

Life history of the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Blennioidei, Tripterygiidae)

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Synopsis

We described aspects of the life history of the small, cryptic, triplefin blenny, *Enneapterygius atriceps*, collected from the mouth of Kaneohe Bay, Oahu, Hawaii. We examined otolith microstructure to construct a von Bertalanffy growth curve, described a length–weight relationship, performed a detailed dietary analysis, used standard histological techniques to determine size at maturity and reproductive patterns, determined batch fecundity, and used an index of gonadal development to examine spawning seasonality. *Enneapterygius atriceps* is a remarkably short-lived species with low fecundity and a short, well-defined breeding season. Dietary analysis suggests this fish lives and feeds around the bases of dead coral heads. This study generated the first otolith-based growth curve for any member of the Tripterygiidae.

Introduction

The life histories of small, cryptic fishes are largely unknown. However, this is often the most abundant and speciose group of fishes found on coral reefs. For instance, blennioids are the major component by species richness, numerical abundance and biomass of the primary resident reef fishes in the Sea of Cortez (Kotrschal & Thomson 1986). It is likely that these fishes have been ignored because they are not important food or ornamental fishery species. However, high abundances, small sizes, small home ranges, and presumptive short life spans make small, cryptic fishes ideal candidates for field experiments evaluating the importance of ecological processes by examining their effects on population demography. The first step in any such study requires detailed information on the autecology of the experimental organism.

Here, we examine the only Hawaiian member of the family Tripterygiidae. The family is composed of about 172 species found primarily in temperate and subtropical waters and, along with five other families (Blenniidae, Dactyloscopidae, Clinidae, Chaenopsidae, Labrisomidae), forms the Blennioidei (Nelson 1984). We described the age and growth, diet, and reproductive patterns for the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Jenkins 1903). It is a small-bodied (to 30 mm standard length) sexually dichromatic species that lives in habitats exposed to moderate surge.

Methods

We collected all specimens, except those used in the otolith increment validation study, during a

rotenone sampling program conducted at the mouth of Kaneohe Bay, Oahu, Hawaii from 1990 to 1993 (Greenfield 2003). Our sampling area encompassed 21 km² of high-energy coral reef habitat. Because our sampling area was exposed to trade winds and frequent large swells, our sampling schedule was dictated by safe boating conditions. For each sample, we released a 2 l aliquot of rotenone (1500 ml Synpren[®] fish toxicant, 500 ml powdered *Derris* root, plus 300 ml clear Ivory[®] dish detergent) in an average 13.2 m² area in depths of 4–11 m. We used SCUBA and hand nets to collect all specimens.

We collected specimens used for age and growth analysis with 10% quinaldine in alcohol, placed them on ice in the field and refrigerated them in the laboratory until processing. We fixed all other specimens in formalin for 24 h and preserved them in 70% ethanol. We used dial calipers to measure standard and total lengths (SL and TL, respectively), to the nearest 0.5 mm, of all 228 specimens.

Age and growth

We removed saggitae, or saccular otoliths, (Figure 1a) and measured their long axis using dial calipers. We prepared transverse sections (Figure 1b) by mounting the otoliths, anterior end up, on glass microscope slides in thermoplastic glue (Crystal Bond[®] #509), wet grinding on a series of 400, 600, and 1200 grit sandpaper to a region just anterior of the core, then polishing with a series of 0.3 and 0.05 μ m alumina slurry on felt. We then flipped the otoliths so that the polished surface faced the slide, and repeated the grinding and polishing process until we reached a region just posterior to the core.

We counted otolith increments at 600 \times on a compound microscope. We calculated the mean standard length and mean age for fish specimens from apparent 10 d age groups. We used these grouped data and followed the methods outlined in Everhart & Youngs (1992) to construct a von Bertalanffy growth curve. Briefly, we estimated L_{∞} using a Ford–Walford plot of standard length data, whereas we estimated K and t_0 from a plot of $\ln(L_{\infty} - l_t)$ vs. age. We examined the relationship between fish and otolith length by linear regression analysis. We used total body mass data from the

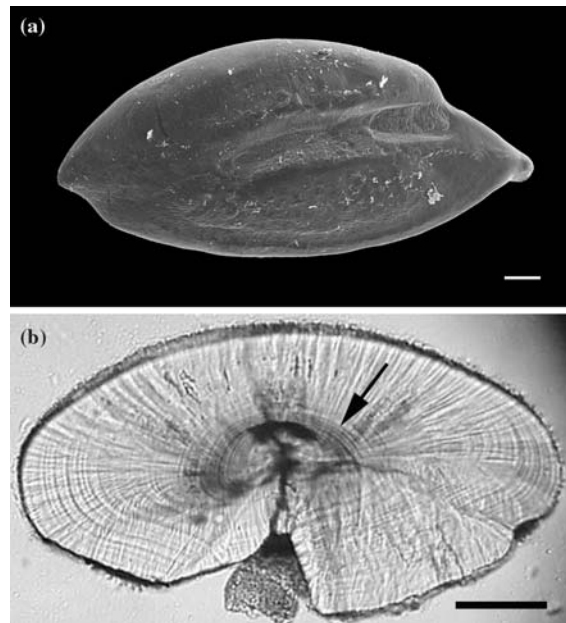


Figure 1. Sagitta of *E. atriceps*. (a) Scanning electron micrograph of medial side. (b) Transmitted light micrograph of a ground and polished transverse section from a 24 mm specimen. We counted 86 increments. Arrow points to an abrupt change in color and increment pattern presumed to result from settlement. Scale bars = 100 μ m.

reproductive patterns and batch fecundity study (below) to generate a length–weight regression.

Diet

We randomly selected 20 specimens from adult-size individuals (≥ 16 mm SL) collected during the rotenone sampling program. We identified all prey items contained within the portion of the gut from the beginning of the esophagus to the moderate constriction posterior to the second turn (representing approximately 2/3 of the entire gut length) of the gut to at least class level and order where possible. Because malacostracan crustaceans were the major prey type, we identified them to species when possible. We used a squash plate modified from Ross (1974) to estimate the volume of prey. Briefly, we compared the diameter of a prey item compressed between two microscope slides held a constant distance apart by coverslips to a regression equation for a known volume of water and its diameter in the same apparatus.

We calculated the Pinkas et al. (1971) Index of Relative Importance (IRI) for each prey class, where:

$$\text{IRI} = (\%N + \%V) \cdot \%FO.$$

Here %N is percent number, the number of prey items belonging to a given class relative to the total number of prey items. Percent volume (%V) is the volume of prey items belonging to a given class relative to the total volume of prey. Percent frequency of occurrence (%FO) is the number of fish containing prey of a given class relative to the number of fish examined. We also calculated IRI values for prey orders where known. For these calculations we used data from class-level identifications when prey could not be identified to order. We present %IRI as an estimate of the importance of each prey class and order.

Reproduction

We determined size at sexual maturity by histological examination of gonads. We removed the head and caudal portions of each fish, noted head color (mature males have black heads, whereas females and immature males have red heads), and decalcified the remaining trunk section in a 1N solution of Cal-Ex[®] for 24 h followed by a rinse in tap water for an equal period. We dehydrated the tissue in a graded methanol series, cleared it with toluene, and embedded it in Paraplast-Plus[®]. We serially sectioned specimens at 7 μm on a rotary microtome, affixed the sections to glass microscope slides, and stained them with Harris hematoxylin and alcoholic eosin. We scored the gonads of each specimen as male or female and recorded their relative development. We considered males sexually mature when spermatids or spermatozoa were present within the testes. We scored ovarian development into four stages according to Wallace & Selman (1981). Briefly, these stages are primary growth (stage I), yolk-vesicle stage (stage II), vitellogenesis (stage III) and maturation (stage IV). We classified ovaries according to the most advanced oocyte stage present. We considered females mature with the onset of vitellogenesis (stage III). We report size at sexual maturity as the size at which 50% of individuals sampled of a given sex are mature. We examined 26 male and 17 female *E. atriceps*.

We used a modified gonosomatic index (GSI) to test for seasonal variation in female reproductive output. We re-hydrated preserved specimens in water for several hours, blotted them dry and weighed them to the nearest 0.1 mg on a digital balance. We removed, blotted dry, and weighed to the nearest 0.001 mg on a CAHN C-30 micro-balance the ovaries of each fish. We estimated the relationship between gonadal and somatic mass (G/S) by the equation: $G/S = (\text{gonad mass} / (\text{total body mass} - \text{gonad mass}))^{-1} \cdot 100$. We used collections containing a majority of gravid individuals for batch fecundity analysis; we measured oocyte diameter to the nearest 0.01 mm using a stage micrometer and grouped each into 0.1 mm size classes for histological validation. Initially we counted all oocytes greater than 0.1 mm diameter in a single ovary. A histogram of these data revealed a bimodal size distribution in oocyte diameters, the larger mode being composed of oocytes 0.4 mm and greater (Figure 2). We assumed (*sensu* Hunter et al. 1985 unpublished data) these oocytes formed the next spawning batch and counted oocytes ≥ 0.4 mm from both ovaries in the remaining specimens.

Results

Age and growth

Despite four attempts at chemically marking otoliths (twice each by 24 h immersion in alizarin

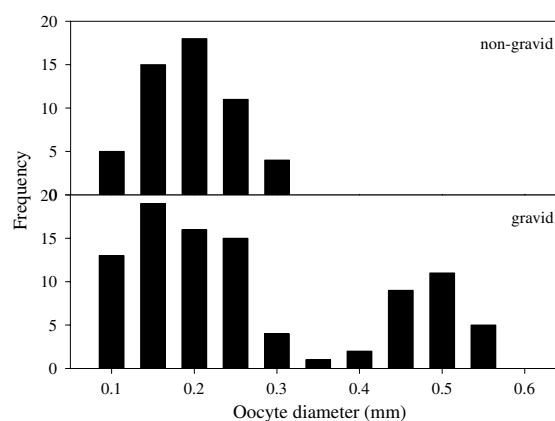


Figure 2. Size-frequency histograms of oocyte diameters from a non-gravid and a gravid 20 mm *E. atriceps* (53 and 95 oocytes examined, respectively).

complexone or oxytetracycline solution), we were unable to validate increment periodicity. Growth of *Enneapterygius atriceps*, assuming each otolith ring represents 1 d in age, can be described by a von Bertalanffy curve (Figure 3a).

The relationship between otolith length and SL is linear (Figure 3b). A power function best described the relationship between SL and total body mass (Figure 3c).

Diet

The diet of *E. atriceps* consists of small, benthic invertebrates. Table 1 shows that most prey are from classes typically thought of as macrofauna (retained on a 500 μm sieve). Small bivalves and gastropods (average volume 0.21 and 0.37 μl ,

respectively), barnacle appendages, mites, chironomids (B. Font, personal communication), ostracods, and polychaetes were occasionally eaten. However, malacostracan crustacea were the dominant macrofaunal prey. Meiofaunal (passing through a 500 μm but retained on a 63 μm sieve) copepods are also important.

Patterns of importance change when prey are grouped into orders. The most important malacostracans are amphipods followed by tanaids, then isopods. However all of these orders are less important than harpacticoids, the only order of copepod eaten by *E. atriceps*. More fish ate harpacticoids (95%) than amphipods (85%) or tanaids (55%). Harpacticoids were also numerically dominant (45%), followed by amphipods (23%) then tanaids (10%). However amphipods were

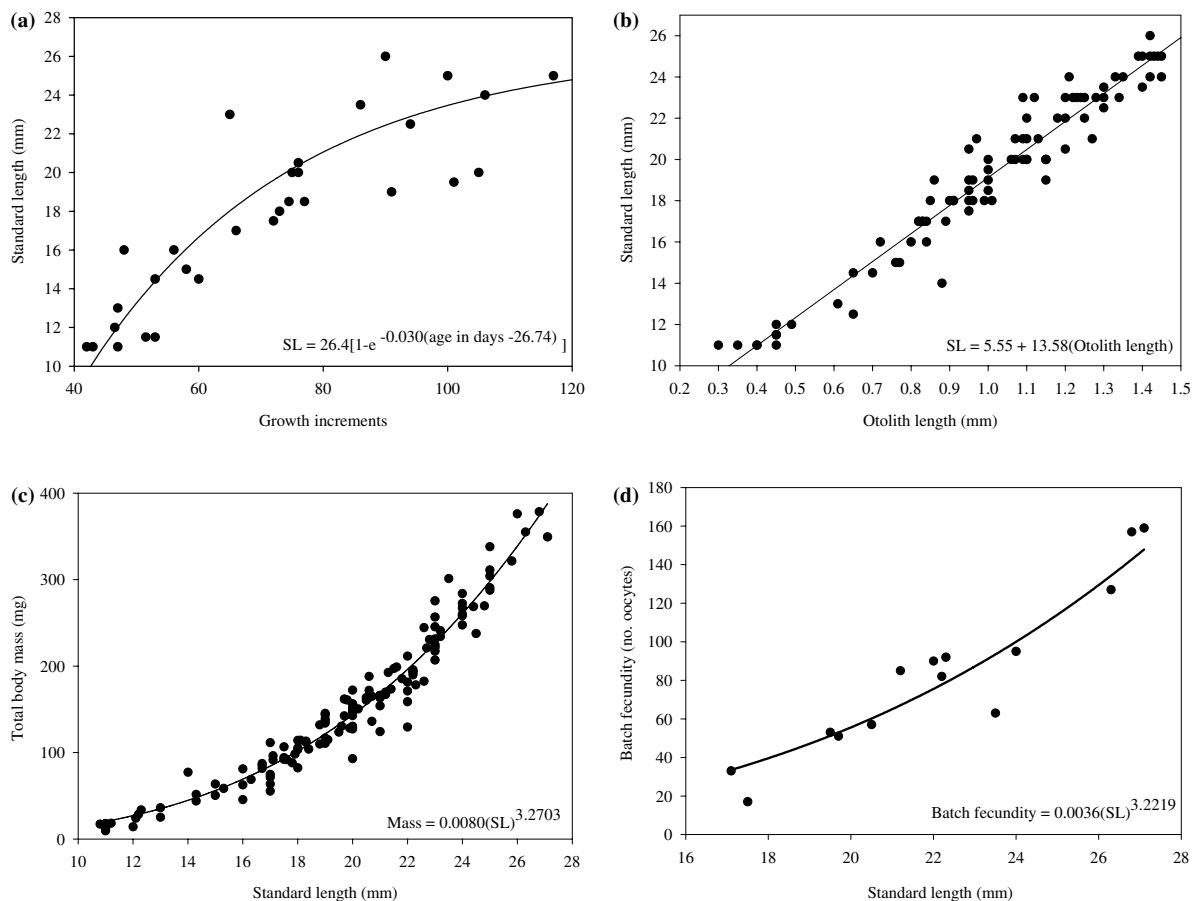


Figure 3. Relationships between standard length (SL) in mm and various life history parameters for *E. atriceps*. (a) Age vs. length and von Bertalanffy growth curve; $R^2 = 0.776$; $n = 30$. (b) Otolith length vs. standard length; $R^2 = 0.939$; $n = 89$. (c) Standard length vs. total body mass; $R^2 = 0.955$; $n = 136$. (d) Standard length vs. batch fecundity; $R^2 = 0.896$; $n = 14$.

Table 1. Percent IRI values for the prey of *E. atriceps* ($n = 20$).

Class	%IRI	Order	%IRI
Arachnida	0.06	Prostigmata	0.07
Bivalvia	0.04	?	0.05
Cirripedia	1.85	?	2.06
Copepoda	42.37	Harpacticoida	47.13
Gastropoda	1.10	?	1.22
Insecta	0.45	Diptera	0.50
Malacostraca	53.54	Amphipoda	38.17
		Isopoda	0.58
		Tanaidacea	9.58
Ostracoda	0.51	?	0.57
Polychaeta	0.07	?	0.08

volumetrically dominant (40%), followed by harpacticoids (25%) then tanaids (14%).

We identified 57% of the malacostracans to taxa lower than order. Five of the amphipods were the caprellid, *Metaprotella sandalensis*. All other amphipods were gammaridean: one *Maera kaiulani*, one *Photis* species, two *Gammaropsis* species (at least one was *Gammaropsis haleiwa*), one *Ischyrocerus oahu*, and eight *Cerapus* cf. *tubularis* (here the genus is first reported for Hawaii). These 18 individuals were 46% of the total number of amphipods eaten. We identified 88% of the tanaids. Fourteen were *Leptochelia dubia* and one was *Anatanais insularis*. One of the four isopods eaten was *Munna acarina*.

Reproduction

Testes of *E. atriceps* were spermiated in individuals as small as 14 mm SL, with 50% of males mature at 16 mm. All males ≥ 17 mm were mature and all mature males had the black head color from which the species gets its common name. Ovaries contained stage III oocytes in individuals as small as 15 mm. Fifty percent of females were mature by 17 mm and all were mature by 18 mm. When data for each sex are combined, 50% of individuals are mature at 15 mm.

The testes of *E. atriceps* are paired and appear crescent-shaped in cross section. The germinal portion of the testis is divided into lobules which themselves contain germ cells in various stages of spermatogenesis (i.e., spermatogonia, spermatocytes, spermatids, and spermatozoa). The medial

part of the testis is centered about a large eosinophilic testicular gland which surrounds a small duct, presumably used in sperm transport. Posteriorly these ducts emerge from the gland, enlarge, and unite to form a median spermatic sinus. In a few individuals this sinus was filled with spermatozoa.

Females also possess a bi-lobed gonad. Immature females have small, ellipsoid ovaries limited to the dorsum of the visceral cavity. Oocytes in these individuals were exclusively stage I. Ovaries of recently matured females (17–22 mm SL) were larger but often unequal in size and relative development. Oocytes in these individuals ranged from stage I to III, and numbers of stage III oocytes often varied significantly between ovaries of a single individual. In contrast, ovaries of the largest females (≥ 24 mm SL) were similar in size, and contained approximately equal number of advanced-stage (III and IV) oocytes. Ovaries in these individuals typically filled the entire visceral cavity posterior to the stomach.

We found no evidence for sequential hermaphroditism in *E. atriceps*. A *t*-test for a sex-based bimodal size distribution was not significant ($p = 0.52$). Likewise, classic histological signs of sex change (see Sadovy & Shapiro 1987) were absent: testes lacked a lumen or brown bodies, and ovaries did not contain spermatogenic tissue. *Enneapterygius atriceps* is apparently a gonochore.

Batch fecundity, as estimated during the spawning peak, is a cubic function of standard length (Figure 3d). However, the data fit a linear regression nearly as well (number of oocytes = $-193.85 + 12.51(\text{SL})$; $n = 14$; $p < 0.001$; $R^2 = 0.889$).

Histological examination of the development of each oocyte size class supports the choice of ≥ 0.4 mm oocytes as the spawning batch. These oocytes corresponded to stages III and IV whereas those ≤ 0.3 mm corresponded to stages I and II. Figure 4 shows the relationship between an index of female gonadal development (G/S) and time of year. G/S is highest in May, but drops considerably in the late summer months of October and November. This trend is apparent over several years, suggesting that *E. atriceps* has a regular spawning season.

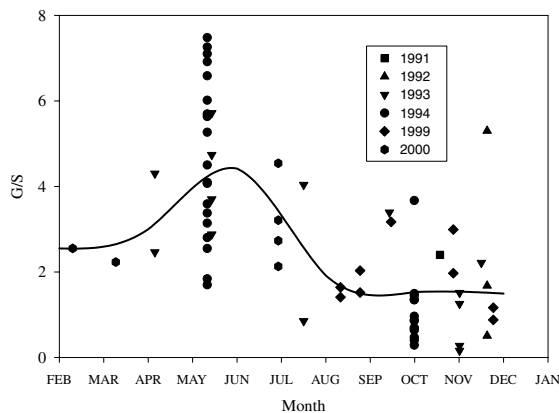


Figure 4. Seasonal trend in gonosomatic index (G/S) for female *E. atriceps*.

Discussion

This study generated the first otolith-based growth curve for any member of the Tripterygiidae. Using the von Bertalanffy equation to describe the growth of *Enneapterygius atriceps* is appropriate because the relationship between $\ln(L_\infty - l_t)$ and apparent age is linear (see Everhart & Youngs 1992). Because we could not validate the periodicity of otolith ring formation, the growth curve we constructed is based on the assumption that rings are formed daily. This assumption seems justified by Shafer's (2000) demonstration that otolith ring formation is daily in a Hawaiian goby, *Bathygobius coalitus*. This and other gobies (Gill et al. 1996, Iglesias et al. 1997) have similar age-length relationships over the size range of the individuals used in this study. If ring formation is daily, *E. atriceps* is a remarkably short-lived species: The oldest fish in our sample lived 117 d (Figure 3a).

Otoliths will be useful to describe the importance of *E. atriceps* in the diets of other fishes. Detailed descriptions of piscivore diets are often difficult because fish remains are digested beyond the point of identification or accurate size measurement. The shape of *E. atriceps* otoliths (Figure 1a) is unique among 160 fishes collected in the same area as this study (Dye & Longenecker 2004) and, because *E. atriceps* is the only Hawaiian tripterygiid, is presumably unique among all Hawaiian fishes. Thus otolith shape allows species-level identification. Longenecker is describing

energy flow on the Kaneohe Bay forereef, and used otolith shape to determine *E. atriceps* is the second most abundant prey item in the stomachs of the mullid, *Parupeneus cyclostomus*, and was eaten by half of the individuals examined. The length (Figure 3b) and weight (Figure 3c) regressions can be used to estimate the size of fish that produced the otoliths (Echeverria 1987, Gamboa 1991).

The diet of *E. atriceps* is similar to those of other tripterygiids. Prochazka (1998) found that caprellid amphipods dominated, by volume and occurrence, the diet of *Cremnochorites capensis* from South Africa. Kotrschal & Thomson (1986) found that 4 of 5 triplefin species from the Sea of Cortez ate primarily amphipods by volume. Gammari-dean amphipods were most important by weight (30%) and frequency of occurrence (92%), while harpacticoids were most abundant in the diet of *Tripterygion dalaisi* from the Mediterranean (Zander 1982).

Results from our species-level identification of malacostracan prey, along with the knowledge that most triplefin blennies are territorial (Mayr & Berger 1992), suggests *E. atriceps* forages in a specific habitat and manner. The amphipod, *Cerapus tubularis*, is tubicolous (Lowry & Berents 1989), and many of the *Cerapus* eaten were still in their tubes. Although we did not find tubes along with the *Leptocheilia dubia* eaten, this ubiquitous tanaid also lives in tubes (Mendoza 1982, Holdich & Jones 1983, Krasnow & Taghon 1997). The distance larger triplefin species will travel from shelter is known to range from 59 cm in *Tripterygion varium* (Jones & Thompson 1980) to 150 cm in *Tripterygion delaisi* (Goncalves & Almada 1998). Because we most frequently found *E. atriceps* in algae-encrusted skeletons of the rose coral, *Pocillopora meandrina*, it appears that this fish concentrates its feeding efforts on tubedwelling organisms found in or around dead coral.

As in other Hawaiian reef fishes (Walsh 1987), spawning intensity in *E. atriceps* appears to vary seasonally, with a peak in early summer and decreased effort in late summer (Figure 4). Otolith microstructure (Figure 1b) suggests that settlement occurs at ca. 30 d. Given that sexual maturation occurs at 15 mm, or ca. 55 d, the time between settlement and maturation is very short (Figure 3a). Furthermore, the oldest individual in

our collections was 117-d-old, suggesting that this species has a 2 mo reproductive life. Certainly, seasonality has been reported in temperate species of triplefins (e.g., De Jonge & Videler 1989). However, maximum lifespan in these species is 2–3 yr whereas the oldest *E. atriceps* we collected was less than 120-d-old. This raises the questions: why is this species so short-lived, what factors trigger annual seasonality in a species with an estimated generation time substantially less than 1 yr, and how do populations persist?

High mortality and thus short life span is frequent among small-bodied fishes. For instance, the goby *Coryphopterus glaucofraenum* appears to have an average adult life span of 10 weeks (Forrester et al. 2002) whereas the endemic Hawaiian ruby cardinalfish, *Apogon erythrinus*, reaches a maximum size of 40 mm SL and has a maximum life span of 120 d (R. Langston, unpublished data). These short life spans may be due to high predation rates. Of all small, cryptic fishes in our study area only a gobiid, *Eviota epi-phanes*, appears to experience more predation (K. Longenecker, unpublished data). This species settles at 7 mm SL, matures at 10 mm and attains a maximum size of 13 mm in our study area (Longenecker 2001). Our preliminary analyses suggest its maximum life span is even shorter than that of *E. atriceps* (ca. 50 d).

Despite the prevalence of an early summer spawning peak among Hawaiian fishes, the adaptive significance of the pattern is unknown. However, it appears that *E. atriceps* may persist throughout the year, despite a short life span and a single spawning peak, from a continuous but reduced spawning effort. GSI analysis shows changes in spawning effort rather than whether spawning occurs. Thus, it is possible that some fish are spawning during the off-peak months, but that batch fecundity and/or egg size is lower, leading to a reduction in GSI values. Langston (2004) examined reproductive seasonality of the small-bodied, short-lived Hawaiian sandburrer, *Crystallodytes cookei*, using both GSI and a histological index of ovarian development. Similar to *E. atriceps*, GSI for *C. cookei* peaked in early summer (March–July) and was depressed during the late summer months (August–November); however, histological evidence of spawning (e.g., presence of mature oocytes and post-ovulatory

follicles) was present in three of four months in which the GSI was depressed.

Batch fecundity is low in *E. atriceps* (Figure 3d), whereas in larger-bodied, temperate tripterygiids, batch sizes may exceed 1500 (Thompson 1986). Based on the relatively low number of oocytes in each batch, it is probable that female *E. atriceps* spawn an entire clutch in a single event rather than partitioning batches between multiple males and nesting sites. Although a cubic function best described the relationship between batch fecundity and standard length, a linear model fit the data nearly as well. This linear relationship makes *Enneapterygius atriceps* a good candidate for studies of environmental effects on recruitment success because the reproductive potential of a population can be modeled on adult abundance. All such models assume a linear relationship, but few fishes have length–fecundity relationships that satisfy this assumption (Everhart & Youngs 1992).

We found no evidence for ‘sneak spawning’ in male *E. atriceps*. All mature males were readily sexed by the dark black coloration on their heads. In contrast, De Jonge & Videler (1989) found *Tripterygion* sneaker males with large testes and female coloration. Although female *E. atriceps* often possessed some slight pigmentation on the head as well, these markings were usually much more diffuse than those for mature males.

The exact function of the testicular gland in male *E. atriceps* is unclear. In other blenniids, it has been hypothesized to serve in nutrition of sperm (Lahnsteiner et al. 1990, Rasotto 1995), differentiation and phagocytosis of spermatozoa (Lahnsteiner & Patzner 1990, Lahnsteiner et al. 1990) and in the production of viscous seminal fluid (Lahnsteiner & Patzner 1990, Lahnsteiner et al. 1990, Rasotto 1995). Whatever the exact function, accessory testicular organs occur widely in demersally spawning species in which males provide parental care. Indeed, all blennioids are thought to deposit demersal oocytes in male-defended shelters (Rasotto 1995). Thompson (1986) found that males of a subtropical triplefin species, *Forsterygion varium*, effectively defended territories from egg predators and excluded other males from the nest area. This male nest-attending is characteristic of all tripterygiids (Mayr & Berger 1992).

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