

EXTREMES, PLASTICITY, AND INVARIANCE IN VERTEBRATE LIFE HISTORY TRAITS: INSIGHTS FROM CORAL REEF FISHES

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Abstract. Life history theory predicts a range of directional generic responses in life history traits with increasing organism size. Among these are the relationships between size and longevity, mortality, growth rate, timing of maturity, and lifetime reproductive output. Spanning three orders of magnitude in size, coral reef fishes provide an ecologically diverse and species-rich vertebrate assemblage in which to test these generic responses. Here we examined these relationships by quantifying the life cycles of three miniature species of coral reef fish from the genus *Eviota* (Gobiidae) and compared their life history characteristics with other reef fish species. We found that all three species of *Eviota* have life spans of <100 days, suffer high daily mortality rates of 7–8%, exhibit rapid linear growth, and matured at an earlier than expected size. Although lifetime reproductive output was low, consistent with their small body sizes, short generation times of 47–74 days help overcome low individual fecundity and appear to be a critical feature in maintaining *Eviota* populations. Comparisons with other coral reef fish species showed that *Eviota* species live on the evolutionary margins of life history possibilities for vertebrate animals. This addition of demographic information on these smallest size classes of coral reef fishes greatly extends our knowledge to encompass the full size spectrum and highlights the potential for coral reef fishes to contribute to vertebrate life history studies.

Key words: age; biomass; body size; coral reefs; Gobiidae; growth; lifetime fecundity; mortality; pelagic larval duration; reproduction; trade-offs; turnover.

INTRODUCTION

Animal life cycles are intimately linked to organism body size (Calder 1984, Stearns 1992), with variation in body size initiating generic responses in many life history traits (Ricklefs and Finch 1995). Among the most important of these are the relationships between body size and growth, mortality, and life span. Overall, larger bodied organisms tend to exhibit slower, more protracted growth, lower rates of mortality, and longer life spans (Calder 1984, Roff 1992). As a group, fishes are the most diverse vertebrate taxa on Earth, with some 25,000 species: half of all the vertebrates (Helfman et al. 1997). Among these, of particular note are the coral reef fishes. Highly diverse and broadly distributed across the tropical and subtropical oceans of the world, familial diversity surpasses that of most other vertebrate groups (Sale 1991). Yet despite this tremendous diversity, their life cycles and their characteristics remain poorly documented (Miller 1984, Caley 1998, Choat and Robertson 2002, Kritzer 2002). In spite of this lack of demographic information, the potential for life history diversity and applicability of testing general life history theory in coral reef fishes appears compelling. Exhibiting a host of reproductive modes, growth trajectories, body

sizes, and life spans within this enormous diversity (~4000 species), research on coral reef fishes has recently expanded the boundaries of vertebrate biological, evolutionary, and life history possibilities (i.e., Kon and Yoshino 2001, Watson and Walker 2004, Depczynski and Bellwood 2005a).

With few exceptions, reef fishes are constrained by evolution to leading complex bipartite lives, which includes a pelagic larval phase, before settling onto a coral reef (reviewed by Thresher 1984, Leis 1991, Bonhomme and Planes 2000), where further growth leading to maturation and reproduction takes place. Within our current state of knowledge on reef fish life cycles, there exist two separate groups of roughly similar diversity and abundance, with each group sharing important life cycle characteristics. The first are those of larger (>100 mm total length [TL]), conspicuous species such as those from the families Scaridae, Labridae, Acanthuridae, Chaetodontidae, and Pomacanthidae. In these families, typical comparative life history traits include asymptotic growth, late maturation, low adult mortality, a pelagic seasonal broadcast spawning regime, and life spans numbering years leading to high lifetime reproductive output (Thresher 1984, Sponaugle and Cowen 1994, Choat and Axe 1996). In contrast, the second group consists of small (<100 mm TL), often cryptic species that typically exhibit steep continuous growth throughout their lives, mature at much younger ages, but have relatively low lifetime

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reproductive output due to their small body size and short life spans. This group is expected to suffer from higher rates of size-related adult mortality and exhibit a benthic spawning reproductive strategy that includes parental care of eggs, a feature which has been associated with enhanced offspring survival, predominantly in small-bodied taxa (Miller 1984, Thresher 1984, Roff 1992, Munday and Jones 1998, Hendry et al. 2001, Neff 2003, but see Robertson et al. 1990, Gladstone 1994). This second group includes species in the families Gobiidae, Blenniidae, Tripterygiidae, and Pseudochromidae. Although both groups exhibit highly successful evolutionary strategies, the smaller cryptic reef fishes have received little attention in the literature. This is despite the fact that members of this group are arguably more trophically interlinked within reef systems, by virtue of their short generation times and higher susceptibility to predation, and are often found in higher densities than their larger counterparts (reviewed in Munday and Jones 1998).

To date, demographic studies on this small, cryptic component have been particularly lacking and restricted to species in the upper size range (50–120 mm TL) (e.g., Kritzer 2002, Wilson 2004, Hernaman and Munday 2005a, b, but see Longenecker and Langston 2005). However, the modal body size of small adult cryptic reef fish communities on the Great Barrier Reef (GBR) is 21.0 mm TL at an inner-shelf location (Orpheus Island), and 15.0 mm TL on a midshelf location (Lizard Island) (Depczynski and Bellwood 2003, 2005b). Given the numerical dominance of these smaller bodied species and the theoretical relationship between body size and life history traits, the smaller size classes of coral reef fishes may be a critically important component of coral reef ecosystems. Furthermore, these fishes represent the extremity of the body size spectrum in vertebrate animals, thereby extending the breadth of life history possibilities and enabling a more complete overview of patterns in life history traits among this diverse assemblage of vertebrates.

Coral reef fishes of the genus *Eviota* are some of the smallest and most abundant fishes on the Great Barrier Reef (GBR), and constitute approximately half of all cryptic individuals on the reefs surrounding Lizard Island (Depczynski and Bellwood 2005b). Numerically ranking 1, 2, and 3 in abundance on these reefs, here we document the complete life cycles of *Eviota sigillata*, *E. queenslandica*, and *E. melasma* in order to quantify the demographic characteristics of this diminutive portion of the reef fish community. Specifically, this study aims to quantify the growth and mortality rates of these three species based on laboratory and field experiments. A further aim is to explore the relative proportion of life span allocation to pelagic larval durations and juvenile and adult stages, across a range of reef fish species based on a meta-analysis of life history data, in order to establish and contrast the full available range of life history strategies exhibited by coral reef fish taxa.

Finally, lifetime fecundity is calculated for the three focal species to investigate the costs of extreme small body size and associated life history traits on lifetime reproductive output and population dynamics. These parameters are then incorporated into an overview of known life history patterns in coral reef fishes in order to assess the contribution of fish assemblages to our understanding of vertebrate life history theory.

MATERIALS AND METHODS

All collections and field studies were undertaken in January and February 2003 and 2004 on reefs around the Lizard Island group (14°40' S, 145°27' E) in the Cairns section of the Great Barrier Reef. Individuals for all studies were collected on SCUBA using the anaesthetic clove oil in a 5:1, ethanol:clove oil mixture and a fine-mesh (2-mm) net, following Depczynski and Bellwood 2004. All size and mass measurements throughout this article are given in total length (TL) and grams (g), respectively.

We used tetracycline-validated daily otolith increment analysis (following Schmitt 1984) on a total of 13 *Eviota sigillata* and 6 *E. queenslandica* individuals to ensure accurate age and growth estimation. Daily periodicity of increments was confirmed by comparing the number of increments with the number of posttreatment days (i.e., postfluorescent rings). For the 17-day trial there were 16.61 ± 0.18 rings (mean \pm SE) for *E. sigillata* and 16.0 ± 0.58 rings for *E. queenslandica*.

For ageing analyses, a total of 319 *E. sigillata*, 189 *E. queenslandica*, and 171 *E. melasma* were collected. Sixty individuals of each species from a full range of available sizes including the 10 largest individuals of each species were used for ageing. Individuals were euthanized within two hours following capture, weighed, measured (to the nearest millimeter) and their sagittal otoliths extracted, cleaned, sectioned, and rings counted three times using a compound microscope (400 \times) along the longest axis. Any discrepancies of >10% between counts on a single individual were excluded from the analysis. Growth trajectories from size-at-age plots were fitted to three growth models: the von Bertalanffy growth function, a linear curve, and a power curve. Goodness of fit of each model was tested using the residual sums of squares (RSS) and coefficient of determination (r^2) calculated from the residual and explained sums of squares and the best model fitted. Fish trunks were fixed in a 4% formaldehyde, 5% acetic acid, and 1.3% calcium chloride (FAACC) solution for later gonad histology.

A meta-analysis of size-at-age data was generated from a comprehensive search of the coral reef fish literature. All maximum life spans and corresponding sizes of coral reef fish species were recorded to compare *Eviota* to known size-at-age data in 111 other species (full list described in Appendix A). The criteria used to assess the integrity of the data was that it had to have gone through an external peer review process. One exception was made for the maximum life spans of 7 of 114 species.

Data from these 7 species were generously donated by a colleague (M. Berumen) and verified by the primary author (i.e., otolith rings and specimen sizes recorded).

Like most reef fishes, species of *Eviota* have complex bipartite lives that include a pelagic open-water phase before settling onto a reef to begin the benthic phase of their lives. *Eviota* settlement rings were distinguished by their abrupt transition from widely spaced presettlement increments (~5.1 μm) to narrower (~2.7 μm) increments, and correspond to type 1a settlement check marks (Wilson and McCormick 1999). Presettlement age was determined by counting the number of rings (days) between hatching (first ring) and settlement. The life spans and pelagic larval durations (PLDs) of these three *Eviota* species were compared with demographic data for a range of coral reef fish species (life spans and maximum sizes (in millimeters) of 111 species; PLDs of 361 species, as described previously and presented in Appendices A and B). Cross-referencing size-at-age data with PLD data identified 27 species in total for which all parameters existed.

Whole fish trunks were sectioned longitudinally in 5- μm sections following decalcification and embedding in paraffin wax. Sections were stained using Myer's haematoxylin and Young's eosin-erythrosin. Gonads were sexed and maturity status assessed under a compound microscope (400 \times). Maturity was defined based on the presence of late vitellogenic and ripe oocytes (stages III–IV) in females (West 1990) and spermatozoa (stages III–IV) in males. Histological samples were cross-referenced with ageing data to determine age and size at first maturity.

Eviota spp. have been successfully bred under artificial conditions and *Eviota queenslandica* and *E. melasma* fecundity data were taken directly from the literature (Sunobe and Nakazono 1987, Sunobe 1998). A similar breeding program was conducted for *E. sigillata*. Four replicates consisting of a single male and two females were placed in 15-L flow-through aquaria (at 27°–28°C) and fed twice daily. In each aquarium, unlidged 50 \times 15 mm clear plastic vial "nests" were buried in sand with their openings exposed. Vial ceiling interiors were checked each morning by moving sand away from vial roofs. The swelling abdomen of each female was clearly visible as egg development progressed, and shrunk following egg-laying, enabling the identity of spawning females to be determined within each replicate aquarium. Vials containing eggs were removed six hours later to ensure the completion of the spawning episode (typically 15–45 minutes) and all eggs counted. The experiment was continued for 39 days or until the death of the male or females, whichever came first. An estimate of the reproductive efficiency (RE) was calculated for each species using the equation

$$\text{RE} = \text{LRO}/M_{\text{max}}$$

where lifetime reproductive output (LRO) = $\overline{\text{SE}} \times \overline{\text{EE}}$; $\overline{\text{SE}}$ = mean number of spawning events; $\overline{\text{EE}}$ = mean

number of eggs per spawning event, and M_{max} = maximum number of mature female days. This provides a comparative estimate between species of the rate of reproductive output per unit time (day), by taking the number of adult reproductive days for each species into consideration. It also provides an estimate of the expected lifetime reproductive output from a single female individual. Frequency of spawning events was taken as semilunar (14 days) for *E. queenslandica* and *E. melasma*, based on Taru and Sunobe (2000) for *E. abax*, and data presented in this study on *E. sigillata*.

Mean generational turnover ($\overline{\text{GT}}$) estimates were calculated using the following:

$$\overline{\text{GT}} = \text{AM} + [(T_{\text{max}} - \text{AM})/2]$$

where AM = age at female maturation and T_{max} = maximum age. This gives a conservative averaged estimate for the time taken for a new generation to be generated, assuming that a stable population exists (i.e., two adults are replaced by two larvae surviving to adulthood; see Gaillard et al. 2005).

Mortality estimates are based on a community-level study that included 36 *E. sigillata*, 20 *E. queenslandica*, and 13 *E. melasma* specimens. In total, 146 small, cryptic, reef gobies were collected on SCUBA from three 4 \times 1 m² field sites. Field sites were pooled following a nonsignificant result in a one-way ANOVA on abundances between sites ($F_{2,9} = 0.329$, $P = 0.727$), providing 12 \times 1 m² replicates. Fish were placed into clip-seal bags and tagged in situ in the dorsal flank using a 29-gauge (0.29-mm) hypodermic filled with elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). Upon full recovery, ~10 minutes (cf. Munday and Wilson 1998), tagged individuals were released at their exact site of capture. To control for movement, recaptures nine days later were conducted using a concentric net arrangement consisting of 1-, 2-, and 4-m² nets. Members within this reef fish community have home ranges of 0.25–2.5 m² (Luckhurst and Luckhurst 1978, Taru and Sunobe 2000, Depczynski and Bellwood 2004). The position (1-, 2-, and 4-m² nets), size, mass, species identification, and the presence or absence of tags for each individual were recorded on recapture. An instantaneous mortality estimate based on Hoenig's equation for mortality rates (Hoenig 1983) was also calculated to supplement field mortality estimates for the three *Eviota* species. Hoenig's equation is based on empirical evidence (and not theoretical estimates) over a wide range of marine taxonomic groups ($r^2 = 0.82$) and utilizes maximum species age to calculate mortality rates over time using the equation

$$\ln Z = 1.46 - 1.01 \ln T_{\text{max}}$$

where Z = instantaneous mortality rate and T_{max} is maximum species age. Previous studies to determine (1) mortality from tagging and (2) increased predation risk to tagged individuals were also conducted and found to

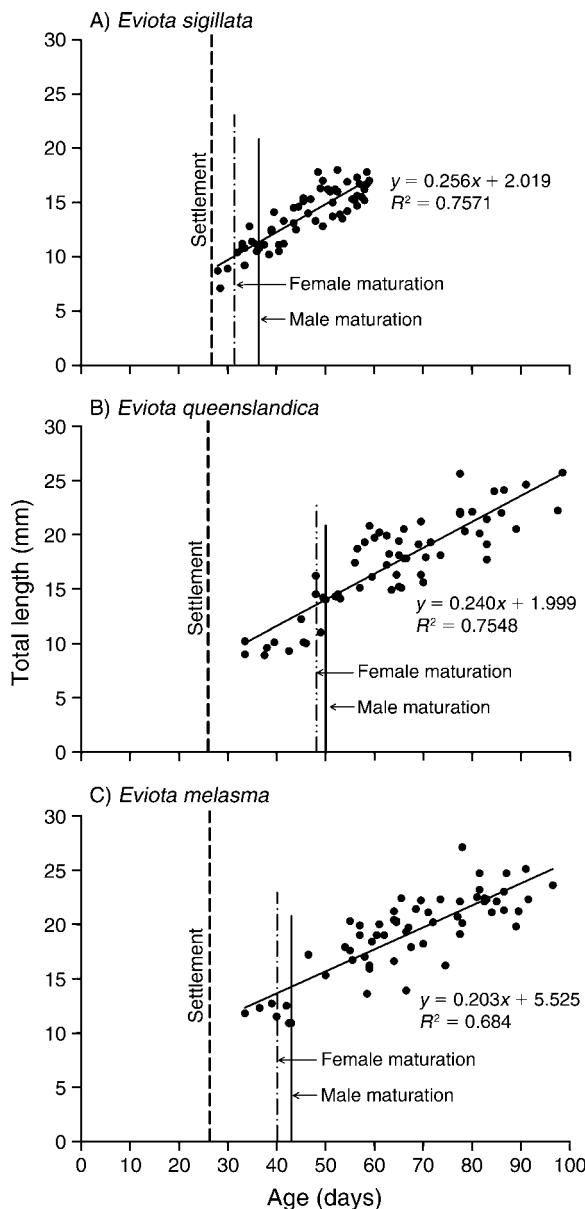


FIG. 1. Size-age regressions summarizing the complete life cycles of three coral reef gobies: *Eviota sigillata*, *E. queenslandica*, and *E. melasma*. Settlement lines denote the mean age and transition point at which each species moves from its pelagic larval phase to a benthic reef-associated phase. Projected rates of growth indicate a linear pattern from postsettlement to death. $N = 60$ for each species.

have no detectable effect (see Depczynski and Bellwood 2005a).

RESULTS

Postsettlement growth in all three species was best described by a linear function with maximum sizes of 18 mm for *Eviota sigillata*, 25.7 mm for *E. queenslandica*, and 27.1 mm for *E. melasma* (Fig. 1A–C). Across all

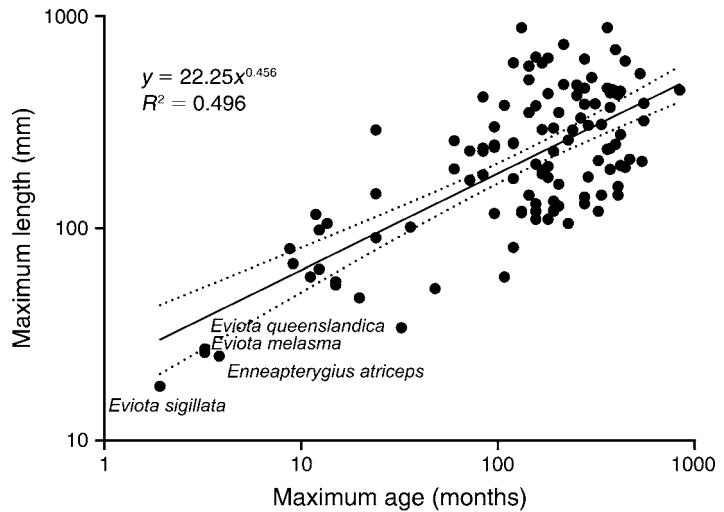
coral reef fish species, the relationship between size and age was highly variable (Fig. 2); however, larger species tended to live longer lives (cf. Nee et al. 2005). Life spans ranged from 59 days in *Eviota sigillata* to 70 years in the surgeonfish *Prionurus maculatus* (447 mm). All three *Eviota* species were located at the extreme bottom end of both the body size and age spectrum. Without exception, all species with life spans of <12 months were smaller than 100 mm.

Maximum life span in *E. sigillata* was 59 days, *E. melasma* 97 days, and *E. queenslandica* 99 days. Projected size at reef settlement in the three species was between 7 and 7.5 mm, with mean pelagic larval durations (PLDs) of 24.2 ± 0.33 days (mean \pm SE) for *E. queenslandica*, 24.7 ± 0.28 days for *E. sigillata*, and 26.2 ± 0.41 days for *E. melasma*. This corresponds to maximum “on-the-reef” postsettlement life spans of 34.3 days for *E. sigillata*, 70.8 days for *E. melasma*, and 73.8 days for *E. queenslandica*. The proportion of total life span represented by PLDs was 41.8% (*E. sigillata*), 27.0% (*E. melasma*), and 24.4% (*E. queenslandica*). For species where longevity and PLD data are available, proportion of total life span equals <1% of total life span (Fig. 3). One notable exception to this pattern exists in another small, cryptic, coral reef fish (*Enneapterygius atriceps*; Longenecker and Langston 2005) where the PLD represents 25.6% of total life span.

Sex ratios showed a strong dominance of females (Table 1) suggesting the possibility of protogyny or harem keeping by males. Already conspicuous by their unusually extreme life history characteristics, the reproductive features of *E. sigillata* stood out among the *Eviota*. Although size at first maturity in both sexes was similar for *E. sigillata* and *E. melasma*, and only marginally larger in *E. queenslandica*, age at maturation occurred earliest in *E. sigillata*. This corresponded to astonishingly short mean generational turnover rates of 46.5 d for this species (*E. melasma* 68.5 d; *E. queenslandica* 74 d). Among the *Eviota*, *E. sigillata* also exhibited the lowest lifetime reproductive output and efficiency, a result of their shorter life spans and the comparatively smaller numbers of eggs they laid at each spawning. Collectively over a lifetime, this equated to a maximum production of just 243 eggs in comparison to the calculated values for *E. melasma* (781) and *E. queenslandica* (1039).

Of the 69 *Eviota* tagged, 27 were resampled, providing a mean mortality rate of 60.9% over the 9-day period. This equates to a daily mortality rate of $6.8 \pm 0.65\%$, $n = 12$). The variance reflects variation among sites, not days. Of these 27 individuals, 77.7% were resampled in the 1-m² net, 14.8% in the 2-m² one, and 7.5% in the 4-m² net, supporting existing evidence of the small home ranges of these fishes. Daily field and expected estimates based on Hoenig’s mortality equation were similar within each of the three *Eviota* species: *E. sigillata* 8.0 and 7.0%, *E. melasma* 5.1 and 4.2%, and *E. queenslandica* 5.6 and 4.2%, respectively.

FIG. 2. Log-log plot of the relationship between maximum size and maximum age in 114 species of coral reef fishes (as described in Appendix A) fitted with 95% confidence intervals (dotted lines). Raw values and corresponding reference sources for each species are in Appendix A.



DISCUSSION

Representing some of the shortest-living and earliest-maturing vertebrates known, the three focal species broaden our understanding of the breadth and range of vertebrate life histories and the potential for reef fishes to contribute to this area of research. Consistent with life history theory, our results demonstrate major shifts in patterns of growth, reproductive strategy, and the pace and timing of sexual development in coral reef fishes, which may help compensate for an exceptionally short life span. Accordingly, maximum size and age in short-lived reef fish species have significant implications for the proportion of the total life span spent in a pelagic larval environment that probably reflects the minimum size at settlement for survival on the reef.

Life spans define the amount of time an organism has to complete all the essential tasks in life, and are therefore of primary importance when examining variations among life history traits and strategies within taxonomic groups. Reef fishes display a wide spectrum of life spans, from surgeonfishes of >60 years (Choat and Axe 1996) to *Eviota sigillata* at 59 days, currently the shortest life span for a vertebrate animal (Depczynski and Bellwood 2005a). At a gross scale, life spans correlate well with body size in animals (Ricklefs and Finch 1995, Brown et al. 2004). However, recent evidence has suggested that this life history relationship is not always applicable to coral reef fishes, because size and age are decoupled within and between reef fish taxa (Munday and Jones 1998, Choat and Robertson 2002). The addition of demographic size-at-age and longevity data for small (<100 mm) cryptic reef fish species at the lower end of the body size spectrum, however, has permitted a reexamination of life history relationships in coral reef fishes.

These additions significantly modify our view of life history patterns in coral reef fishes. First, it establishes that the relationship between size and longevity is maintained at a gross level (cf. Nee et al. 2005), much

as they are in other taxonomic groups, and as predicted by life history theory (Blueweiss et al. 1978, Calder 1984, Brown et al. 2004). Second, the decoupling of size and age may not be applicable to many smaller species due to linear patterns of growth. Third, in spite of the variation in reef fish size-at-age data, growth trajectories themselves appear to share a strong relationship with species life span. In the vast majority of cases, longer-lived species (years) exhibit curving trajectories appropriately modeled by von Bertalanffy growth curves (e.g., Choat and Axe 1996, Choat and Robertson 2002); medium-lived species (months) may exhibit a paired linear model with a break point (sometimes referred to as the broken stick model [see Toms and Lesperance 2003]) marking a distinct slowdown in growth at or around maturity (e.g.,

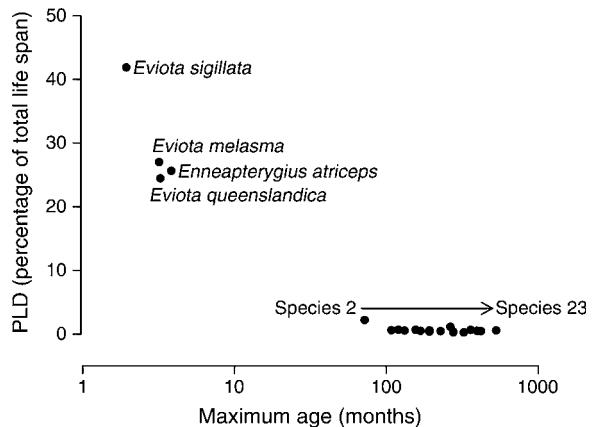


FIG. 3. Relationship between pelagic larval duration (PLD) and maximum longevity (in months, plotted on a logarithmic scale) in 27 species of coral reef fishes for which published estimates of both variables are available. Data shown are the percentage of the total life span. Except for *Eviota* and *Enneapterygius atriceps*, species names and values are listed in Appendix C and correspond to species data points, numbered from left (number 2) to right (number 23). Species 2–23 are further plotted in Appendix D to show the degree of variability within these data points.

TABLE 1. Demographic and reproductive rates of female *Eviota* species.

Species	<i>n</i>	♂:♀ sex ratio	Size and age at first maturity		No. eggs per spawning event		<i>n</i>	Frequency of spawning and interlude range (days)		Lifetime reproductive output (LRO)	Reproductive efficiency (RE)
			Size (mm)	Age (days)	No. eggs (mean ± SE)	Range		Frequency (mean ± SE)	Range		
<i>E. sigillata</i>	75	1:1.6	♂ 11.1 ♀ 11.2	36 34	136.15 ± 4.9	108–163	13	14 ± 0.8	11–17	243	9.7
<i>E. queenslandica</i>	70	1:1.7	♂ 13.1 ♀ 13.9	50 49	291 ± 40.3†	160–374	5	14†		1039	20.8
<i>E. melasma</i>	79	1:1.4	♂ 10.9 ♀ 11.5	43 40	192 ± 26.1†	104–270	7	14†		781	13.7

Notes: Mean frequency of spawning events (*n*) in *Eviota queenslandica* and *E. melasma* were estimated using Taru and Sunobe's (2000) observations on semilunar spawning frequencies in *E. abax* and *E. sigillata*. Lifetime reproductive output (LRO) is based on mean number of spawning events possible in an adult female life span × mean number of eggs per spawning event. Reproductive efficiency (RE) is a measure of the comparative efficiency of reproductive output per day, when adult female life span of each species and lifetime reproductive output are taken into consideration.

† Data from Sunobe and Nakazono (1995).

Hernaman and Munday 2005a); while the shortest-lived species (days) exhibit linear patterns of growth (Fig. 4). These points highlight the importance of including the entire body size spectrum when looking at life history relationships within taxonomic groups. This is particularly important in coral reef fishes where >40% of species are within this <100-mm body size threshold (Ackerman and Bellwood 2000).

All three *Eviota* species exhibit linear growth. Linear growth trajectories in reef fishes are becoming increasingly common as the demography of smaller species is revealed (cf. Kritzer 2002, Hernaman and Munday 2005a). From a life history perspective, the evolution and maintenance of linear growth is remarkable in that there is no apparent trade-off between somatic growth

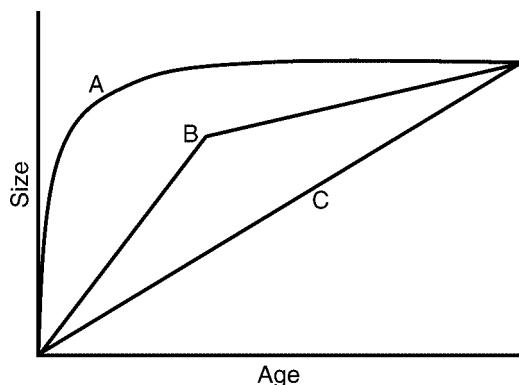


FIG. 4. Reef fish growth models. (A) Von Bertalanffy growth, suited to many longer-lived (years) fish species. In this model, initial growth is rapid and linear before (often abruptly) reaching an asymptotic size. Under this growth scenario, size and age become decoupled at (or approaching) asymptotic size. (B) Breakpoint growth, applicable to many medium-lived (months) fish species. This model consists of two joined straight lines with a "breakpoint" coinciding with (or around) sexual maturation. Further growth slows noticeably at this stage but remains linear. (C) Linear growth as seen in *Eviota* and other short-lived (days) fish species. In this model, size and age share a consistent and ongoing relationship, making size a reliable predictor of age.

and reproduction. The somatic growth/reproduction association is arguably one of the best evidenced of all life history trade-offs in both plant and animal taxa, making the lack of such a relationship here particularly interesting (reviewed in Roff 1992, Stearns 1992, Aday et al. 2003). Supporting reproduction at the same time as maintaining prereproductive growth rates requires substantial amounts of additional energy. There are several lines of evidence to suggest that the energy requirements necessary for linear growth and reproduction are available to these small taxa. Studies on a range of small vertebrates provide good evidence of the capacity of these taxa to amass additional surplus or additional energy, as required. In small species, the capacity to cost-effectively tap into and utilize potentially abundant and ubiquitous small food items is enhanced due to their ability to exploit microhabitats not available to larger-bodied organisms (Churchfield 1996, Clarke 1996, Miller 1996). Thus, the nutritional needs of small ectothermic vertebrates may be quickly and easily met (Clarke 1996). The probability of ready access to an abundant and nutritionally rich diet has been described in *Eviota queenslandica*. This species is able to procure and utilize a broad range of ubiquitous food items (Depczynski and Bellwood 2003). Furthermore, they do so with minimal foraging effort (<5% of their daily activities) (Depczynski and Bellwood 2004). Based on these observations, energetic demands supporting both rapid linear growth and reproduction may be easily met in *Eviota* and other small, linear-growing coral reef fishes.

Rapid linear growth in the young stages of fishes has traditionally been viewed as a strategy to escape size-related predation, the growth-predation theory (Anderson 1988). However, this concept does little to explain the growth patterns seen in *Eviota* species, as their small size ensures that they remain at high risk of predation throughout their lives. The trade-off between female body size and fecundity provides a more realistic explanation for the rapid growth patterns of *Eviota*. Because the relationship between body size and clutch size

is a volumetric one (Wootton 1990), even small increases in female body size may equate to proportionally large gains in clutch size. Under these circumstances, batch fecundity in linearly growing species is expected to increase with maternal age. Unfortunately, our breeding program data are inadequate to elucidate these patterns for *Eviota*. However, the female expectation of producing only two (*E. sigillata*) to four (*E. queenslandica* and *E. melasma*) clutches over a lifetime would directly increase the fitness value of maintaining rapid linear growth throughout life. Overall, the lifetime reproductive output of *Eviota* individuals is extremely low by reef fish standards, an inevitable by-product of their short lives and small body size. In this situation, linear growth to maximize reproductive effort and output via early maturity, a frequent semilunar spawning regime (regardless of season), and parental care of eggs is probably critical for the maintenance of local populations and the continued existence of these three species.

In reef fishes with nonlinear adult growth, the early (prereproductive) portion of life is characterized by steep linear growth, inviting the possibility that small, rapid-linear-growing species such as *Eviota* may simply never reach an asymptotic size due to premature death on the reef, and have simply readjusted the timing of their life cycle events to compensate for their short lives. Three lines of evidence exist in support of this hypothesis. First, *Eviota* kept in aquaria often live substantially longer lives than they would in the wild, reaching an asymptotic size some time after the maximum life spans recorded in wild individuals (M. Depczynski, *personal observation*). However, after an extended period these captive individuals often show an increasingly wasted appearance, decreased locomotor activity, loss of coordination, and a general disinterest or cessation in courting and reproduction with increasing "postnormal" age, all recognized signs of advanced senescence (Ricklefs and Finch 1995, Delbono 2003) and entirely incompatible with survival in the wild. Second, all of the oldest *Eviota* individuals from all species had active gonads with germ cells in varying stages of development, indicating their ability and willingness to continue reproducing despite approaching their maximum longevities. Third, we recorded extremely high daily mortality rates and short life spans of <100 days in all three *Eviota* species, indicating the severe biological time constraints and selective pressure imposed on these small species.

Among life history traits, mortality is probably the least well documented aspect of an animal's life history (Pauly 1980, Purvis and Harvey 1996). Experimental and theoretical results show that high extrinsic mortality throughout prey life selects for rapid growth (Arendt 1997), earlier size and age at maturity co-occurring with higher early-life reproductive investment (Reznick and Endler 1982), and shorter intrinsic life spans (Williams 1957, but see Reznick et al. 2004). Unfortunately, few studies document the entire life cycle of coral reef fish species, incorporating growth, maturation, reproduc-

tion, and rates of mortality (but see Hernaman and Munday 2005a, b), making it difficult to assess how mortality rates shape reef fish life history patterns. We documented extremely high daily field mortality rates of 7–8%, which match estimated otolith-based rates, in all three *Eviota* species, along with the three key life history traits. Size at female maturity, typically an event that happens at 65% of average asymptotic size in fishes (Charnov 1993), happens at 51% of the mean size of the largest 10% of *Eviota queenslandica* individuals (sensu Hernaman and Munday 2005b) and 44% for *E. melasma*, both reductions being consistent with life history theory. Considering *E. sigillata* is the smallest of the three species, we would expect size at maturity to decrease further still. However, size at maturity takes place at ~11–12 mm, representing 63% of the life span in the largest 10% of individuals. Perhaps accounting for this deviation from the expected, Miller (1984) points out that there appears to be a functional body size threshold in gobioid fishes of ~10 mm (e.g., the coral reef species *Trimmaton nanus*: Winterbottom and Emery 1981), below which the teleost frame is unable to support reproduction.

For a coral reef fish species, the lengths of *Eviota* pelagic larval durations (PLDs) are unremarkable (24–26 days). However, as a proportion of the total life span, the PLD is striking. While the PLDs of most reef fish species typically make up <1% of their expected life span (see Appendix C), they make up a quarter to nearly half in *Eviota*. *Eviota* do not represent an isolated case. The PLD of *Enneapterygius atriceps* in the Tripterygiidae is ~25% of its total life span (Longenecker and Langston 2005). This phenomenon suggests that there is a lack of response to reduced life spans that crosses taxonomic boundaries. Under these circumstances, the fixed range of PLDs obviously represents a consistent and real constraint among coral reef fishes, with a pelagic larval phase that places more pressure on very short-lived species to successfully complete all the necessities of life within a narrow postsettlement time frame.

It is interesting to note that despite their very short life spans, we see no reduction in *Eviota* PLD's. The complete lack of any interspecies correlation between reef fish life spans and PLD's overall (Fig. 3), suggests that a minimum functional state (i.e., developmental condition or size) may be necessary before pelagic young are capable of surviving and persisting on the reef (cf. Searcy and Sponaugle 2000). It is clear from the short 7–17 day PLDs of the anemone-fish genera *Amphiprion* and *Premnas*, that PLDs and corresponding size at settlement can be significantly reduced (i.e., *A. melanopus*, 8.1 mm; *P. biaculeatus*, 6.8 mm [Job and Bellwood 2000]). However, as noted by Job and Bellwood (2000), anemone-fish species may be exceptional in that they settle directly into the protective habitats provided by their anemone hosts. For those taxa that do not settle into a protective microhabitat, however, the chances of surviving on a coral reef at such a minute size may be

limited. It is noteworthy that very small (maximum 9.1–30 mm) gobies from the genus *Schindleria* live entirely pelagic lives, despite their close association with coral reefs, and retain juvenile traits rather than undergoing metamorphosis and settlement (Kon and Yoshino 2001, Watson and Walker 2004). Therefore, the size at which *Eviota* recruit to a coral reef likely represents the approximate minimum at which a “free, open-living” pelagic-stage fish is able to settle onto a coral reef.

Overall, our study has shown that the three species of *Eviota* live on the ecological and evolutionary fringe of current life history possibilities for vertebrates. Nevertheless, these miniature species are simply an extension of, rather than a departure from, a life history continuum in vertebrate animals. Life history theory aims to provide evolutionary and ecological explanations for the variability in organism design and trait diversity. Given their extensive range of life history traits, coral reef fishes present us with an ecologically diverse assemblage of vertebrates in which to test basic life history theory.

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APPENDIX A

A list of the 111 species plus three *Eviota* species included in Fig. 2, their maximum age, lengths, and sources (*Ecological Archives* E087-188-A1).

APPENDIX B

A list of the pelagic larval durations (PLDs) of 361 coral reef fish species and their source (*Ecological Archives* E087-188-A2).

APPENDIX C

A list of species for which published estimates of both maximum age and pelagic larval duration are available (*Ecological Archives* E087-188-A3).

APPENDIX D

Log-log plot of the percentage of total life span and maximum ages in months of the 23 larger species (*Ecological Archives* E087-188-A4).