

Abstract.—Squirrelfish of the genus *Myripristis* are valued in small-scale fisheries throughout much of the tropics. The life history and species biology of most of these soldierfishes is poorly known. For the brick soldierfish, *M. amaena*, in Hawaii and Johnston Atoll, we found that sexual maturity for both sexes was reached between 145 and 160 mm standard length at about six years of age — a large fraction of the apparent maximum size and lifespan. Fecundity was relatively low and increased as the fifth power of body weight. Spawning peaked from about early April to early May, and a secondary peak occurred in September. *Myripristis amaena* is a nocturnal predator, feeding mostly on meroplankton, especially brachyuran crab megalops, hermit crab larvae, and shrimps, but also taking a variety of benthic prey. In pristine fish communities, holocentrids were abundant, quantitatively important (often dominant) reef predators and prey. *Myripristis amaena* (and probably other common and important soldierfish) seems to be relatively long lived (at least 14 years), slow growing, and late maturing. The populations suffer considerable natural predation and depend mainly on the largest and oldest fish for reproduction. Heavy, unregulated fishing of these soldierfish, especially at prereproductive size, may severely reduce populations.

Reproductive and trophic ecology of the soldierfish *Myripristis amaena* in tropical fisheries

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Soldierfish, Myripristinae, of the squirrelfish family, Holocentridae, occur widely throughout the tropics (Greenfield, 1965, 1968, 1974). They are typically abundant and are an important component of commercial, recreational, and subsistence fisheries in much of the world's tropics. Throughout most of the central and western Pacific Ocean, the brick soldierfish, *Myripristis amaena* (Castlenau), is an important member of this group (Greenfield, 1968). It contributes significantly to fish communities and to fishery catches in shallow reef and rocky habitats. It is particularly important in the recreational fishery at Johnston Atoll (JA), where it is typically the species caught in greatest abundance (Irons et al.¹). It is also common in catches throughout the Hawaiian archipelago.

Relatively little quantitative information has been published about the life history and biology of species of the genus *Myripristis*, and very little is available about *M. amaena* in particular. Data about diets are available for only a few species of *Myripristis*; for most of these, sample sizes are small (e.g. 14 specimens for *M. amaena*; Hobson, 1974). Results on age and growth from our studies of the JA population of *M. amaena* have been

reported (Dee and Radtke, 1989). There have been no thorough published studies of the reproduction of *M. amaena* or closely related species. Because of the wide distribution, considerable abundance, and substantial fishery importance of *M. amaena*, we undertook to describe more fully its food requirements and trophic position in the community and to quantify the reproductive characteristics that affect the dynamics of its populations. The parameters we determined may also provide reasonable first approximations for similar *Myripristis* species that are less well studied. The results will contribute to an informed approach to management of species that are now typically unmanaged and probably overfished in most localities with even moderately dense human populations.

The JA population of *M. amaena* was the major focus of this study for several reasons. Many biological and ecological characteristics of *M. amaena* (e.g. size, morphology, habits, habitat used, fishery value) seem to be representative of a num-

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¹ Irons, D. K., R. K. Kosaki, and J. D. Parrish. 1990. Johnston Atoll resource survey. Final report of Phase Six (21 July 1989–20 July 1990). Project rep. to U.S. Army Engineer District, Honolulu, HI, 150 p.

ber of common soldierfish species. Johnston Atoll provided a logistically good base for study, where *M. amaena* was the dominant *Myripristis* species, with populations not seriously depressed by fishing. The species was plentiful and easily collected at many locations throughout the year, and a good range of sizes was readily available. The importance of *M. amaena* in the fishery at JA facilitated collection of specimens and fishery data.

Materials and methods

Specimen collection and handling

Most specimens used in all analyses were taken at Johnston Atoll, a remote, coral-rich, oceanic pinnacle about 1250 km SW of Honolulu (Halstead and Bunker, 1954; Amerson and Shelton, 1976; Randall et al., 1985; Maragos and Jokiel, 1986). Smaller collections were made from a rich, fringing coral reef tract at Puako in South Kohala on the leeward coast of Hawaii Island (Hayes et al., 1982). A few specimens were collected from the almost uninhabited Northwestern Hawaiian Islands (NWHI), primarily from shallow, coralline areas at French Frigate Shoals and Midway (located about 750 and 2000 km, respectively, northwest of Honolulu).

Specimens from all three locations contributed to size-frequency analysis, visual assessment of gonad condition (maturity), and analysis of gut contents. At JA and Puako, gonad weight was taken to determine reproductive season and size at first reproduction; at JA, gonad samples were preserved for histological examination and estimation of fecundity.

Most specimens at all locations were collected from shallow waters (<15 m). The major methods of collection were spearing, bait casting with a line, and some spot applications of ichthyocide. At JA, we collected specimens from several sites inside the lagoon and just outside the barrier reef. Collections and extensive underwater observations were made at frequent intervals between February 1984 and January 1986. Sampling was less intensive in some months because of constraints on travel to JA. At Puako and in the NWHI, specimens were collected rather widely within coralline habitats. At Puako, about half the specimens were collected as quickly as feasible (May–June 1981), once the species was found to be in reproductive season. Other collections there were distributed throughout the year. In the NWHI, specimens were collected in March, April, May, August, and November.

Standard (SL), fork (FL), and total (TL) lengths of all captured specimens were measured to the nearest millimeter, and weights were taken to the near-

est 0.1 g. (Appendix A provides functions, fitted by regression, to convert between SL, FL, and TL.) Whole guts and gonads were excised and preserved in 10% buffered formalin for further analysis. Some specimens were frozen whole and stored for some weeks or months before processing.

Source of size-frequency data

At JA, Puako, and the NWHI, length and weight data from all specimens collected for other purposes were available for size-frequency estimation. In addition, at JA, creel census data were obtained from fishermen's catches on many days over the period of study. Fish landed by boat and shore fishermen were examined, and each specimen was measured and weighed as above. These data provided a much larger and possibly more representative sample than our collections alone.

Feeding

The volume of each complete gut specimen was measured by displacement of water before and after the gut was opened and all contents removed. The total volume of contents was determined by difference. All diet items were sorted into systematic categories and identified to the lowest possible taxa. For each prey category, the number of individuals, length, extent of digestion, location in gut, and volume were recorded. Whole reference specimens were used as an aid in identifying prey items and estimating the original size of the prey by comparison of the dimensions of recognizable parts. Volume of remains in each prey category was estimated by displacement of water (Wolfert and Miller, 1978).

A measure of overall importance of each prey category was calculated by using the Index of Relative Importance (IRI), as defined by Pinkas et al. (1971):

$$\text{IRI} = \text{frequency } \% \times (\text{numerical } \% + \text{volume } \%),$$

where frequency % = (the number of guts containing prey of one category divided by the total number of guts that contained any identifiable prey) \times 100;

numerical % = (the number of individuals of one prey category divided by the total number of prey individuals found in all the guts) \times 100;

and volume % = (the volume of one prey category divided by the total volume of all prey found in the guts) \times 100.

Reproduction

Gonads of 430 specimens from JA were visually examined macroscopically and classified (based on their size, color, texture, and morphology) as male, female, immature, or unknown. A subsample of these gonads from specimens collected during probable reproductive and nonreproductive periods was removed, wet weighed to the nearest 0.001 g, and preserved in 70% isopropyl alcohol for further examination. Gonads selected for histology were prepared and embedded by using Kahles solution (Guyer, 1953, p. 236) with a graded series of ethyl alcohol and butyl alcohol dehydration. Embedded subsamples taken from the anterior, middle, and posterior regions of the selected gonads were then sectioned at 5 and 10 μm , mounted on plain microscope slides, and stained by using Delafield hematoxylin and eosin Y techniques (Humason, 1979, p. 112, 119–123).

Size at first reproduction (SFR) was estimated based on visual examination of gonads and by using the gonadosomatic index (GSI), where:

$$\text{GSI} = (\text{gonad wet weight/whole body wet weight}) \times 100.$$

The GSI was plotted against SL for male and female *M. amaena* collected from periods during which the species seemed to be reproductively active. A sharp rise in the GSI at some length indicated the SFR. The SFR was also estimated based on histological examination of gonads from specimens collected during the April 1984 spawning peak. Eggs were examined for size and stage of development from sections of 11 females representing a range of sizes. Staging was based on size, morphology, and staining proper-

ties of eggs (Khoo, 1978; Wallace and Selman, 1981). Testes from five males were examined histologically for presence of sperm.

Spawning season was estimated by plotting GSI against month of capture for 99 sexually mature males and females (larger than 145 mm SL) collected throughout the sampling period. Histological sections of samples from March, April, May, July, and August 1984 were examined for further validation of reproductive periods.

We did not identify individual clutches of ova in females. Based on the histology, we identified ova ≥ 0.4 mm on the major axis as being in an advanced stage of yolk development and defined this stage as mature (Table 1, See Fig. 3). Our fecundity value is an estimate of the number of such ova in a female specimen. Ovaries from 12 gravid females collected at JA during the January 1986 spawning peak were used to estimate fecundity. Three 0.02-g aliquots were taken from the midsection of each ovary. All mature ova (≥ 0.4 mm on the major axis) were counted with the aid of a binocular dissecting microscope. Fecundity, F , was estimated for each female from the formula:

$$F = ((N_1 + N_2 + N_3)/3) \times (G/A),$$

where N_1, N_2, N_3 = the number of mature ova in each aliquot;

G = total gonad weight (g);

A = weight of a gonad aliquot (0.02 g).

For specimens from Puako, the same procedures were followed except that no histological preparation or examination was done, and ripeness was estimated simply on the basis of visual appearance of

Table 1
Stages of development of oocytes in the brick soldierfish, *Myripristis amaena* (also see Fig 3).

Stage	Oocyte diameter (mm)	Description
oogonia and primary growth	0.01–0.04	scant cytoplasm; centrally located nucleus; single large nucleolus; stains dark red
perinuclear	0.04–0.056	multiple nucleoli around inner side of nuclear membrane; stains dark purple
secondary growth and yolk vesicle	0.056–0.14	clear-staining cortical alveoli begin as ring at cytoplasm periphery, then increase in size and occupy whole cytoplasm
yolk granule	0.14–0.40	true vitellogenesis; red-staining yolk granules begin to form around cytoplasm periphery (early vitellogenesis) then increase in size and occupy whole cytoplasm (late vitellogenesis); zona radiata first appears
maturation	0.40–0.54	yolk granules fuse into yolk "plates" which stain light blue; fusion begins at center and spreads throughout cytoplasm

the gonad and GSI. The SFR, but not spawning season, was estimated quantitatively by using these measures. Egg sizes were not measured, and fecundity was not estimated.

Results

Feeding

Guts from 64 specimens collected at JA at night contained identifiable prey items (Table 2). Crab larvae

dominated the diet, producing much larger IRI values than any other major systematic group (Table 3). Brachyuran megalops (mostly Portunidae) were found in over 90% of the analyzed guts. Despite their relatively small size, they were important in volume (28%) as well as numbers (38%). Hermit crab larvae (Paguroidea) were present in over half the guts, and alpheid shrimp in slightly less than half. Both these groups provided significant fractions of all prey numbers and volume and had large IRI values; hermit

Table 2

Diet of *Myripristis amaena* based on 64 specimens from Johnston Atoll, 9 from the Northwestern Hawaiian Islands, and 22 from Puako, Hawaii Island. Results reported by Hobson (1974) based on 14 specimens from Kona, Hawaii Island, are also included for comparison. Table shows the percent of predator individuals that consumed each prey (F), and the percent of all numbers (N) and volume (V) provided by each prey. Values for the highest systematic levels are printed in bold. (See Table 3 for Indices of Relative Importance for these highest level groups.)

Prey category	Numerical percent ¹			Volume percent ¹				Frequency percent			
	Johnston Atoll	N.W.	Puako	Johnston Atoll	N.W.	Hawaii Island		Johnston Atoll	N.W.	Hawaii Island	
		Hawaiian Islands	(Hawaii Island)		Hawaiian Islands	Puako	Kona ²		Islands	Puako	Kona ²
Crabs ³	60.8	33.3	71.2	50.3	8.4	35.0	75.1	100	11.1	68.2	100.0
Portunidae	37.8			27.6				90.6			
Paguroidea (hermit crab)	23.0		0.3	22.7		4		59.4		4.6	
Galatheididae			8.5			7.7				4.6	
Shrimp	11.8	22.2	11.4	10.8	8.4	>2.0	9.3	46.9	11.1	27.3	28.6
Alpheidae	11.8		3.5	10.8		0.4		46.9		13.6	
Palaemonidae			2.0			0.6				13.6	
Hippolytidae			3.0			>0.8				13.6	
Caridea unidentified			0.6			4				4.6	
Shrimp larvae			0.9			4				4.6	
Shrimp unidentified			1.5			0.2				4.6	
Stomatopods	1.6	11.1	4.1	6.7	8.4	6.5	0.1	37.5	11.1	22.7	7.1
Lobsters	0.06		0.9	4		21.5		3.1		13.6	
Polychaetes	12.0		0.3	15.3		0.4	0.4	70⁵		4.6	7.1
Eunicidae	6.7			11.7				60 ⁵			
<i>Nematonereis</i> sp.	6.3			2.8				59.4			
<i>Eunice</i> sp.	0.4			8.9				9.4			
Opheliidae	5.3			3.6				43.8			
(<i>Polyophthalmus</i> sp.)											
Fish	2.4	33.3	1.8	10.5	33.6	5.8	2.9	32⁵	22.2	22.7	21.4
Eels, unidentified	2.2			8.5				21.9			
Mysids	5.9		0.3	4.3		4	0.3	18.8		4.6	28.6
Amphipods	0.1		5.0	0.1		>0.2	0.2	9.4		18.2	7.1
Gammaridea			4.7			0.2	0.2			13.6	7.1
Tanaids	5.4			2.0				50.0			
Copepods			1.2			4	0.1			9.1	7.1
Isopods							0.1				7.1
Cephalopods			0.3			1.5	1.4			4.6	7.1
<i>Octopus</i> sp.			0.3			1.5				4.6	
Gastropods			3.5			1.4	0.4			22.7	14.3
Crustacean parts, unidentified		⁶	⁶		41.2	25.8	9.7		66.7	77.3	57.1

¹ Data for unidentified crustacean parts are excluded from the calculation.

² Data from Hobson (1974); numerical percents were not reported.

³ Larvae (mostly megalops), except those from the Northwestern Hawaiian Islands that were juvenile majids.

⁴ Data are missing.

⁵ Calculated from a subset of 31 specimens.

⁶ Not countable.

Table 3

Summary of the diet of *Myripristis amaena* at the highest systematic levels of prey. Results are shown as percents of the summed Index of Relative Importance (IRI). (See Table 2 for details at these and other systematic levels.)

Prey category	Johnston Atoll (n=64)	Northwestern Hawaiian Islands (n=9)	Puako (Hawaii Island) (n=22)
Crabs	72.3	18.5	84.8
Shrimp	6.9	13.6	4.3
Stomatopods	2.0	8.6	2.8
Lobsters	¹		3.6
Polychaetes	12.4		0.04
Fish	2.7	59.3	2.0
Mysids	1.2		¹
Amphipods	0.01		1.1
Tanaids	2.4		
Cephalopods			0.1
Gastropods			1.3
Crustacean parts, unidentified	Few ²	Very many ²	Very many ²

¹ Data are missing.

² Not countable; not included in computation of IRI.

crabs were more important by all measures. Two *M. amaena* specimens contained a total of three lobsters. Fish were moderately important prey by frequency and volume. Many prey specimens appeared to be eels, probably mostly ophichthids. Polychaetes were the most important benthic prey, present in about 70% of all fish and providing over 10% of all prey by numbers and volume.

Twenty-two specimens from Puako contained prey identifiable to some level (Table 2). Nearly 70% of these contained crab megalops larvae; a hermit crab was identified in one of these and a galatheid crab, *Galathea spinosorostis*, in another. Crab larvae were also the major prey in numbers (over 70%) and volume (35%) and were strongly dominant in the IRI (Table 3.). Shrimp were eaten by the second largest number of fish (nearly 30%) and were second in importance numerically (over 10%), but minor in volume. They were far less an important prey at Puako than at JA, and were more evenly divided among Alpheidae, Palaemonidae, and Hippolytidae (including two *Saron marmoratus*). Lobsters (three individuals) appeared in only three guts (14%), but they accounted for over 20% of total prey volume. Both the slipper lobster, *Scyllarides squamosus*, and the Hawaiian clawed lobster, *Enoplometopus occidentalis*, were eaten. No other groups made major individual contributions to the diet. However, sto-

matopods and fish accounted for at least several percent of the number of consumers (frequency %) and volume. One octopus appeared in the diet at Puako. Benthic prey included at least a few percent gastropods (by the various measures) and a polychaete specimen. Nearly 80% of all fish also contained some quantity of unidentifiable crustacean parts, which accounted for over 25% of the total prey volume. Calculated as a percent of only the total prey identifiable to more specific groups, the volume % of each of those groups was considerably higher.

Only nine specimens from the NWHI contained prey identifiable to any level (Table 2). The total amount of prey recovered was small. Fish (including at least one pomacentrid), shrimp, juvenile crabs (including majids), and stomatopods were found in one or two guts each in total numbers of one to three individuals each. Six guts contained unidentifiable crustacean parts, which accounted for over 40% of the total diet volume. Fish were next in volume, and the other three groups contributed little volume.

At all three locations, the diet of *M. amaena* was heavily dominated by small juvenile stages of crustacean species that become much larger as adults. These prey included all the major groups of large crustaceans that are dominant in the diets of many demersal species of reef fishes studied in Hawaii (Parrish et al., 1985). Besides the crab and shrimp prey — quantitatively important in the diet of *M. amaena* at all three locations — stomatopods were eaten at all locations, and were the dominant prey of the Myripristinae generally in the NWHI (Parrish, unpubl. data). *Pseudosquilla oculata* was a stomatopod species identified in our *M. amaena* specimens that also was prominent in the diets of other Myripristinae and other demersal reef fishes in our studies in Hawaii.

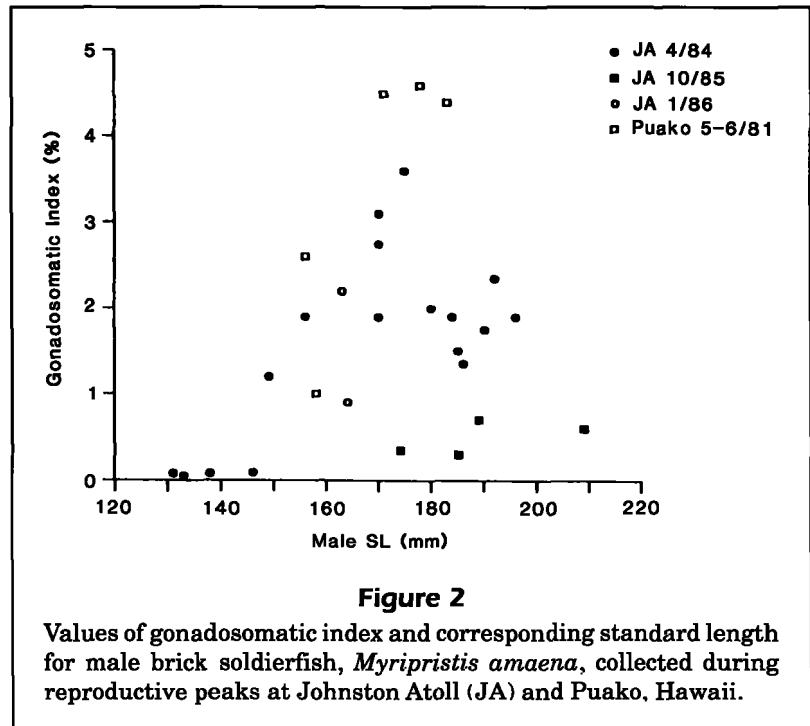
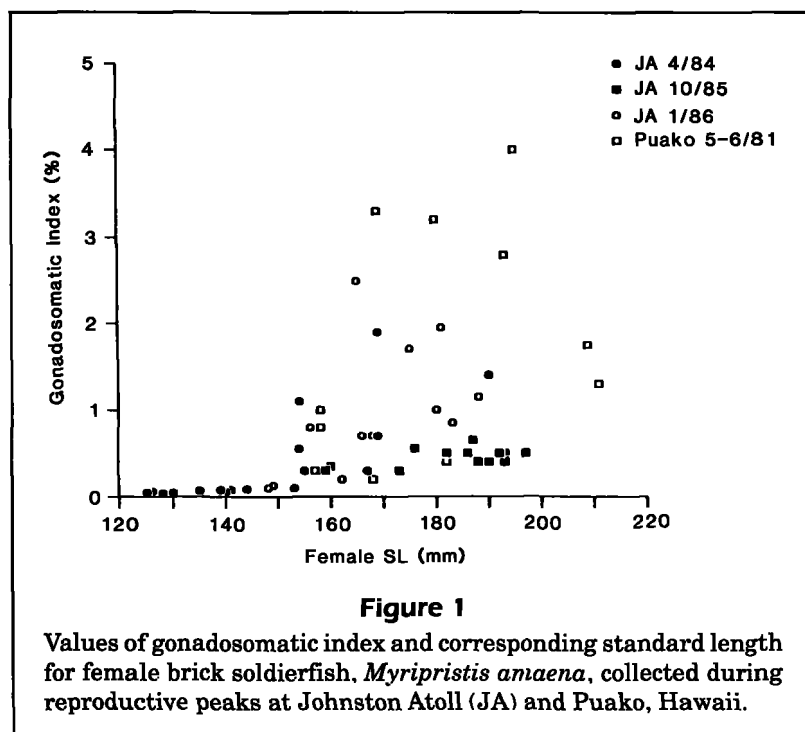
Small peracaridan crustaceans were conspicuous in the diet at JA (Table 2). Mysids and tanaids were present in the gut contents of many fish specimens, and each group contributed a few percent of the total number and volume of prey. Only one individual of each was identified at Puako. Amphipods were somewhat less widely found as diet components at JA and their abundance was trivial. At Puako they were present in about 18% of the fish and made up about 5% of numbers but were trivial in volume. Most of those identified were gammarids. A few isopods were found in JA specimens, and traces of copepods were found in Puako specimens. More peracaridans and other small crustaceans were very likely part of the residue of unidentifiable crustacean parts that appeared widely at all locations.

Myripristis amaena showed the expected strongly nocturnal feeding habit. At JA, guts from all 64 speci-

mens taken between 2000 and 0200 hours contained identifiable prey items. From 62 guts collected in the daytime, only four (taken at 0730 hours) contained more than one identifiable food item. At Puako, all 11 guts collected between 2300 and 0930 hours contained identifiable prey items, all of which might reasonably be the result of night or dawn feeding. Eleven specimens taken between 1000 and 1300 hours contained some food, much of it only unidentified crustacean parts. Sixteen specimens collected between 1100 and 1500 hours contained no identifiable prey. Of 61 specimens from the NWHI, only nine (collected between 0800 and 1100 hours) contained identifiable prey, mostly considerably digested. The remaining 52 specimens, collected between 1000 and 1600 hours, were empty or contained well digested, unidentifiable material.

Reproduction

The GSI of each sex collected during reproductive periods throughout the year from JA and Puako combined indicated an increase in the range of 153–156 mm SL for females (Fig. 1) and in the range of 149–156 mm SL for males (Fig. 2). Based on histological examination of developing oocytes in JA females, five developmental stages were identified (Table 1).



Sexual maturity was defined based on the presence of ovaries with oocytes in the late yolk granule stage for females (≥ 0.4 mm diameter; see Fig. 3) and on the presence of mature sperm in males (Fig. 4). The 11 ovaries and five testes examined histologically indicated that first sexual maturity occurred near 154 mm SL for females and 149 mm SL for males.

The results were consistent with those from visual examination of 24 total gonads (males and females) from Puako.

When GSI of mature specimens (larger than 145 mm SL) from JA was plotted against month of capture, with data from all months except September, spawning peaks were discernible in January, April, May, and October; the major peak was in April (Fig. 5). Based on visual examination, GSI, and histology, no gravid individuals were recorded among specimens collected during any other month. (Samples were rather small in some months.)

The fecundity estimated from the 12 ovaries sampled at JA ranged from 12,400 mature ova for a 156-mm SL fish to 69,200 for a 181-mm SL fish (Appendix B). Regressions were performed with fecundity, F , in number of mature eggs as a function of standard length, SL, in millimeters, and alternatively as a function of whole wet body weight, W , in grams. The fit was

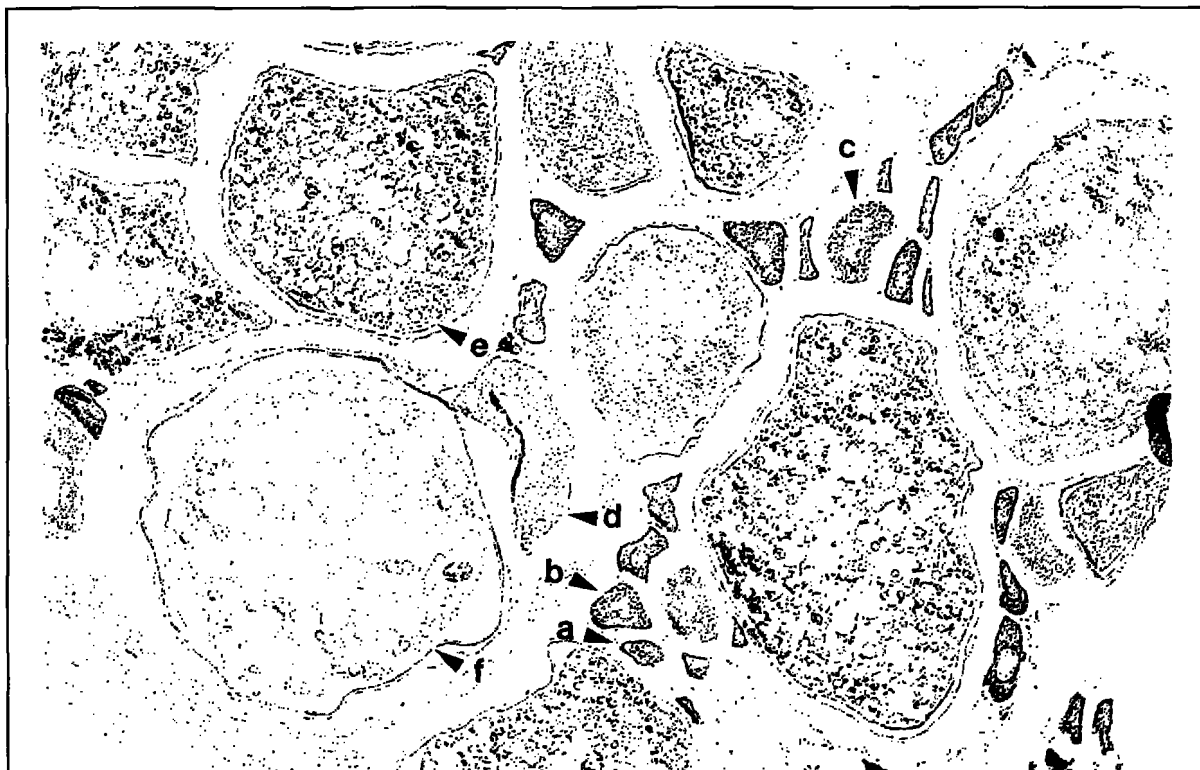


Figure 3

Light micrograph of a section of ovary from a brick soldierfish, *Myripristis amaena*, showing oocyte development stages: (a) primary growth, (b) perinuclear, (c) early yolk vesicle, (d) late yolk vesicle, (e) yolk granule, and (f) maturation.

slightly better for power functions than for linear functions in both cases:

$$F = 5.029 \times 10^{-20} (\text{SL})^{10.614}, \quad r^2 = 0.75$$

$$F = 1.447 \times 10^{-7} W^{5.0038}, \quad r^2 = 0.86 \quad (\text{Fig. 6}).$$

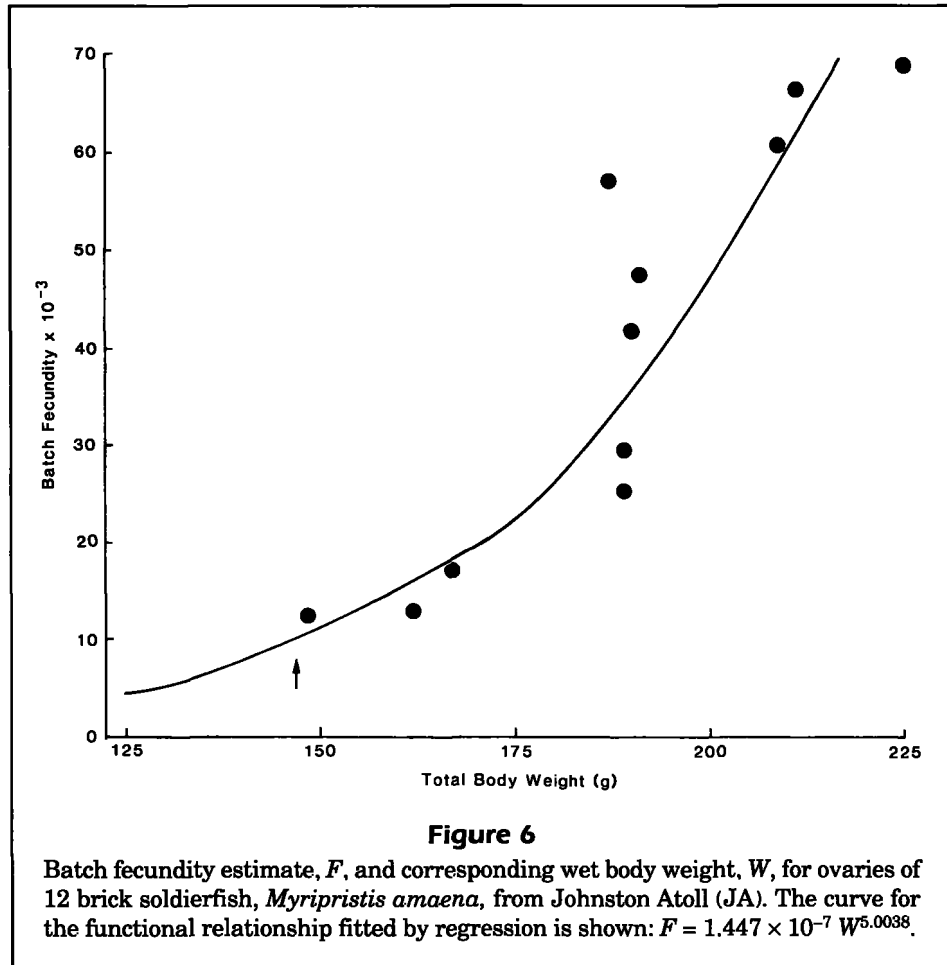
Based on the weight-frequency distribution of the recreational catch sampled at JA (Fig. 7A) and our weight-fecundity expression, in an average year, the reproductive output of the population is distributed as shown in Figure 7C. Thus, for example, about 54% of all eggs are produced by fish of 250 g and larger (over 13 years old)—the oldest 20% of the population. Weight classes between 200 and 250 g (ages of about 10 to 13 years) constitute about 38% of the reproductive population and produce about 35% of all eggs. Smaller fish—over 41% of the reproductive population—produce only about 11% of all eggs. Fishing pressure (all recreational) is light at JA, and many large fish remain.

Discussion

Feeding

With the possible exception of some of the larger shrimp and stomatopod specimens, the dominant

prey found in our *M. amaena* samples at all three locations were in some sense planktonic. The large number of crab, shrimp, and stomatopod larvae eaten, as well as the presence of prey such as copepods and mysids, strongly indicates that *M. amaena* does much of its feeding in the water column. Hobson (1974) found generally the same prey groups dominant and concluded that *M. amaena*, *M. berndti*, and *M. kuntee* were planktivores at Kona on Hawaii Island. A similar suite of prey items found in *M. kuntee* at Puako in the present work and at Oahu (Oda and Parrish, 1982) indicated that zooplankton were the dominant food source. Our diet studies of *M. berndti* at Puako show a similar result. Brecknock (1969) found that *M. berndti* was primarily zooplanktivorous at Oahu. The results of Harmelin-Vivien (1979) for *M. bowditchae* in Madagascar and of ter Kuile (1989) for *M. murdjan* in the Flores Sea indicate a large proportion of meroplanktonic prey in the diets. These soldierfishes seem morphologically adapted for picking small prey individuals from the water column (Hobson, 1972, 1974), and they have often been observed foraging extensively well above the bottom (Brecknock, 1969; Hobson, 1972, 1974).



A large fraction of all food eaten by *M. amaena* and most other *Myripristis* species appears to be taken from the water column, often at some distance above the substrate. However, relatively little of what we found or of what has been reported in the diets of these species in Hawaii appears to be holoplanktonic. Among the many small crustacean groups identified in the diets, few copepods were found. A number of the common crustacean prey were from groups such as mysids and amphipods that migrate vertically (often on a diel schedule) within shallow water, and may shelter on or near benthic substrate, within caves, cavities, rubble, or other cover during part of the day. Larval and young juvenile forms of larger benthic crustacea, such as crabs, lobsters, stomatopods, and some shrimp, may be components of this migrating "semitplankton." Some shrimps may be intermittently sedentary or free swimming as adults. What is known of this semiplankton (Aldredge and King, 1977; Porter and Porter, 1977; Parrish, 1989) and of the diet and feeding of *Myripristis* suggests that these squirrelfishes are not restricted to either planktonic or benthic feeding, but that they consume these prey groups wherever they are accessible.

The dominance of this semiplanktonic, probably vertically migrating, fauna in the diet of these fishes has important implications for their trophic linkage to the surrounding systems. Whatever the spatial and temporal details of their residence in the water column, the dominant "zooplankton" seem characteristic of an inshore aggregation, probably tied closely to shallow water. Therefore, these squirrelfishes depend for their trophic support largely on local sources of secondary production and possibly even primary nutrients (Parrish, 1989). This trophic arrangement is in contrast to the traditional concept of shallow-water planktivorous fishes supported by holoplankton of open ocean origin brought to the coast by prevailing oceanic currents.

There are reports of some *Myripristis* species feeding close over the substrate (Brecknock, 1969; ter Kuile, 1989). Hiatt and Strasburg (1960) noted that *M. microphthalmus* (= *violaceus*; Greenfield, 1974) in the Marshall Islands "takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this...fish secludes itself." They also found that some of their specimens had eaten tube-dwelling polychaetes—clearly a benthic

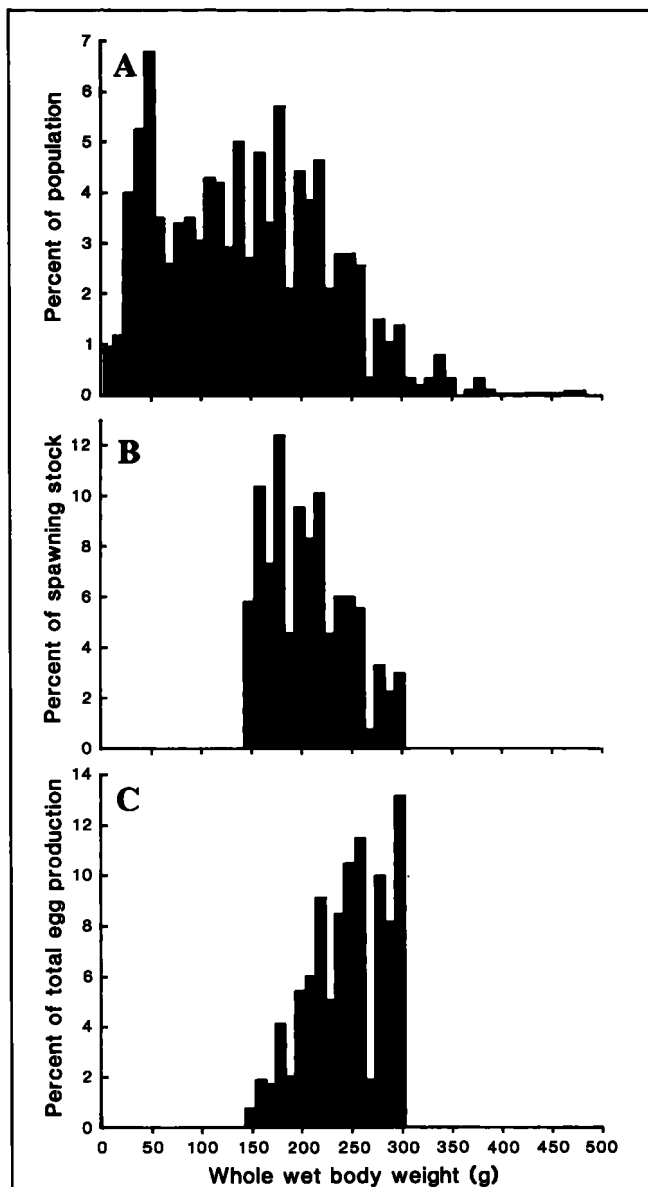


Figure 7

Size-frequency distribution of population numbers and population egg production of the brick soldierfish, *Myripristis amaena*, at Johnston Atoll (JA). (A) Distribution of whole wet body weights of all 855 specimens measured from recreational catches and scientific collections combined. (B) Distribution of wet weights of only the reproductively mature portion of the population up to 300 g ($n=396$). (C) Distribution of egg production by wet weight of spawners ($n=396$) based on the spawning population distribution in (B) and the fecundity vs body weight relationship developed from gonad samples. The fish population is arbitrarily truncated at 300 g for (B) and (C), which excludes 25 specimens distributed very irregularly over 18 weight classes, and with sizes much larger than those used to develop the size-fecundity relationship.

prey that was common in adjacent sandy patches. Harmelin-Vivien (1979) reported that polychaetes were the major prey by weight found in *M. bowditchae* (= *murdjan*; Randall and Gueze, 1981) in Madagascar, and she specifically noted that this fish sometimes fed on the bottom. Polychaetes were a minor prey of *M. berndti* at Oahu (Brecknock, 1969) and were fairly abundant in *M. murdjan* in the Flores Sea (ter Kuile, 1989). A polychaete was found in a *M. amaena* specimen from Kona (Hobson, 1974) and in one from our collections at Puako. In our JA collections, they were much more common and abundant, producing the second largest IRI value of the major systematic groups (Table 3). The JA taxa were Seditaria, which must certainly have been benthic dwellers. At Puako, at least five of our 36 specimens of *M. berndti* and two of our 21 specimens of *M. kuntzei* with prey contained polychaetes. Three specimens of *M. berndti* contained several polychaete individuals each.

Gastropods (presumably benthic species) were reported by Hobson (1974) in the diets of *M. amaena* and *M. berndti* from Kona. A benthic gastropod was found in the gut of a *M. berndti* at Puako, and they were fairly common in our *M. amaena* specimens there. Brecknock (1969) found a few gastropods in guts of *M. berndti* from Oahu and reported foraging by this species on the bottom of aquaria. One *M. berndti* specimen from Puako contained part of an arm of a bottom-living ophiuroid.

It seems clear that *M. amaena* and some other *Myripristis* species eat some fully benthic taxa. It is unlikely that such prey make up a major part of the diet for more than a very few *Myripristis* species. However, the ability of these squirrelfishes to employ this feeding mode enables them to exploit a greater range of food resources, at least on an opportunistic basis. Again, the trophic source seems to be local.

Trophic role of squirrelfishes in tropical communities

Holocentrids commonly make up a significant portion of the total natural fish community and are important predators throughout their range. In the uninhabited NWHI, nine species of holocentrids, including *M. amaena*, made up 4.5% of all individuals in the fish community (Norris and Parrish, 1988). In Tulear, Madagascar, three species of holocentrids represented 2.2% of the total fish population (Harmelin-Vivien, 1981). At JA, *M. amaena* alone provided about 2% of all individuals in the fish community. Together with three other species of holocentrids, it accounted for about 3% of the total fish community there (Dee et al.²).

² Dee, A. J., D. K. Irons, and J. D. Parrish. 1985. Johnston Atoll resource survey; a final report of the initial phase (19 Jan 1984–20 Jul 1985). Project report to U.S. Army Engineer District, Honolulu, 70 p.

The importance of holocentrids as predators has been well documented (Randall, 1967; Hobson, 1974; Vivien and Peyrot-Clausade, 1974; Gladfelter and Johnson, 1983). Gladfelter and Johnson (1983) found that seven species of squirrelfishes made up >99% of the nocturnally active, benthic crustacean-feeding fishes at St. Croix, U.S. Virgin Islands. Randall (1967) reported that holocentrids accounted for about 14% by number and 11% by weight of all zooplankton consumed as prey by the fish community at St. John, U.S. Virgin Islands. In the NWHI, holocentrids, including *M. amaena*, are among the most successful families of fish predators. Holocentrids accounted for nearly 40% by number, over 60% by weight, and about 50% by volume of the large crustacean community (crabs, shrimps, stomatopods, and lobsters) taken as prey by the 78 fish species from 28 families that contained large crustacean prey in our NWHI diet studies. Holocentrids also were responsible for about 2.5% of all the individual fish eaten. The fraction of the complete food consumption (all prey in the community combined) by this entire fish community that is eaten by holocentrids was about 13–17% (Parrish, unpubl. data).

Holocentrids also are an important element of the community as prey for other fishes. In the NWHI, 4% of all identified fish prey individuals were holocentrids (Norris and Parrish, 1988). In the western Atlantic, Randall (1967) found evidence that seven species of fishes from four families had eaten holocentrids; three species from three families had eaten Myripristinae (*Myripristis jacobus*). Dragovich (1970) also found that postlarval holocentrids (including Myripristinae) were fairly common prey of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the western Atlantic. As a widespread and abundant group that is an active predator and vulnerable prey, holocentrids play a major role in the trophic structure of tropical marine ecosystems.

Reproduction

For specimens from JA, the results from the three independent analyses of gonads (histology, GSI, and visual examination) indicated that sexual maturity of *M. amaena* occurs at 153–156 mm SL for females and at 149–156 mm SL for males. These results correspond closely to SFR estimates from our specimens collected at Puako: 145–160 mm SL, sexes combined (Hayes et al., 1982). Data from both locations are included in Figures 1 and 2. These values of SFR correspond to about 75–80% of L_{∞} (as determined by fitting data from length measurements and otolith increment counts to a von Bertalanffy growth model)

and to an age of about six years (Fig. 8 in Dee and Radtke, 1989). Dee and Radtke (1989) aged specimens up to nearly 14 years old. Their oldest specimen (of many available for analysis) was somewhat larger than the L_{∞} derived from the regression, so it seems unlikely that many individuals live much longer. Therefore, the age at first reproduction (AFR) is probably about 40% (or a little less) of the maximum lifespan commonly attained, and some individuals may reproduce for as many as eight years.

The relation between SFR and maximum body size has been investigated by several workers in a number of locations. The only results reported for squirrelfishes are estimates, based on large sample sizes, for two species of Holocentrinae from the Caribbean Sea (Wyatt, 1976). For *Holocentrus adscensionis*, FL at sexual maturity was about 175 mm, asymptotic (maximum) FL about 265 mm, and the ratio about 0.66; for *Holocentrus rufus*, FL at sexual maturity was about 130–135 mm, asymptotic FL about 230 mm, and the ratio about 0.59. Both these species reach considerably larger sizes than *M. amaena*, and *M. amaena* has the largest SFR/ L_{∞} ratio of the three species. The ratios for these squirrelfishes seem to be in the high portion of the range of published values for tropical fishes (Munro, 1974; Loubens, 1980). *Myripristis amaena*, in particular, matures at an advanced absolute age and at a surprisingly large fraction of its maximum age and size.

Spawning of *M. amaena* at JA seems to occur primarily in April–May; a secondary peak probably takes place in late September. All specimens collected during the fall peak showed GSI values above the inactive (off-season) level, but considerably below the mean value for the spring peak (Fig. 5). Although no collections were possible in September, visual examination and GSI data from collections made throughout October 1985 suggested the late stages of a spawning period that probably peaked in late September. Back calculation using the total number of otolith increments counted for the two smallest individuals aged by scanning electron microscope examination (Dee and Radtke, 1989) indicated that one individual was spawned in late September and the other in early October. A spawning peak also was observed in specimens collected in January 1986, but not in January 1985. The 1986 event may have resulted from unseasonably calm conditions that occurred during that period. Spawning also was recorded during January 1986 for *Chaetodon trifascialis*, an unusual time of year for that species. Values of the GSI for *M. amaena* collected in January 1986 were generally as high as those of specimens collected during the April spawning peak.

Data were not collected at Puako in a way that would permit a comparable assessment of seasonal

distribution of reproduction. Instead, small collections of specimens were made at regular, frequent intervals only long enough to discern a time of active reproduction. At only that time, a large collection of specimens was made quickly to permit estimation of SFR, and seasonal collections were not continued (Hayes et al., 1982). Thus, the Puako results serve only to establish that reproductive development (e.g. GSI, Fig. 5) is high in May and June. Those months probably represent a peak, but the data do not well define its limits or the pattern for the rest of the year. This early summer high at Puako is contiguous with the late spring high at JA.

Many tropical marine species show a collective spring spawning peak and a second peak in fall (Munro et al., 1973; Watson and Leis, 1974; Johannes, 1978; Walsh, 1987). For Hawaiian fishes, the most dominant seasonal spawning pattern, based on numbers of spawning records, is a peak spawning period in about April and May, with a secondary peak in October for some species. Based on numbers of recruitment records, the dominant recruitment period occurs in June and July, and a secondary peak in February and March (Walsh, 1987). Many studies indicate that there can be considerable variability in the timing of recruitment from year to year, and that the timing and intensity may vary at small spatial scales (Victor, 1982; Williams, 1983; Sale, 1985; Schroeder, 1985; Walsh, 1987; Doherty, 1991).

Larval and newly settled *M. amaena* were elusive throughout the present study, and few data could be collected regarding recruitment. The youngest specimen for which we counted short period (apparently daily) increments in otoliths (Dee and Radtke, 1989) showed a discontinuity that probably represented settlement from the plankton. Back calculation based on the number of increments after the assumed settlement mark suggests that the specimen settled in early February. Although our data regarding settlement are minimal, both these and our spawning results are consistent with the above seasonal reproductive periods summarized by Walsh (1987). Walsh suggested that changes in water temperature or photoperiod, or both, are most likely responsible for observed seasonal patterns of spawning and recruitment in Hawaiian reef fishes. For *M. amaena* at JA, there was no indication that water temperature affected the time of spawning. The full annual range of temperature is very small (24.5–26.5°C). Temperatures during the reproductive period of January 1986 were among the coldest recorded during the entire study, whereas temperatures during spawning in April 1984 were among the highest recorded.

Wyatt (1976) reported on spawning seasons of two Holocentrinae species in Jamaican waters. He re-

corded ripe *Holocentrus adscensionis* collected in all months except June, and only 2% (one specimen) ripe in July. Most spawning occurred in January, February, and March, but October was also a peak month. Besides ripe fish, "sexually active" gonads were common (14–37% of all gonads) in September through May. The seasonal pattern was similar for *H. rufus*; highest peaks of ripe gonads occurred in October (44%) and February (32%). "Sexually active" gonads were found in all months except July. May, June, and July were the months of lowest gonad development. In Bermuda (15° farther north in mid-ocean), Winn et al. (1964) reported breeding by both these Holocentrinae species in June, July, and August. Variability in timing of spawning due to factors such as lunar periodicity, water temperature, plankton productivity, photoperiod, currents, and rainfall occurs commonly, and spawning time can vary from year to year, even at the same location (Watson and Leis, 1974; Wyrski, 1974; Johannes, 1978; Walsh, 1987).

The fecundity of *M. amaena* is relatively low compared with many marine species. The most fecund specimen examined contained fewer than 70,000 maturation stage eggs, and the length-fecundity function predicts that a specimen of length L_{∞} would contain fewer than 100,000 such eggs. Fecundity increases sharply with body size; it rises with the fifth power of weight and more than the tenth power of SL. (The sample size used for the regressions was not large, but the values of r^2 indicate a reasonably good fit.) These changes with size are much greater than those found in many marine species. These results, together with the results for SFR and the oldest specimen aged, indicate that the species matures slowly. With a relatively long life and steeply increasing fecundity, a very large fraction of the reproductive output of the population is provided by old fish.

The number of spawnings per year is unknown. There was no clear evidence in ovaries examined under direct light microscopy or histologically of a distinct series of distinguishable groups of ova in a graded-size sequence that might represent serial batches spawned within a season. However, production of such serial clutches is commonplace in tropical, nearshore fishes. Unless individual females spawn a good many batches (of the full number of maturation stage eggs estimated) within each year, the total or lifetime fecundity of individuals is relatively low compared with many common marine species. For example, an individual maturing at age six and spawning once annually through age 14, according to the body sizes indicated by our von Bertalanffy expression (Dee and Radtke, 1989) and the fecundity indicated by our length-fecundity expression, would produce fewer than 300,000 eggs during such

a reproductive life. Clearly, determination of the number of clutches spawned in a reproductive season is an important subject for research on *M. amaena*.

Most types of fisheries tend to produce higher mortality of older age classes. Certainly this is true of the common spear fisheries for squirrelfish in the tropics, where larger specimens are individually selected. For a species in which sexual maturity and fecundity are related to age (size) as they are in *M. amaena*, this means that substantial fishing pressure applied to the population can severely reduce egg production (see Fig. 7). The risks of recruitment overfishing are therefore especially great, particularly when maturity occurs late enough that fish of prereproductive size are still a desirable catch. The expected trend as fishing pressure on such a stock increases is the appearance of an increasing fraction of prereproductive fish in the catch. At JA, despite low total fishing effort, about 51% of all *M. amaena* in our creel sample of the fishery were prereproductive; in the small-scale, recreational-subsistence fishery at Puako, about 46% were prereproductive ($n=24$). Near many centers of human population, fishing intensity is much greater, and great declines in populations of soldierfish are unofficially reported. Clearly the life history of *M. amaena*, and perhaps soldierfishes in general, creates high vulnerability to conventional, unregulated fishing. It seems essential that fisheries for such species be managed to conserve the largest, oldest spawners to protect the reproductive potential of the stock.

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Appendix A

Relationships between standard length (SL), fork length (FL), and total length (TL) in millimeters, based on linear regressions for 377 specimens of the brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA).

$$SL = 0.9013 FL - 3.22, \quad r^2 = 0.991$$

$$SL = 0.7811 TL - 3.23, \quad r^2 = 0.992$$

$$TL = 1.1493 FL + 0.65, \quad r^2 = 0.991$$

Appendix B

Size measured and batch fecundity estimated by counting ova in aliquots from the ovaries of 12 specimens of the brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA).

Standard body length (mm)	Whole body wet weight (g)	Estimated batch fecundity
156	149	12402
166	162	12925
168	167	17077
169	166	17618
175	189	29505
175	187	57200
177	191	47680
179	190	42003
180	189	25301
181	225	69221
187	209	61000
188	211	66719