

## Reproductive biology and female parental care in the cockscomb prickleback, *Anoplarchus purpurescens* (Pisces: Stichaeidae)

Ronald M. Coleman

Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada

Received 8.11.1990      Accepted 24.9.1991

**Key words:** Field, Aquarium, Guarding, Fanning, Intertidal, Marine, Parental investment, Evolution, Phylogeny, Behavior

### Synopsis

Reproduction and parental care in the cockscomb prickleback, a Pacific coast intertidal fish, were examined using a combination of field and laboratory observations. The sexes were dimorphic, particularly during the breeding season, and males competed with other males for access to females. Males performed lateral and spasm displays. In the wild, the breeding season extended from January to March on cobblestone beaches. Assortative mating was positive with respect to body size. Females exhibited solitary parental care of the eggs. Each female coiled around, guarded and fanned a single egg mass that likely represented her total reproductive effort for the year. The number of eggs in the mass increased linearly with female size (weight or length). Males did not remain after spawning. Aquarium observations revealed that males spawn with more than one female given the opportunity. It is not known whether this occurs in the wild. Incubation to hatching took 29 days. Upon hatching, the young swam towards the surface. Parental care did not extend beyond hatching.

### Introduction

Fishes exhibit a diversity of parental-care patterns, including the absence of care, biparental care, solitary male care, and solitary female care (reviewed in Gittleman 1981, Blumer 1982, Gross & Sargent 1985). Of those that show parental care (21% of bony fish families), male care prevails. Female care and biparental care are less common (Blumer 1979, 1982). Few studies have examined the reproductive biology of a species with solitary female care (e.g., Balon 1977, van den Berghe & Gross 1986, Mrowka & Schierwater 1988, Yanagisawa & Sato 1990).

The family Stichaeidae, found exclusively in temperate marine waters, contains 31 genera with

approximately 60 species (Nelson 1984, Follett & Powell 1988). Little is known about the reproductive behavior of any species of this family, but the few existing studies show that some species exhibit male parental care (e.g., Green et al. 1987) whereas other species exhibit female parental care (e.g., Peppar 1965, Shiogaki 1987). Biparental care has not been found in this family; this pattern of parental care is found in only six families of bony fishes (Blumer 1982).

The high cockscomb prickleback, *Anoplarchus purpurescens*, is a small (to 20 cm total length) eel-like, intertidal fish that occurs from California to Alaska (Hart 1973). Its most distinguishing feature is a fleshy crest or cockscomb on the dorsal surface

of the head (Eschmeyer et al. 1983). Two previous reports have indicated that cockscombs exhibit female care of the eggs. Schultz & DeLacy (1932) found female cockscombs coiled around their egg masses in the intertidal zone and reported egg size and female size from Seattle, Washington. The second study, an unpublished M.Sc. thesis by Pepar (1965), reported on some aspects of reproduction from a population in Burrard Inlet, Vancouver, British Columbia. The purpose of this investigation was to confirm and extend the results of these two previous studies for comparison with studies on pricklebacks exhibiting male parental care.

## Materials and methods

### *Field observations and collections*

I used a combination of field and aquarium studies. I observed cockscombs at four intertidal sites (Lighthouse Beach, Mermaid Beach, Second Beach, and Cates Park) in Burrard Inlet, Vancouver, British Columbia (Latitude 49°N, Longitude 123°W). Although all sites were in marine waters, they received regular inundation with freshwater. Collection and observation periods were severely limited by the tidal cycle. During the winter, the lowest tides occurred at night, approximately every two weeks. I did field work between 1800 and 0300 h, concentrating on the 15 minutes prior to low tide and in the 30 minutes following it. Tide heights were taken from Canadian Tide and Current Tables for 1985, 1986, 1987 and 1989, Vol. 5, Juan de Fuca Strait and Strait of Georgia, Fisheries and Oceans Canada. Using flashlights, I observed or collected specimens on a total of fourteen nights in 1985, 1986, 1987 and 1989 (Table 1). Not all specimens found were collected. Seven additional trips were made to Cates Park in 1986 and 1987, but adult pricklebacks were rare there. I collected a total of 32 males and 49 females (32 ripe and 17 guarding egg masses).

Cockscombs were observed or collected at low tide by turning over rocks just above the water line. The complex, three-dimensional structure of the beach, plus the rapid receding and advancing of the

water line made systematic searching impossible. Instead, I turned over as many rocks as I could before the tide returned, typically at a rate of about 10 rocks per minute. Once a specimen was located, it was captured by hand. In some cases, a small pool of water lay under the rock but most frequently pricklebacks were found on top of the moist gravel or crushed-shell substrata. Because large rocks could not be turned over, collections were biased toward rocks of less than approximately 25 kg. A ripe female was sometimes found in a pair with a ripe male; 16 such pairs were collected.

Collected specimens were measured and weighed, their gonads were dissected, weighed and measured, and their sex and coloration noted. Somatic weight was calculated as total weight minus the weight of the gonads and gonosomatic index was calculated as the ratio of gonad weight to somatic weight. Egg masses were collected, weighed and all eggs in the ovary or egg mass were counted

*Table 1.* Reproductive status of cockscomb pricklebacks in the field based on 14 sampling trips. The symbols P, R, M, and N indicate that pricklebacks of that status were found in the population on that date. Ripe females (R) were sometimes found alone, and sometimes in a pair (P) with a male. Females guarding egg masses (M) were never found in a pair. On some dates, e.g. 31 January 1985, both ripe females and females guarding egg masses were found at the same site.

| Date               | Low tide (m) | Pairs | Ripe | Mass | Only non-reproductive |
|--------------------|--------------|-------|------|------|-----------------------|
| <i>Winter 1985</i> |              |       |      |      |                       |
| Jan 26             | 2.2          |       | R    |      |                       |
| Jan 31             | 1.3          | P     | R    | M    |                       |
| Feb 3              | 0.7          | P     | R    | M    |                       |
| Feb 7              | 0.8          |       | R    | M    |                       |
| Feb 8              | 1.2          |       |      | M    |                       |
| <i>Winter 1986</i> |              |       |      |      |                       |
| Jan 3              | 2.2          |       | R    |      |                       |
| Jan 24             | 0.8          | P     | R    |      |                       |
| Feb 7              | 0.5          | P     | R    | M    |                       |
| <i>Winter 1987</i> |              |       |      |      |                       |
| Nov 5              | 0.3          |       |      |      | N                     |
| Dec 2              | 0.0          |       | R    |      |                       |
| Dec 30             | 0.0          | P     | R    |      |                       |
| Jan 26             | 0.5          | P     | R    |      |                       |
| Jan 26             | 0.5          | P     | R    |      |                       |
| <i>Spring 1989</i> |              |       |      |      |                       |
| May 23             | 0.5          |       |      |      | N                     |

individually. Egg size was measured on 20 fresh eggs using a dissecting microscope fitted with an ocular micrometer.

### *Aquarium studies*

Aquarium studies were performed at the Vancouver Public Aquarium (Stanley Park, Vancouver) from December 1986 to March 1987. The purpose of these observations was not to provide a detailed quantitative description of prickleback behavior, but rather to determine the qualitative response of males and females to each other under two different sex ratios and to observe parental behavior. I used five 100 l glass aquaria (75 × 30 × 45 cm) on a flow-through natural seawater system at ambient temperature (7–10°C). Flow rate varied from 1.31 min<sup>-1</sup> to 9.31 min<sup>-1</sup>. Each aquarium had a substratum of gravel (average diameter 4.2 mm, *SD* = 2.0, *N* = 85, range = 2–12 mm) and was covered on the back and sides by black plastic to facilitate observations and to reduce distractions for the fish. Fish in one aquarium were visually isolated from fish in any other aquarium. Illumination was provided by overhead fluorescent fixtures.

To simulate the natural habitat, I placed two plastic rocks (a piece of clear 20 × 20 × 0.6 cm Plexiglass with 3 cm legs glued on each corner) in each aquarium to allow fish to hide under cover while remaining visible to me. The corner legs were pushed into the gravel substratum leaving a space roughly the height of a prickleback under the rock. When the rocks were first put in the aquarium, they were clear and the pricklebacks did not spend much time under them. Once debris and algae accumulated on the rocks, blocking much of the light, the pricklebacks adopted them. I cleaned the rocks occasionally but never removed all the debris.

Pricklebacks collected on the night of 2 December 1986 were transferred from holding tanks to the observation aquaria on 9 December. Each of two aquaria contained 1 female and 2 males, whereas another three aquaria contained 2 females and 1 male each. These fish were observed daily for the next 3 months, during which time spawning occurred in all aquaria. A systematic observation

schedule was not employed because preliminary observations revealed that most of the time cockscombs remained immobile. Rather, observations were taken when the animals were observed to be active. Animals were fed brine shrimp and frozen krill and excess food was siphoned out.

## **Results**

### *Habitat use*

Cockscomb pricklebacks were found on cobblestone beaches (e.g., photographs 98 and 115 on p. 192 and 210 in Snively 1978) consisting of jumbles of rocks varying in size from 10 cm to 30+ cm in diameter. A typical evening of 45 min of constantly turning rocks yielded 15–20 cockscomb pricklebacks. They were seldom found under rocks of less than 15 cm in diameter. The typical rock under which specimens were found was about 30–60 cm across, had a flat or concave under-surface creating a shallow cave underneath it, and was lying on gravel, crushed shells, other rocks, or a mixture of these substrata. Cockscombs were not found under well rounded rocks, or rocks that were submerged in mud.

### *Body size and sexual dimorphism*

The sexes were dimorphic in head shape (males had a larger, more prominently displayed cockscomb than females) and color, particularly when the fish were reproductively active. Males varied from brown to black, with intense red/orange on the pectoral and anal fins and some red on the dorsal fin. Females had a slight purple color over a brown background and had more spots and markings on the body, giving them a speckled or grainy appearance. Gravid females had visibly distended abdomens. Some females had orange on the pectoral fins, but never of the intensity of those of the males. Females had patterns on the pectoral, anal and caudal fins that the males lacked.

For a sample of 11 males and 14 females, total length and standard length were highly correlated.

The following regression relates the two: TL (cm) = 1.086 SL (cm) + 0.052 ( $r_{25} = 0.999$ ,  $p < 0.001$ ). When males and females were analyzed separately, this relationship did not differ by sex (Analysis of Covariance, slopes:  $F_{1,21} = 1.31$ ,  $p = 0.26$ ; intercepts:  $F_{1,22} = 2.26$ ,  $p = 0.15$ ). There was a curvilinear relationship between total weight (W) and total length (TL) for males,  $W = 0.004 \times TL^{3.14}$ ,  $r_{32} = 0.95$ ,  $p < 0.001$ ; females with ripe ovaries,  $W = 0.0092 \times TL^{2.85}$ ,  $r_{32} = 0.96$ ,  $p < 0.001$ ; and females guarding an egg mass,  $W = 0.0058 \times TL^{2.93}$ ,  $r_{17} = 0.86$ ,  $p < 0.001$ .

Males and females did not differ in total weight, somatic weight or total length (unpaired t-tests:  $t_{79} = 0.97$ ,  $p > 0.05$ ;  $t_{79} = 1.79$ ,  $p > 0.05$ ;  $t_{79} = 0.77$ ,  $p > 0.05$ , respectively). Furthermore, ripe females and females guarding eggs did not differ with respect to any of the three parameters ( $t_{47} = 0.43$ ,  $p > 0.05$ ;  $t_{47} = 0.54$ ,  $p > 0.05$ ,  $t_{47} = 1.79$ ,  $p > 0.05$ , respectively).

When males and females were found together as pairs prior to spawning, the sexes did not differ in total length, total weight or somatic weight (paired t-tests;  $t_{15} = 0.056$ ,  $p = 0.96$ ;  $t_{15} = 0.329$ ,  $p = 0.75$ ;  $t_{15} = 0.631$ ,  $p = 0.53$ , respectively). There was a significant correlation between males and females in pairs for all three factors ( $r_{15} = 0.50$ ,  $p = 0.049$ ;  $r_{15} = 0.60$ ,  $p = 0.014$ ;  $r_{15} = 0.60$ ,  $p = 0.014$ ). Thus, they mated assortatively with respect to size.

### Gonads and fecundity

The gonosomatic index for females decreased significantly after oviposition (Table 2; unpaired t-test,  $t_{11} = 11.12$ ,  $p < 0.001$ ). Females guarding an egg mass invariably had a much reduced ovary. They never contained ripe eggs. In a few cases, numerous tiny unripe eggs (< 0.05 mm diameter) were present. Unripe eggs were pale yellow and opaque, and tended to be irregular in shape rather than smoothly spherical.

The number of eggs in the bi-lobed ovary of a ripe female (F) was significantly related to the somatic weight (W) of the female:  $F = 275 W$  (g) - 43 ( $r^2_{29} = 0.94$ ,  $p < 0.001$ ); and to her total length (TL):  $F = 439 TL$  (cm) - 2768 ( $r^2_{29} = 0.96$ ,  $p < 0.001$ ). Polynomial regressions revealed that a polynomial of degree 2 (i.e., an  $x^2$  term) did not explain significantly more of the variance than did a linear regression for either somatic weight or total length, which is not surprising given the high value of  $r^2$ . Thus, fecundity increased only linearly with body size; it did not accelerate with body size (see Discussion).

### Aquarium behavior and intrasexual aggression

Prior to spawning, males became increasingly agonistic towards each other in the presence of a female. Such males performed lateral displays and

Table 2. Summary of body size and reproductive variables for male and female cockscomb pricklebacks. Data are means  $\pm$  1 SD. For females guarding an egg mass, the egg size and number of eggs values are for eggs in the egg mass.

|                       | Males            | Ripe females                | Guarding females             | All females                 |
|-----------------------|------------------|-----------------------------|------------------------------|-----------------------------|
| n                     | 32               | 32                          | 17                           | 49                          |
| Total weight (g)      | 6.45 $\pm$ 2.95  | 5.97 $\pm$ 2.64             | 5.65 $\pm$ 2.23              | 5.86 $\pm$ 2.49             |
| Somatic weight (g)    | 6.39 $\pm$ 2.93  | 5.24 $\pm$ 2.21             | 5.60 $\pm$ 2.22              | 5.37 $\pm$ 2.20             |
| Gonad weight (g)      | 0.06 $\pm$ 0.03  | 0.73 $\pm$ 0.47             | 0.04 $\pm$ 0.02              |                             |
| Total length (cm)     | 10.02 $\pm$ 1.32 | 9.53 $\pm$ 1.44             | 10.26 $\pm$ 1.18             | 9.78 $\pm$ 1.39             |
| Gonosomatic index (%) | 1.0 $\pm$ 0.3    | 13.0 $\pm$ 4.5              | 0.8 $\pm$ 0.2                |                             |
| Egg size (mm)         |                  | 1.00 $\pm$ 0.09             | 1.57 $\pm$ 0.05              |                             |
| Number of eggs        |                  | 1382 $\pm$ 640 <sup>a</sup> | 1382 $\pm$ 447               | 1382 $\pm$ 572 <sup>b</sup> |
| Egg mass weight (g)   |                  |                             | 4.23 $\pm$ 1.52 <sup>c</sup> |                             |

<sup>a</sup>n = 30; <sup>b</sup>n = 47; <sup>c</sup>n = 16.

spasm displays to each other. In a lateral display, the body was oriented parallel to the fish being displayed at and the fins and crest were fully erected. The front portion of the body was raised off the substratum. Lateral displays were followed by spasms, biting or both. During a spasm display, the fish oriented either directly at an opponent or, more typically, laterally to an opponent and the whole body jerked in a single spasm. It was either done once or in a series of 2 or 3 spasms spaced by 1–2 s. It was not done continuously, i.e. it was not a shaking motion. During male-male agonistic encounters, the fins of the males became deep red/orange and the spot at the anterior of the dorsal fin became outlined in gold.

The act of spawning was not observed in the aquaria; however, courtship behavior was observed for two pairs. The male and female swam around and over each other, occasionally nudging. The female's ovipositor became visible and the male positioned himself upside down under the female and pressed his genital area against hers. The female was right-side up, pressed against the underside of the rock. The male performed a spasm in this position. This behavior was observed in R3 on 22 January and in R5 on 14 January and again on 22 January. Egg masses were not seen in these aquaria until 2 February, and 25 February respectively, possibly suggesting a lengthy courtship period, although this may be an artifact of the fish being confined to a relatively small space.

### *Spawning*

From the observations of when egg masses were first seen, and the rarity of gravid females after these times, it appears that cockscomb pricklebacks spawn during late January to February (Table 1): in 1985 the first egg mass was discovered on 31 January, but by the 8th of February, all females that were found had spawned. In late 1986, females collected on 2 December already had visibly distended abdomens with a slight yellow coloration. Since these females did not spawn for at least 6 weeks (no egg masses were found in the field before 26 January 1987), this indicates that egg matu-

ration occurs over a period of many weeks prior to spawning. In 1989, a sampling trip in mid-May confirmed that no animals were in reproductive condition at this time of year. Poor tidal conditions made it impossible to sample in March or April to determine if any females spawned then, though it seems unlikely since all females appeared to have spawned by mid-February.

Seven spawnings occurred in the laboratory between 30 January and 28 February. Three of these were either infertile (no male present in one aquarium at the time of spawning), or the egg mass was neglected and the eggs showed no signs of development (two aquaria). Of the four other egg masses, all embryos hatched, those in three masses in 29 days and those in the fourth in 28 days. At hatch, distinct gold eyes were visible in the eggs, and the embryos twisted inside the eggs and then broke free. Immediately upon hatching, the embryos swam to the surface, covering a distance of 150 mm in less than 5 seconds. They measured approximately 9 mm and the yolk sac, if present, was not visible to the unaided eye.

### *Polygyny*

One of the main purposes of the aquarium observations was to determine whether one male could mate with more than one female. Aquarium R5 contained two females and one male. On 25 February, one female was found caring for an egg mass and on 28 February, the other female was caring for an egg mass. In both egg masses embryos eventually hatched, indicating that the male had successfully spawned with both females. The male did not provide care for either egg mass.

### *Parental care*

Female cockscomb pricklebacks cared for the eggs. Parental care consisted of the female coiling around the egg mass, sometimes with the head coiling past the tail, but typically forming only a single coil. Females were found guarding either on the substratum directly, or occasionally, in upturn-

ed clam shells, but always under a rock. Males were never found coiled around an egg mass and were not found in close association with guarding females in the wild, although occasionally a male was found within a metre of such a female. No female was found guarding more than one egg mass simultaneously. Undefended egg masses were never seen in the wild.

In aquaria, males ignored guarding females. Such females were observed to coil around the eggs, though sometimes they left the eggs alone. Some females moved around on the substratum moving their egg mass with them by nudging it with their tail.

Females fanned the egg mass using the posterior portion of the body and the caudal fin. Over a series of four fanning bouts, one female fanned with a mean tempo of  $72.5 \text{ beats min}^{-1}$  ( $SD = 2.4$ ). After several minutes of fanning, a female usually changed her position and moved the eggs around as well. Sometimes the beating tail was directed at the eggs, and in other fanning positions it was not. In these cases the female coiled only the anterior portion of the body around the eggs and the tail fanned away from the egg mass. Females continued to fan up to and during hatching.

### *The egg mass*

Egg masses were found in a variety of shapes, but they shared a number of features. First, the eggs adhered to each other more strongly than they adhered to a surface such as the overlying or underlying rock, and it appeared that often the egg mass extended between these two surfaces. Second, the egg mass was usually wider at the top and bottom than in the middle, i.e. hour-glass shaped, or it was in the shape of a truncated cone. Both shapes showed a constriction around the middle of the egg mass, marking where the female's body wrapped around the eggs, as confirmed by aquarium observations.

The eggs in an egg mass stayed together until hatching, although they changed color and became more loosely connected as time progressed. Soon after laying, an egg mass was white, it then turned

yellowish, and finally had a distinct green tint when the eyespots of the embryos became visible. The egg mass was close to neutrally buoyant; in aquaria if the female stopped coiling around an egg mass it drifted around on the bottom.

The average number of eggs in the ovaries of ripe females was the same as the average number of eggs in the egg masses of guarding females [(1382 in both cases), Table 2]. In addition, because no large ripe eggs were found in the ovaries of guarding females, I conclude that each female spawned all of her eggs into a single egg mass. The number of eggs in an egg mass ( $N$ ) was significantly related to the weight of the mass ( $W$ ):  $N = 266W \text{ (g)} + 253$  ( $r^2_{15} = 0.77$ ,  $p < 0.001$ ). The number of eggs in an egg mass ( $N$ ) was also significantly related to the somatic weight ( $SW$ ) of the guarding female:  $N = 177SW \text{ (g)} + 393$  ( $r^2_{16} = 0.77$ ,  $p < 0.001$ ) and to the total length ( $TL$ ) of the guarding female:  $N = 291TL \text{ (cm)} - 1604$  ( $r^2_{16} = 0.58$ ,  $p < 0.001$ ). As with fecundity of ripe females, polynomial regressions revealed that a second degree polynomial did not explain significantly more of the variance in number of eggs for guarding females than did a linear regression for either somatic weight or total length. When I compared ripe females versus guarding females, there were significant differences in the slopes of the linear regressions of number of eggs on somatic weight and number of eggs on total length (Analysis of Covariance,  $F_{1,43} = 15.19$ ,  $p < 0.001$ , and  $F_{1,43} = 8.84$ ,  $p < 0.01$  respectively), precluding comparison of adjusted means.

### *Egg size*

The eggs in an egg mass were approximately 60% greater in diameter than the eggs in the ovary of a ripe female (Table 2). Egg size in the ovary was significantly correlated with both somatic weight and total length of the female (somatic weight:  $r_{31} = 0.392$ ,  $p = 0.026$ ; total length:  $r_{31} = 0.389$ ,  $p = 0.028$ ), whereas egg size in masses was not (somatic weight:  $r_{16} = 0.363$ ,  $p = 0.152$ ; total length:  $r_{16} = 0.390$ ,  $p = 0.122$ ), although this may be the result of smaller sample sizes in the latter.

### Male reproductive success

Assuming that each male found in a pair would spawn only with that female, I examined the expected male success with body size, using the female's fecundity as the measure of male success. There was a significant relationship between expected male success and somatic weight ( $r_{15} = 0.511$ ,  $p = 0.052$ ) although only a marginally non-significant relationship existed between expected male success and total length ( $r_{14} = 0.467$ ,  $p = 0.079$ ).

### Discussion

Female cockscomb pricklebacks exhibit solitary parental care of the eggs. A female coils around, guards and fans a single egg mass that likely represents her total reproductive effort for the year. She continues this behavior until the embryos hatch (an average of 29 days) but she provides no care of the young. These results agree with the earlier work of Schultz & DeLacy (1932) and Peppar (1965). Cockscomb pricklebacks are one of the few species known to display this particular combination of parental care behavior.

Positive assortative mating for size (larger males were found paired with larger females) may represent mate choice by both sexes for the largest available mate of the opposite sex, or it may result if individuals of both sexes of a certain size occupy similar habitat. In aquaria, males were seen to battle intensely over a female, using displays, chases and biting. Because larger females contained more eggs than smaller ones, the advantage to the male of mating with large females is obvious. The converse is not true. Since any male is probably capable of fertilizing any female's eggs, it is less clear that females should choose among males. Males do not provide parental care nor do they appear to offer females resources such as access to feeding territories, though this latter possibility should be investigated further.

In the wild, spawning occurred from late January to early February. This may be due to favorable wave exposure, as Marliave (1975) has postulated

for the black prickleback, *Xiphister atropurpureus*, or it may be that the young pricklebacks enter the plankton at a specific time of the year. Upon hatching, the young have little yolk reserves and therefore must find suitable food rapidly. They have well-pigmented (and presumably well-developed) eyes at hatch, which would allow them to see prey. Peppar (1965) described the newly-hatched young. He also found that the young show a marked positive phototaxis for three to five days, but then they became negatively phototactic.

Female cockscombs providing parental care are periodically exposed to the air when the tide recedes. Horn & Riegle's (1981) study of survival time out of water shows that cockscombs of 10 cm SL can withstand approximately 20 hours out of water. This tolerance far exceeds that experienced by guarding females in this study. In addition, the overlying rock and the underlying moist gravel may reduce the likelihood of desiccation.

This choice of guarding site also restricts predators to those that are either small enough to fit under the rock or large enough to move the rock (possibly bears and raccoons). Those that can fit under the rock are barred from the eggs by the female's body. The most abundant potential egg predators in the vicinity of the guarding females were shore crabs (*Hemigrapsus* spp.), with dozens of individuals present under a single rock, but it is not known if they prey on cockscomb eggs.

Besides guarding, I observed females fanning the eggs. Peppar (1965) reported fanning by cockscombs but Schultz & DeLacy (1932) did not. The tail of the female cockscomb was not always directed at the eggs while fanning. This is understandable in the context of the natural spawning site of pricklebacks under rocks. In the planar space under a rock, fanning in any direction creates a current that passes over the eggs.

Reproductive biology and parental care have been examined in a few other species of stichaeids (Table 3). LeDrew & Green (1975) and Green et al. (1987) reported on male parental care in the radiated shanny, *Ulvaria subbifurcata*. The mean number of eggs found in ovaries was 1512 ( $n = 6$ ) and in egg masses was 2706 ( $n = 11$ ), higher than in the cockscombs studied here. The mean diameter

of unfertilized eggs was 1.07 mm and for fertilized eggs 1.55 mm, similar to cockscombs. They also found no partially spent females, suggesting that all eggs were spawned into one mass. Spawning occurred later than in cockscombs, predominantly in May and incubation to hatching took 35 days in the field at temperatures ranging from 4 to 9° C (LeDrew & Green 1975) but 29 days in aquaria (Green et al. 1987). Male shannies often guarded more than one egg mass (13 cases of a male with a single egg mass, 4 with 2, and 1 with 4 egg masses) which was never the case for female cockscombs in this study.

Marliave & DeMartini (1977) reported on male parental care in two species of eastern North Pacific stichaeids, the rock and black pricklebacks (*Xiphister mucosus* and *X. atropurpureus*). Females were completely spent after spawning and egg masses contained the same number of eggs as ovaries. They concluded that females spawned only

once per year. They also noted that males sometimes guarded more than one egg mass. These masses were in different stages of development, suggesting that males spawned with different females at different times. Fecundity for black pricklebacks was similar to cockscombs, while fecundity of the much larger rock pricklebacks was greater (7039 eggs per egg mass).

Shiogaki (1981, 1982, 1983, 1985, 1987) described reproduction and parental care in five species of stichaeids from Japan (*Opisthocentrus tenuis*, *O. ocellatus*, *Chirolophis japonicus*, *Alectrias mutsuensis*, and *A. benjamini*), all of which exhibited female parental care. For the first two, the spawning season extended from early December to late January. In the third, spawning occurred from late November to December. In the last two, aquarium spawnings occurred in January and February, respectively. The female guarded a single egg mass in all species.

Table 3. Distribution of parental care in those stichaeid species for which it is known. The classification is following Makushok (1958) and Yatsu (1986). ? indicates that no species in the subfamily has been studied for parental care. Multiple egg masses refers to whether the parent guards more than one egg mass simultaneously. \* indicates that the information was taken from Shiogaki's (1981) summary.

| Subfamily<br>Species            | Parent | Multiple egg masses | Reference  |
|---------------------------------|--------|---------------------|--|
| Stichaeinae                     |        |                     |  |
| <i>Ulvaria subbifurcata</i>     | Male   | Yes                 | LeDrew & Green (1975), Green et al. (1987)         |
| Chirolophinae                   |        |                     |  |
| <i>Chirolophis japonicus</i>    | Female | No                  | Shiogaki (1983)                                    |
| <i>Chirolophis ascanii</i>      | Female |                     | Shiogaki (1981*)                                   |
| Lumpeninae                      | ?      |                     |  |
| Opisthocentrinae                |        |                     |  |
| <i>Opisthocentrus tenuis</i>    | Female | No                  | Shiogaki (1981)                                    |
| <i>Opisthocentrus ocellatus</i> | Female | No                  | Shiogaki (1982)                                    |
| Cebidichthyinae                 |        |                     |  |
| <i>Dictyosoma burgeri</i>       | Male   |                     | Shiogaki & Dotsu (1972)                            |
| Xiphisterinae                   |        |                     |  |
| <i>Xiphister atropurpureus</i>  | Male   | Yes                 | Marliave & DeMartini (1977)                        |
| <i>Xiphister mucosus</i>        | Male   | Yes                 | Marliave & DeMartini (1977)                        |
| <i>Ernogrammus hexagrammus</i>  | Male   |                     | Shiogaki (1981*)                                   |
| Alectriinae                     |        |                     |  |
| <i>Anoplarchus purpureus</i>    | Female | No                  | Schultz & DeLacy (1932), Peppar (1965), this study |
| <i>Alectrias alectrolophus</i>  | Female |                     | Shiogaki (1981*)                                   |
| <i>Alectrias mutsuensis</i>     | Female |                     | Shiogaki (1985)                                    |
| <i>Alectrias benjamini</i>      | Female |                     | Shiogaki (1987)                                    |
| Azygopterinae                   | ?      |                     |  |
| Eulophinae                      | ?      |                     |  |

### *Parental care in the Stichaeidae*

The Stichaeidae is one of the few families known to contain species with male-only care and other species with female-only care, but no species with biparental care. Understanding the evolution of this unusual state will be important for understanding and testing general models for the evolution of parental care in fishes. The distribution of these states appears to follow phylogenetic lines (Table 3); care states being the same within subfamilies but differing among subfamilies. However, the systematics of the Stichaeidae are uncertain (Anderson 1984, Stoddard 1985, Follett & Anderson 1990). Makushok (1958, see Gosline 1959 for English translation) divided the superfamily Stichaeoidea into four families, the Anarhichadidae (wolf-fishes), monotypic Ptilichthyidae (quillfish), Pholididae (gunnels) and Stichaeidae (pricklebacks). Within the Stichaeidae, Stoddard's (1985) analysis showed the tribe Xiphisterini and the tribe Alectrini to be sister taxa, together forming the monophyletic Xiphisterinae. According to this view, the subfamily Xiphisterinae contains both species with male care (Xiphisterini) and some with female care (Alectrini). Parental care patterns in the other families in the superfamily are as follows: Anarhichadidae, male-only or biparental (Keats et al. 1985, Marliave 1987, personal observation); Pholididae, biparental though possibly facultatively female-only (Hughes 1986, personal observation); and Ptilichthyidae, unknown. Thus, while the superfamily is known to exhibit a diversity of parental care patterns, a detailed analysis of which state is primitive and which derived must await further studies both on parental care in other species and on the intrarelations of this group.

Ridley (1978), Gittleman (1981) and Gross & Sargent (1985) suggest that solitary male care arises from the absence of care while solitary female care may arise from either biparental care or from no care. The extant stichaeids show no sign of biparental care suggesting that either female care did not evolve from biparental care or that biparental care is unstable and evolves quickly into female care. Gross & Sargent (1985) presented a model for the

evolution of male and female parental care in fishes, recognizing that parental care has only one benefit, the increased survivorship of the young, whereas it has three costs: a mating cost, an adult survivorship cost and a future fertility cost. From their model, female-only care is likely to evolve if the following conditions hold: (i) female fecundity does not accelerate with body size, (ii) male fertility accelerates with body size, and (iii) males are not territorial. The results of this study suggest that the first condition may be true. Fecundity increased only linearly with body size. The second condition cannot be addressed until we know if males in the wild mate with more than one female. My aquarium observations show that a male will spawn with more than one female given the opportunity. If they do this in the wild, and it is the larger males that get multiple mates, then the second condition might also be satisfied. The third condition will need to be addressed by further field observations.

### **Acknowledgements**

I thank R. Whittall and I. Fleming for field assistance, S. Forbes for acquainting me with the Cates Park site, and E. Cooper, M. Kerr, and R. Giroux for assistance with the aquarium observations and maintenance. I am grateful to J. Marliave for sharing his knowledge of and enthusiasm for pricklebacks, E. Crossman for comments on the manuscript, the Department of Fisheries and Oceans (Canada) for a collecting permit, and the Vancouver Public Aquarium (director M. Newman) for permission to use their facilities.

### **References cited**

- Anderson, M.E. 1984. On the anatomy and phylogeny of the Zoarcidae (Teleostei: Perciformes). Ph.D. Thesis, College of William and Mary, Williamsburg. 253 pp.
- Balon, E.K. 1977. Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *Env. Biol. Fish.* 2: 147-167.

- Blumer, L.S. 1979. Male parental care in the bony fishes. *Q. Rev. Biol.* 54: 149–161.
- Blumer, L.S. 1982. A bibliography and categorization of bony fishes exhibiting parental care. *Zool. J. Linn. Soc.* 76: 1–22.
- Eschmeyer, W.N., E.S. Herald & H. Hammann. 1983. A field guide to Pacific Coast fishes of North America. Houghton Mifflin, Boston. 336 pp.
- Follett, W.I. & M.E. Anderson. 1990. *Esselenia*, a new genus of pricklebacks (Teleostei: Stichaeidae), with two new species from California and Baja California Norte. *Copeia* 1990: 147–163.
- Follett, W.I. & D.C. Powell. 1988. *Ernogrammus walkeri*, a new species of prickleback (Pisces: Stichaeidae) from south-central California. *Copeia* 1988: 135–152.
- Gittleman, J.L. 1981. The phylogeny of parental care in fishes. *Anim. Behav.* 29: 936–941.
- Green, J.M., A.-L. Mathisen & J.A. Brown. 1987. Laboratory observations on the reproductive and agonistic behaviour of *Ulvaria subbifurcata* (Pisces: Stichaeidae). *Nat. Can.* 114: 195–202.
- Gross, M.R. & R.C. Sargent. 1985. The evolution of male and female parental care in fishes. *Amer. Zool.* 25: 807–822.
- Hart, J.L. 1973. Pacific fishes of Canada. *Bull. Fish. Res. Board Can.* 180: 1–740.
- Horn, M.H. & K.C. Riegler. 1981. Evaporative water loss and intertidal vertical distribution in relation to body size and morphology of stichaeid fishes from California. *J. Exp. Mar. Biol. Ecol.* 50: 273–288.
- Hughes, G.W. 1986. Observations on the reproductive ecology of the crescent gunnel, *Pholis laeta*, from marine inshore waters of southern British Columbia. *Can. Field-Nat.* 100: 367–370.
- Keats, D.W., G.R. South & D.H. Steele. 1985. Reproduction and egg guarding by Atlantic wolffish (*Anarhichas lupus*: Anarhichidae) and ocean pout (*Macrozoarces americanus*: Zoarcidae) in Newfoundland waters. *Can. J. Zool.* 63: 2565–2568.
- LeDrew, B.R. & J.M. Green. 1975. Biology of the radiated shanny *Ulvaria subbifurcata* Storer in Newfoundland (Pisces: Stichaeidae). *J. Fish Biol.* 7: 485–495.
- Makushok, V.M. 1958. The morphology and classification of the northern blennioid fishes (Stichaeoidea, Blennioidei, Pisces). *Proc. Zool. Instit. Acad. Sci. U.S.S.R.* 25: 3–129. (In Russian, English transl. by A.R. Gosline, U.S. Fish Wildl. Serv.: 1–105.)
- Marliave, J.B. 1975. Seasonal shifts in the spawning site of a northeast Pacific intertidal fish. *J. Fish. Res. Board Can.* 32: 1687–1691.
- Marliave, J.B. 1987. The life history and captive reproduction of the wolf-eel *Anarrhichthys ocellatus* at the Vancouver Public Aquarium. *Int. Zoo Yearb.* 26: 70–81.
- Marliave, J.B. & E.E. DeMartini. 1977. Parental behavior of intertidal fishes of the stichaeid genus *Xiphister*. *Can. J. Zool.* 55: 60–63.
- Mrowka, W. & B. Schierwater. 1988. Energy expenditure for mouthbrooding in a cichlid fish. *Behav. Ecol. Sociobiol.* 22: 161–164.
- Nelson, J. 1984. *Fishes of the world* (2nd Edition). John Wiley & Sons, Toronto. 523 pp.
- Peppar, J.L. 1965. Some features of the life history of the cockscomb prickleback, *Anoplarchus purpureus* Gill. M.Sc. Thesis, University of British Columbia, Vancouver. 159 pp.
- Ridley, M. 1978. Paternal care. *Anim. Behav.* 26: 904–932.
- Schultz, L.P. & A.C. DeLacy. 1932. The eggs and nesting habits of the crested blenny, *Anoplarchus*. *Copeia* 1932: 143–147.
- Shiogaki, M. 1981. Notes on the life history of the stichaeid fish *Opisthocentrus tenuis*. *Jap. J. Ichthyol.* 28: 319–328.
- Shiogaki, M. 1982. Life history of the stichaeid fish *Opisthocentrus ocellatus*. *Jap. J. Ichthyol.* 29: 77–85.
- Shiogaki, M. 1983. On the life history of the stichaeid fish *Chirolophis japonicus*. *Jap. J. Ichthyol.* 29: 446–455.
- Shiogaki, M. 1985. Life history of the stichaeid fish *Alectrias mutsuensis* in Mutsu Bay, northern Japan. *Sci. Rep. Aquaculture Cen., Aomori Pref.* 4: 11–20.
- Shiogaki, M. 1987. Life history of the stichaeid fish *Alectrias benjamini*. *Sci. Rep. Aquaculture Cen., Aomori Pref.* 5: 9–20.
- Shiogaki, M. & Y. Dotsu. 1972. Life history of the blennioid fish, *Dictyosoma burgeri*. *Contrib. Fish. Exp. Station Nagasaki Univ.* 34: 21–38.
- Snively, G. 1978. Exploring the seashore in British Columbia, Washington and Oregon. Gordon Soules Ltd., Vancouver. 240 pp.
- Stoddard, K.M. 1985. A phylogenetic analysis of some prickleback fishes (Teleostei, Stichaeidae, Xiphisterinae) from the North Pacific Ocean, with a discussion of their biogeography. M.Sc. Thesis, California State University, Fullerton. 88 pp.
- van den Berghe, E.P. & M.R. Gross. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* 64: 1482–1486.
- Yanagisawa, Y. & T. Sato. 1990. Active browsing by mouthbrooding females of *Tropheus moori* (Cichlidae) to feed the young and/or themselves. *Env. Biol. Fish.* 27: 43–50.
- Yatsu, A. 1986. Phylogeny and zoogeography of the subfamilies Xiphisterinae and Cebidichthyinae (Blennioidei, Stichaeidae). pp. 663–678. *In*: T. Uyema, R. Arai, T. Taniuchi & K. Matura (ed.) *Indo-Pacific Fish Biology*, Ichthyological Society of Japan, Tokyo.