well-developed hatchlings with fully formed caudal fins; no scales at hatch/settlement; a distinctly high and variable number of vertebrae; very extended and intense biparental care; parent-juvenile interactions such as glancing; and selection of mates of extremely similar size

and color (see Table 4). While these traits diverge significantly from other pomacentrids, there is a moderately high level of variability in many of the traits among pomacentrid species, making them an interesting group for comparative studies. A phylogeny of the damselfishes would allow a greater level of interpretation of the significance of the trait co-variance, but is currently unavailable. Furthermore, the populations observed of *Acanthochromis* in this study differed from those presented in previous reports in several key life-history traits: egg-clutch size, age at maturity, size at fledging, and mode of dispersal. These data suggest intriguing intraspecific, possibly population-level, differences in *Acanthochromis* on the Great Barrier Reef.

ACKNOWLEDGMENTS

I am grateful to H. Choat, J. Leis, D. Bellwood, J. Caley, G. Allen, P. Doherty, A. Lewis, S. Purcell, J.-L. Solandt, J. Werry and A. Felton for fruitful discussions and comments, and/or for field and laboratory assistance. I thank L. Smith for the illustrations. This research was supported by an Overseas Postgraduate Research Scholarship from the Australian Government, and an Australian Museum Postgraduate Research Grant.

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DATE SUBMITTED: February 15, 1999.

DATE ACCEPTED: December 2, 1999.

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