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## Behavioral Ecology of the Sailfin Blenny, *Emblemaria pandionis* (Pisces: Chaenopsidae), in the Caribbean off Belize

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ABSTRACT

The sailfin blenny, *Emblemaria pandionis*, is a shallow-water, colony-dwelling shore fish that ranges from Florida to South America. Both sexes occupy holes in coral rubble fragments. Females have no fixed homes, but breeding males guard shelter cavities in which eggs are deposited by one or more females. This species is sexually dimorphic; females are cryptically colored and have low dorsal fins, whereas males have much higher spinous dorsal fins and paddle-shaped pelvic fins and are very dark in color when guarding shelters. During daylight hours, males periodically emerge from their shelter cavities and raise and lower their large dorsal fins several times in quick succession. A male may complete more than 1100 such flagging episodes in a single day. Flagging is most intense early in the morning and late in the afternoon and often is highly synchronized

among several males, but the signals do not appear to be answered directly by a particular nearby male. However, the likelihood that flagging by a particular male will be followed by flagging by a specific other male is statistically significant. During presentation experiments, males showed a strong flagging response to females but only weak or no responses to other species. Courtship signals, triggered by the approach of a female, differ markedly from routine crepuscular flagging in that they are a series of unevenly spaced fin lifts while the male remains close to the bottom. Males also perform an aggressive display, and males placed close to each other may engage in combat. Our objective was to determine the biological significance of the flagging behavior of the sailfin blenny. We postulate that flagging episodes are

signals that attract conspecifics of both sexes, whereas aggressive displays and combat maintain the distances between males. The benefits of colonial aggregations include a ready supply of

mates and possible attraction of recruits to a suitable habitat. Cyclical flagging, as distinct from courtship signaling, has not been reported for other chaenopsids.

## INTRODUCTION

The sailfin blenny, *Emblemaria pandionis* Evermann and Marsh, 1899, has both a specialized microhabitat and a social structure that is conspicuous and easy to study. It also adapts well to aquarium conditions so that field observations and manipulations can be supplemented with more controlled experiments. These characteristics make it possible to describe in detail its adult life style.

The sailfin blenny is widely distributed in the Florida Keys, the Bahamas, the Antilles, and along the continental coasts from Texas to northern South America (Stephens, 1970; Robins and Ray, 1986). It lives in shallow rubble-bottom areas near coral reefs, from shorelines to depths of at least 30 m (Böhlke and Chaplin, 1968; Greenfield and Johnson, 1981). Individuals aggregate into colonies that are dispersed in patches within larger expanses that appear to offer equally suitable habitat. Within the colony, males guard shelters in cavities in coral and other limestone fragments, whereas females occupy similar shelters but are far less closely tied to specific shelter sites and move more or less freely about the area.

The flagging of the male sailfin blenny (fig. 1) is one of the most conspicuous behavior patterns of fishes associated with western Atlantic coral reefs. Males spend most of the daylight hours relatively motionless, with their heads protruding from their shelter hole in a rubble fragment. Their heads, fins, and anterior parts of the body are almost black and thus are conspicuous against the pervading pale grayish tan sand of the background. Periodically they emerge to raise and lower their dorsal, anal, and pelvic fins several times in quick succession, after which they rapidly return to their holes and resume a position of vigilance. These display episodes occur hundreds of times each day and are highly stereotyped, with little variation in duration or number of fin lifts. This constancy suggests that they are signal

displays, and, because they occur with and without other species present, they probably are directed to other sailfin blennies in the immediate area. The flagging occurs so many times throughout the early morning and late afternoon hours that it must surely consume a large fraction of the energy budget of males.

The flagging behavior of the sailfin blenny previously has been described briefly by Longley and Hildebrand (1941) and has been photographed by Wickler (1963), David Doubilet (*in* Clark, 1988), and Humann (1994). For the related *E. hypacanthus* from the Pacific coast, female choice of male size as well as response to predators have been studied by Hastings (1991a, 1992) and his investigations of the behavior and ecology of that species continue.

Our objective was to determine the biological significance and adaptive value of the flagging behavior of the sailfin blenny. To do this, we have tried to describe the life style of the sailfin blenny as fully as possible. We have used a combination of field and aquarium observations, experimental field manipulations, and a survey of literature reports of chaenopsid behavior to attempt to understand the social structure of this species.

## METHODS

Our studies were conducted at the Smithsonian Institution marine laboratory on Carrie Bow Cay, Belize (called Ellen Cay on navigation charts of the area). Located at 16° 48'N, 88° 05'W, Carrie Bow Cay is a small, sandy islet on the outer edge of the barrier reef, about 18 km off the coast and 30 km southeast of the city of Dangriga (Rützler and Macintyre, 1982). Our main study area was between 30 and 170 m off the west side of Carrie Bow Cay where the water depth was slightly more than 1 m. We also recorded data on sailfin blennies at a second site about 1000 m south of Carrie Bow Cay



Fig. 1. Male sailfin blenny during an episode of low flagging (photo by Chip Clark, USNM).

where the water depth was approximately 10 m. David Greenfield of the University of Hawaii (personal commun.) has suggested that specimens from deeper water might be a second species, but we have not been able to find any convincing differences between our specimens from deep and shallow waters.

We made preliminary observations in March 1986 and began rigorous data collection in March 1987, with additional studies from 1988 to 1996. General observations at the main study site were made with mask and snorkel and, occasionally, with SCUBA. However, after unsuccessful attempts to record time and duration of the flagging activities with a stopwatch and notebook, we switched to a Panasonic video camera in a specially constructed waterproof housing (fig. 2). Cables supplied power and transmitted the signals to the laboratory on the island, where the activities were recorded on VHS

videotape by means of a JVC time-lapse videocassette recorder (model BR9000U). Most of the data were recorded in 12:2 time-lapse (12 hours of observations recorded on 2 hours of tape), except when special circumstances required more detailed real-time records. At the deepwater site, the data were recorded on a self-contained, 8 mm Sony camcorder in an Amphibico 11 housing and later transferred to VHS tape for review in the laboratory at the American Museum of Natural History.

The starting and ending times of each flagging episode were recorded along with notes on the type of signal and any other unusual events, such as feeding excursions, the approach of swimmers, and visits by larger fish. Real-time records showed that the individual flagging episodes lasted 1 to 8 seconds but most were either 2 or 3 seconds in duration. Therefore, there was no loss of information





Fig. 2. Photograph of video camera in underwater housing (photo by Chip Clark, USNM).

in the time-lapse recordings, which recorded six frames per second. In the laboratory, the tapes were played at regular speed, which provided good definition, until a flagging episode was detected. The tape was then switched to search mode, and the exact time the episode commenced was recorded. Search mode also enabled the observer to step through an episode frame by frame to determine the number of fin lifts and duration of selected episodes. Frequently, the episodes were paired; that is, one episode was followed by another with only 1 or 2 seconds separating them. We listed and scored these as two episodes rather than as a single prolonged display. The duration of the episodes was taken from the tape recordings, which displayed the time in hours, minutes, and seconds. Displays that lasted less than 1 sec were entered as 0.5 sec; those that lasted longer than 1 sec were entered as the difference between the reading at the beginning and at the end of the episode.

Altitudes and azimuths of the sun and times of sunset and sunrise were calculated

using the computer program ACECALC (Astrosoft Inc., Hayward, CA). Intensity of light reaching the bottom at the study site was measured with a Biospherical Instruments QSI-140 integrating quantum scalar irradiance meter. We recorded water temperature with a Peabody Ryan Model J recording thermograph that was attached about 0.5 m below the surface to a pier piling located 45 m from the center of the study area.

During the 1988 and 1989 visits to Carrie Bow Cay, we laid out rectangular grids marked with nylon cord. Easily recognizable characteristics of the edge of the seagrass beds enabled us to set the grid in the same place during each visit. The grid area was 15 m by 25 m (375 m<sup>2</sup>) divided into three rows of five quadrats, each 5 m on a side. Individual nests and shelters were marked by placing painted coral fragments, color coded for either flagging males or females and immatures, next to the shelter rock and plotting the shelter locations on a scale drawing.

Live specimens of sailfin blenny from the main study site were transported to the

American Museum of Natural History in September 1990 and maintained for several years for studies by H. Andreyko of courtship and breeding. Her as yet unpublished manuscript is complementary to our field studies and we refer to it frequently here.

Abbreviations used here include: D—number of spines (Roman numerals) and rays (Arabic numerals) in dorsal fin, A—number of spines and rays in the anal fin, P—number of spines and rays in pelvic fin, SL—standard length, SD—standard deviation, N—number, DF—Degrees of Freedom, CI—95% Confidence Interval, USNM—U.S. National Museum of Natural History, and AMNH—American Museum of Natural History.

#### MATERIALS

The following specimens have been deposited in the AMNH and USNM fish collections. AMNH 220560, AMNH 220562–220583, and AMNH 220585–220590: 217 specimens from the main study site; AMNH 220561: 19 specimens from the deepwater site and AMNH 220570: 3 specimens from Glovers Reef. Cleared and stained specimens include AMNH 220560 (1), AMNH 220579 (2), and USNM 320805 (1).

#### BIOLOGY OF THE SAILFIN BLENNY

Many special aspects of the biology of the sailfin blenny, including its morphology, general ecology, and population dynamics, offer clues to the role of signaling in its ecology.

#### MORPHOLOGY

Sailfin blennies are scaleless. The lack of scales would seem to be advantageous for a species that lives in holes that most often are not much wider than the fish themselves. Sailfin blennies are almost constantly in contact with either the irregular surface of their coral fragment shelter cavities or with rough sandy or rocky bottom. Although it would appear that the expanded dorsal fin of males and even the smaller, but still large, dorsal fin of females would be disadvantageous for a species that lives in small holes, videotapes made in the laboratory and in the field show

that males often rapidly enter their burrows tail first, apparently without difficulty.

#### Description

Body slender, tapering, and slightly compressed. Head blunt. Dorsal and anal fins long, with higher anterior lobes. Tail truncate. Orbital cirrus straplike, simple or weakly bifid. Nasal cirrus flat, trifold or bifid, sometimes bifid with a bulge on the longest branch, suggesting a third branch. Teeth on dentary large and compressed, about 24 on each ramus; 5th to 10th teeth enlarged and slightly recurved; a secondary patch of smaller, conical teeth on each side of the symphysis. Premaxillary teeth similar, about 20 in the main row on each side, the anterior 7 large, compressed and recurved, the rest about half as long. Palatine teeth in a single row of nine, stout and bluntly pointed. Vomer edentulous. A row of about four rather prominent rakerlike papillae on the hyoid bar opposite the gill rakers of the first arch.

The fin spines are generally slender and flexible (fig. 3). Distal parts of the dorsal and anal spines stain blue with alcian and are probably primarily collagen fibers.

Hildebrand (in Longley and Hildebrand, 1941) recorded the counts of the largest of 20 males, 27 to 50 mm long, from Tortugas, Florida, as D XXII,16; A II,24; and P I,3; and the counts of the holotype from Puerto Rico as D XXII,15; A. II,23; and P I,3 (These differ from the counts in the original description, which were given as D VII,17; A II,23; and P I,2.)

Dorsal and anal counts for 85 specimens from Carrie Bow Cay are as follow: D XX,14 (3); XX,15 (12); XXI,12 (1); XXI,13 (7); XXI,14 (48); XXI,15 (14); and A II,20 (1); II,21 (8); II,22 (46); II,23 (30). Pectoral counts for 40 specimens are 11–12 (1); 12–13 (3); 13–13 (34); 13–14 (0); 14–14 (2). Vertebral counts from three cleared and stained specimens are USNM 320805, male 41.1 mm SL, 40; AMNH 220560, female 29.3 mm SL, 40; and AMNH 220579 female 29.4 mm SL, 39.

#### Sexual Dimorphism

The sailfin blenny is strongly sexually dimorphic in color and in body and fin proportions. Proportional measurements of

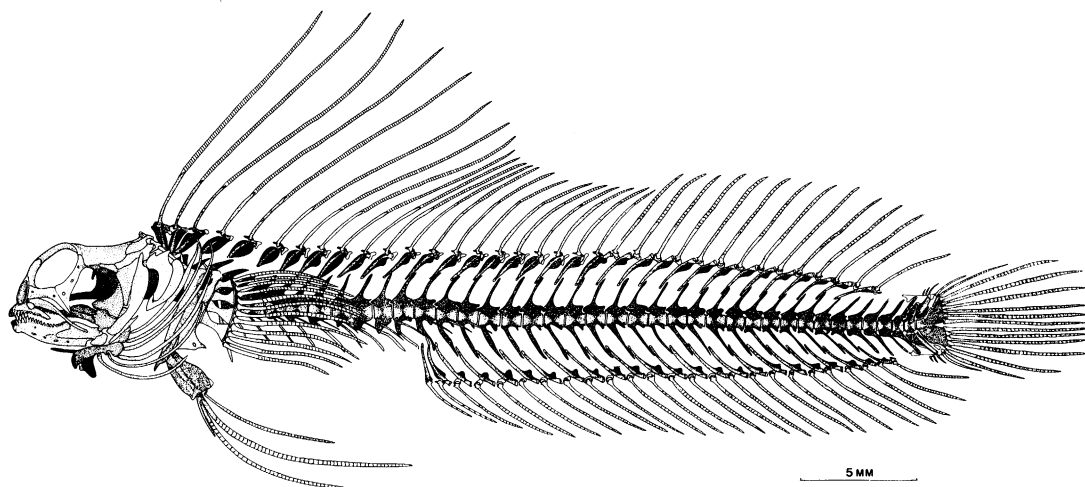


Fig. 3. Lateral view of entire skeleton of a male. The illustration shows the cartilage of the fins and the fin supports that enhance flexibility for flagging and for movement in and out of the hole; all ossifications are stippled. Outlined but not stippled are cartilages, those shown being the distal ends of the 21 dorsal- and 2 anal-fin spines (with parallel cross hatching); the posterodistal and basal ends of all the basal pterygiophores of the spiny and soft dorsal and anal fins; the spherical nubbins partially enclosed between the two halves of the ossified distal pterygiophores of all the soft dorsal- and anal-fin rays; the distal ends of the neural and haemal spines of the 24th and more posterior caudal vertebrae (i.e., those of the caudal peduncle); and the distal ends of all elements of the last vertebral complex (i.e., the fused parhypural-hypural plate, the uppermost free or fifth hypural, and the epural), with especially large cartilages between the distal ends of the neural and haemal spines of the 25th to 27th (penultimate) caudal vertebrae. Illustration of USNM 320805, 41.1 mm SL, Carrie Bow Cay, Belize.

males and females are presented in table 1. The clearest distinction between the sexes is that the anterior dorsal-fin spines are longer in males than in females. The pelvic fins (fig. 4) of males are paddle shaped, with the rays widely separated distally and the interradyal membranes little incised between the tips of the rays. Females have the pelvic rays nearly parallel and the membranes deeply incised. The color patterns are distinctive (see below), although in the field the differences are not always reliable because males have transient color phases in which they become momentarily pale, blotched, and similar to females. The color of immature males is similar to that of females. Males tend to be slightly larger than females. The mean standard length of 64 females was 26.25 mm (SD 4.65) and the mean standard length of 117 males was 31.89 mm (SD 5.48) ( $F = 22.83$ ,  $P = 0.001$ ). Longley (in Longley and Hildebrand, 1941) noted dimorphism in the urogenital papillae; in males the urogenital pa-

pilla is conical and free from the anal rugae, whereas in females there are more (about 12) radial folds that are emarginate ventrally, forming a brush of fleshy processes in two concentric rows of about a dozen papillae each around the vent, and two additional conspicuous papillae just behind the vent in a transverse plane.

**COLOR OF FEMALES** (in preservative): Head mottled, punctate dorsally, with a short, vertically elongate dark bar just behind the ventral limb of the preopercle. Another poorly defined dark bar or spot at the posteroventral rim of the eye, and a transverse bar across the anterior end of the hyoid apparatus. Body pale gray with numerous groups of melanophores forming scattered irregular bars and stripes. Side with about 15 irregular bars and spots along the midside, the anterior two relatively complete bars joining the gray punctate area of the belly. Above all 15 bars there are irregular spots. A clear area around anus. Pectoral fin hyaline. Pelvic fin with a few

TABLE 1  
**Proportional Measurements of Males  
and Females**  
(all proportions in thousandths of the standard length)

Attribute	Males	Females
Standard Length (mm) <sup>a</sup>	33.47	28.57
Longest dorsal spine <sup>b</sup>	356	163
Longest anal spine	163	163
Body depth	163	169
Head width <sup>a</sup>	155	166
Head length <sup>a</sup>	268	286
Pelvic fin length	229	243

<sup>a</sup> Males and females significantly different (*t*-test, *P* < 0.05).  
<sup>b</sup> Males and females significantly different (*t*-test, *P* < 0.001).

melanophores scattered across the middle of the fin. Prepectoral area with four spots arranged in a diamond pattern, the ventral spot a crescent. Caudal fin clear. Anal fin mostly clear, with a band of melanophores extending from the anterior margin of the fin to about the 18th ray. This band about one-fourth the length of the rays and located on the distal third quarter of the fin. Dorsal fin crossed by

alternating diagonal black and white bars, with the anterior five reasonably distinct, the rest mere rows of spots. The first of the bars runs from the middle of the anteriormost spine to the base of the 3rd spine; the fifth black bar runs from the distal end of the 3rd spine to the base of the 10th spine.

**COLOR OF MATURE MALES:** Head and body generally black (brown in preservative) with the melanophores more widely spaced on the caudal peduncle. About 14 pearly blue irregular spots on each side along the base of the dorsal fin. Lips and lower surface of the head with scattered smaller pearly spots, tending to be in rows across the gill membranes. Pectoral fins generally clear with two rows of melanophores along each ray. Pelvic fins entirely dark. Dorsal fin generally the same color as the body, becoming hyaline posteriorly, with groups of melanophores forming irregular bands that slope diagonally downward posteriorly. There are also darker bands in the anterior lobe of the dorsal fin. Anal fin uniformly dark, with white tips on the soft rays. No white tips on the anal spines. A pearly spot at the base of each of rays 1 through 10, these spots becoming indistinct

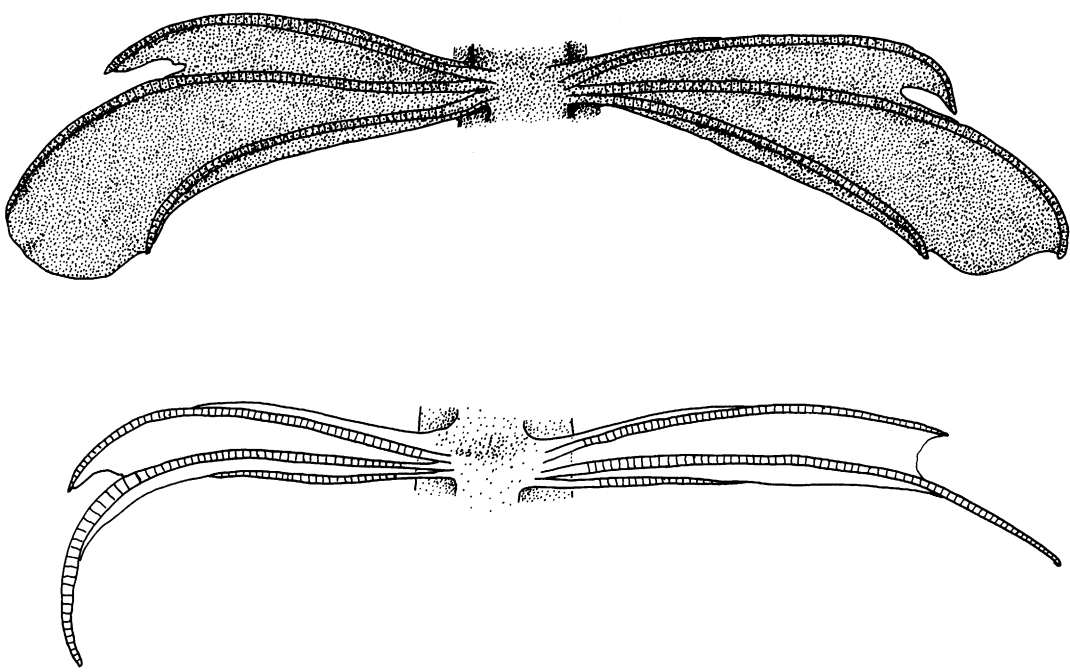


Fig. 4. Sexual dimorphism of pelvic fins. Top, male; bottom, female.

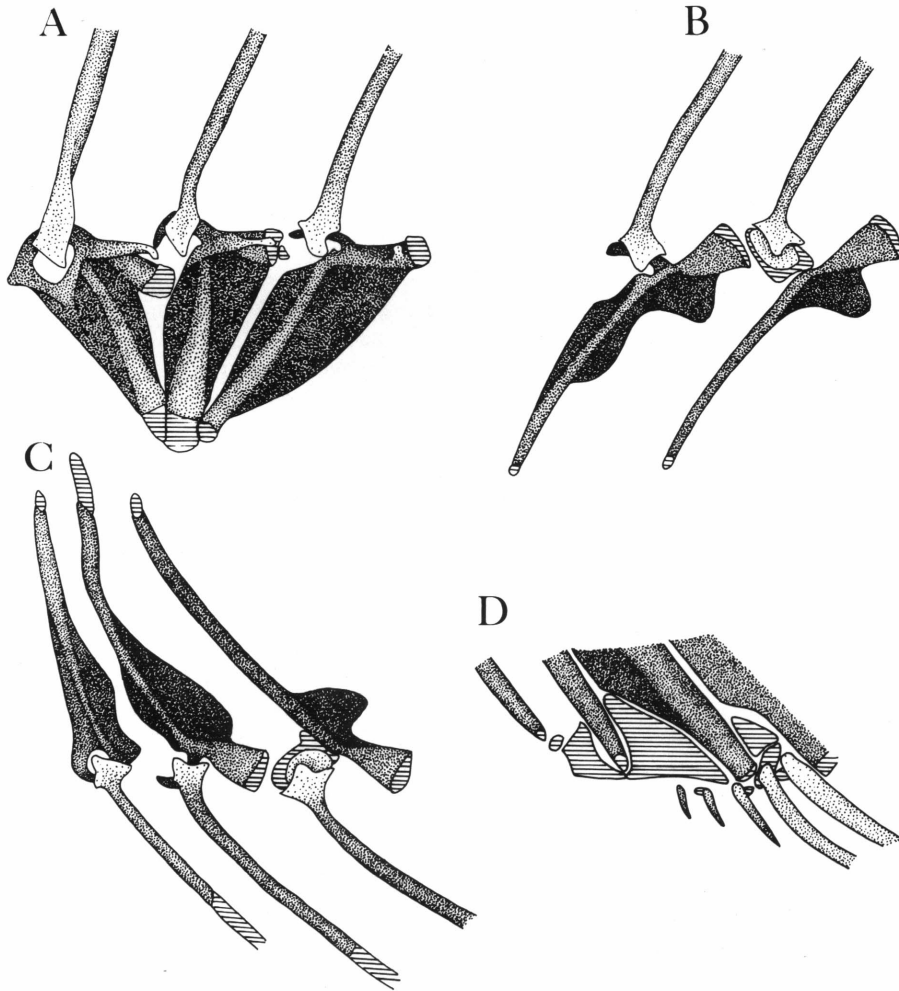


Fig. 5. Details of articulations of representative spines and rays in the fins: **A**, first three dorsal spines; **B**, last spine and first ray of the dorsal fin; **C**, the two anal spines and the first anal ray; and **D**, the four lower procurent rays and the first caudal-fin ray, at the distal ends of the 25th to 27th caudal vertebrae and the lower edge of the fused hypural plate. Cartilages shown by parallel line crosshatching. Illustration of the specimen in fig. 3.

posteriorly. Males also have a paler mottled phase when disturbed (fig. 21).

#### Osteology

In both sexes the intermediate segments of the dorsal and anal pterygiophores are ligamentous (figs. 3, 5). This apparently gives the body sufficient flexibility to enable the fish to turn around in their shelter cavities, which are often little wider than twice the diameter of the occupant. The incompletely ossified and flexible dorsal-fin spines are ap-

parently advantageous to fishes that live in confined spaces. Hastings and Springer (1994) list the incomplete ossification of the dorsal and anal spines and the absence of a secondary lateral ridge on the proximal dorsal pterygiophores as synapomorphies of the Chaenopsinae.

#### FEEDING

Males sometimes made short excursions from their shelters without raising their fins.

They usually appeared to capture something from the bottom or just off the bottom, and we believe that most of these excursions were feeding episodes. However, the excursions were relatively infrequent and may not represent the entire feeding strategy of males. Videotape records indicate that the average male has about 475 flagging episodes in a full day and that the average duration of an episode is 1.55 sec. Therefore, during a 13-hour daylight period, the average male spent approximately 1.54% of its time signaling and far less than 1% making excursions. In view of the high level of signaling by males guarding shelters, it is of interest that so little feeding activity was observed.

The sailfin blenny is a carnivore with a short gut. Although we would not expect the blennies to feed constantly, as herbivorous animals do, we would expect more feeding than we were able to observe. Because males appeared to spend so little time feeding, we can well ask where they obtain the bulk of their nourishment. Andreyko (MS) has demonstrated that males remove eggs from their shelters but never observed them to spit the eggs out. Thus, it appears that the males feed on eggs in their nests, and it is possible that a substantial fraction of their energy requirement could come from eggs consumed in the nests. This would mean that females gather energy and materials for both sexes, transferring them to males in the form of eggs. If this were the case, we would expect to find (1) egg remnants in males' stomachs, (2) few other prey items in the males' stomachs, and (3) a greater variety of items in the stomachs of females. We therefore examined the stomachs of 18 males, 10 females, and 2 juveniles. The results are presented in table 2. Both males and females fed on a variety of items but only two eggs were found in the stomach of one male. Therefore, the hypothesis that egg cannibalism is a common mode of feeding was not born out. In this small sample there is very little difference between the diets of males and females. The absence of chironomids and cumaceans, which live in the sand, in the stomachs of males may indicate that the males rarely prey on organisms that are not at the surface of the sandy bottom.

From time to time, males appeared to crop

TABLE 2  
**Stomach Contents**  
(number of stomachs containing each item)

Items	Females and juveniles	
	N = 10	Males N = 18
Copepods	10	6
Amphipods	3	7
Crab megalops	1	2
Isopods	1	2
Chironomidae	1	0
Crab	1	0
Mysids	0	1
Stomatopods	0	1
Cumaceans	1	0
Decapods	2	1
Snail	0	1
Blenny eggs	0	1
Unidentified	2	2
Number of different items	9	10
Empty stomachs	1	2

particles that drifted past the burrow entrance. Such feeding activity is difficult to see on the tapes, and we were not able to obtain reliable quantitative data, but apparently it is the more common mode of feeding.

#### PREDATORS

Although males are extremely conspicuous in their shelters and would appear to be vulnerable to predation as they perform their signaling, we have recorded only one instance of actual predation. On 20 September 1990 at 05:52, during an experiment in which a male had been isolated by removing all other blennies in the area, a reef squid, *Sepioteuthis sepioidea*, captured the male as it emerged to signal. On one other occasion, a male that was being moved through mid-water escaped from its shelter hole and started to swim to the bottom. Almost immediately a peacock flounder, *Bothus lunatus*, struck at the swimming blenny but missed. Typically, adult male blennies seem to be relatively safe from the many potential predators that pass over the colony. We saw no indication of predators stalking or otherwise attempting to attack blennies as they were signaling. We saw little indication that the



Fig. 6. Primary study site viewed from Carrie Bow Cay. The buoys mark the corners of the sampling grid.

approach of a potential predator even inhibits signaling. We have no data on predation on females as they move about the colony or on the young as they leave the nests.

#### HABITAT

The main study site (fig. 6) is located on the west side of the island at the southern limit of a large area of sand and rubble in the shallow lagoon behind the barrier reef. The location of the colony changed between our observations in 1987 and 1988. In March 1987 the primary colony was centered about 120 m west of the island, but by March 1988 that area had been mostly abandoned and the larger coral fragments had dense algal growth. The colony center had moved closer to the island by about 20 m, where it remained through March 1996. The location was in a notch in the margin of a dense bed of sea grasses, *Thalassia* and *Syringodium*, which limited it on the west, south, and east. The distribution of sea grasses and some artifacts secured in the open sand areas provided reliable landmarks for repetitive obser-

vations. The depth of the primary study area ranged from 111 to 125 cm at low tide.

The preferred habitat of the sailfin blenny is areas where the bottom is nearly flat sand and has coral fragments with sparse algae encrustations and ample cavities for shelter sites. The colonies are in open areas near the edges of beds of *Thalassia testudinum*, where the plants are sparse. Sometimes the shelters are in rocks that are among the plants but most often they are out in the open. Sailfin blennies seem to avoid solid rocky bottom areas, and colonies seldom occur within about 5 m of live reefs. At the main study area (fig. 7) the bottom was coarse sand with abundant fragments of corals and eroded *Strombus* shells. Table 3 shows the relative abundance of large and small rubble fragments in typical one-fourth-square-meter quadrats in the colony zone.

Most rubble fragments in the study area had some low algae, which apparently was kept cropped by herbivorous fishes, including schools of surgeonfishes *Acanthurus* spp., parrotfishes *Sparisoma* and *Scarus* spp.,

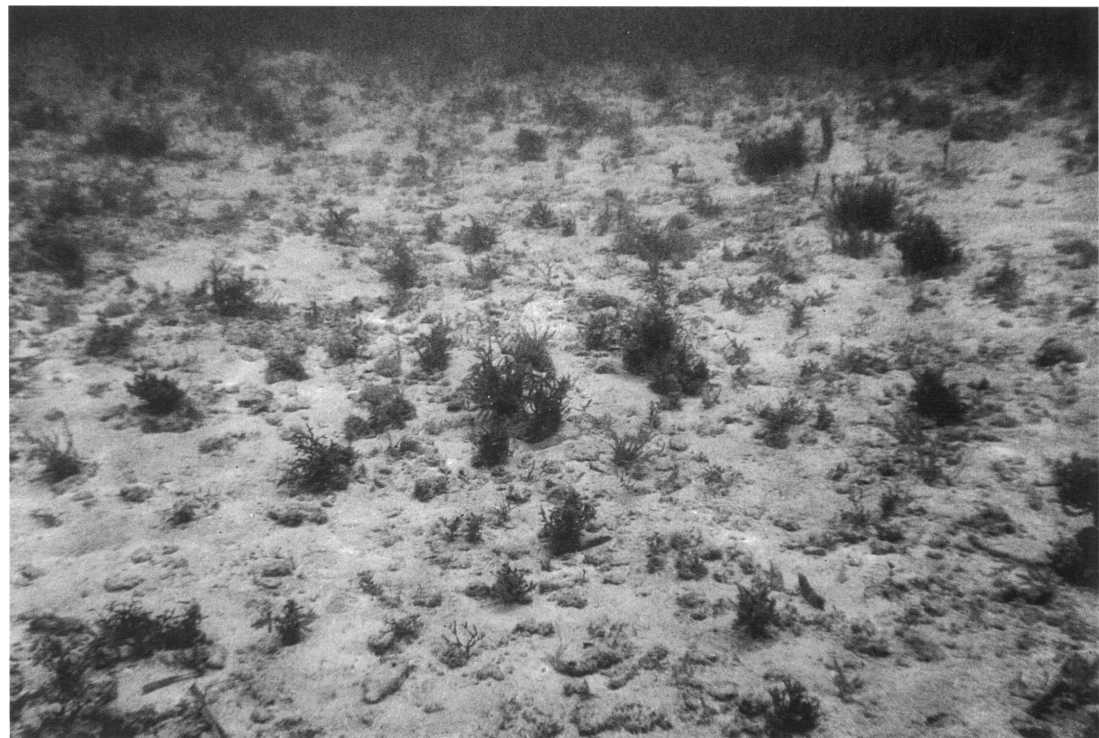


Fig. 7. Underwater view of the study site.

and the queen triggerfish, *Balistes vetula*, that regularly patrolled the area. A few shelters were found in rubble a short distance into the seagrass bed, one in a waterlogged palm tree trunk.

This open and flat habitat offers little shelter for larger fish and therefore supports a rather limited fish fauna, although many larger species visit the area regularly. Some of these are predators, including the yellowtail snapper, *Ocyurus chrysurus*, grunts (species

of the family Haemulidae), and the peacock flounder. Most of the fishes seen on the tapes are transient or visitor species; few, other than the sailfin blenny, are permanent residents. Two burrowing species, a jawfish, *Opisthognathus aurifrons*, and a pike blenny, *Chaenopsis limbaughi*, were represented by single individuals resident for short periods. Small individual damselfishes, *Stegastes* spp., were present and sometimes established territories around the television camera and its supports. The sand-dwelling gobies *Coryphopterus glaucofraenum* and *Gnatholepis thompsoni* were common. Barracudas, *Sphyraena barracuda*, and nurse sharks, *Ginglymostoma cirratum*, were recorded occasionally, and once a manatee, *Trichechus manatus*, passed in front of the camera. Foraging southern sting rays, *Dasyatis americanus*, came into the area and scattered sand and rubble that contained shelters, and herbivorous fishes cropped algae from the shelter rocks. Larger fishes frequently moved and sometimes accidentally inverted the blenny's

TABLE 3  
Relative Frequency of Rubble Fragment Sizes  
(counts for five 0.25 m<sup>2</sup> quadrats)

Sample number	>50 mm	20–50 mm	Total
1	7	23	30
2	6	33	39
3	15	34	49
4	3	59	62
5	9	31	39
Average	7.8	36.0	43.8



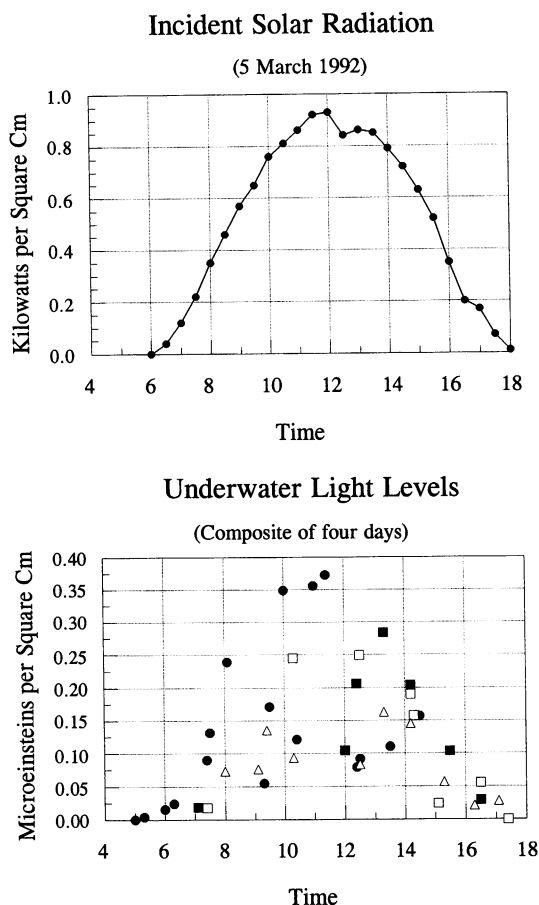


Fig. 8. Top, Solar radiation at Carrie Bow Cay, 5 March 1992. Bottom, Light intensity at the bottom, composite of 4 days' observations.

shelter rocks. Additional species seen at the site are listed in the appendix.

The shallow water of the study area receives intense sunlight. Figure 8 (top) shows the intensity of solar radiation received by the Carrie Bow Cay station throughout the day on 5 March 1992. This was a generally clear day and the values are probably near maximum for that season. Cloud cover caused some dips in the solar radiation curve, most noticeable between 12:00 and 13:00 hours. Light levels at the bottom for four days are shown in figure 8 (bottom). In general, the amount of light reaching the bottom parallels the incoming radiation, reaching maximum at about local apparent noon. The small scale of measurement (microeinsteins

per square centimeter) emphasizes the variations caused by different amounts of cloud cover.

Mean temperatures ranged from 23.9°C in February–March 1992 to 27.6° in mid June 1988. Mean November temperatures showed some variation (26.6° in 1988, 24.7° in 1989), whereas March and April temperatures were less variable (25.3° in March–April 1989, 25.5° in March 1991). The temperature fluctuates about 4°C during a typical diel cycle. In the shallow main study site, the water is well mixed, and there is no indication of a thermocline. Temperatures are also influenced by winds and cloud cover.

The semidiurnal tides in the Carrie Bow area are small, with an average range of 15 cm. The tidal regimen of Carrie Bow Cay was studied by Kjerfve, Rützler, and Kierspe (in Rützler and Macintyre, 1982).

The main study area had a consistent current flowing from north to south. On 27 and 28 February and 3 March 1992, days typical for the season with winds that were neither especially strong nor exceptionally calm, we estimated water velocities by timing the movement of a plastic jug, weighted until it was barely afloat, over a measured line laid along the bottom in the direction of the current. We also timed the movement of fluorescein dye released near the bottom along the same line. Surface velocities during four trial periods ranged from 0.067 to 0.166 m/sec, and bottom velocities (two trials) were 0.106 and 0.104 m/sec.

During the normal trade winds, the study area is sheltered by the island, protected from strong currents and direct wave action. Winds from the northwest or north, which can occur as much as 32% of the time in January and February (Rützler and Ferraris, in Rützler and Macintyre, 1982), can cause sufficient surge to limit blenny activity in the area. Sometimes the currents are strong enough to shift the shelter fragments and transport sand through the area.

### FLAGGING BEHAVIOR

Our descriptions of flagging behavior are based on analysis of videotapes from 109 periods ranging in length from less than 1 hour to more than 13 hours. In total, 774 hours

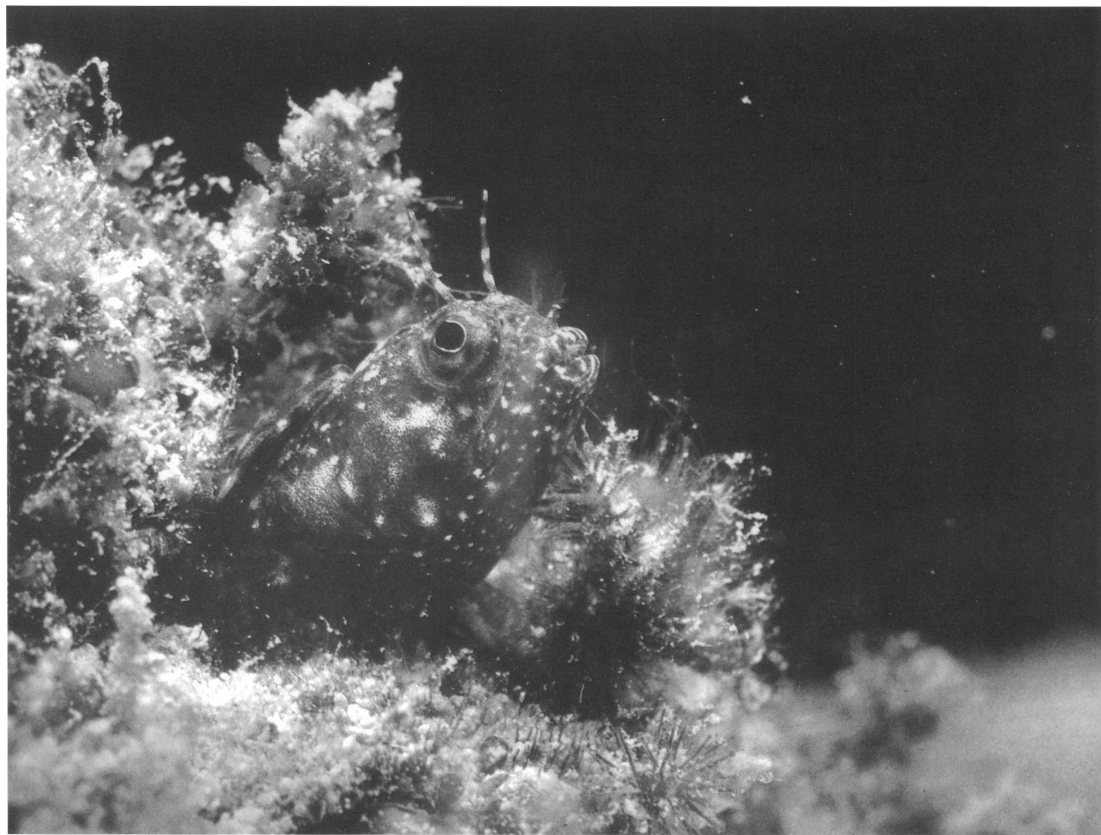


Fig. 9. Male blenny maintaining vigilance in shelter burrow between flagging episodes (photo by Chip Clark, USNM).

and 36 min of tapes were analyzed, most of which included more than one fish. During these periods 34,596 flagging episodes were recorded.

#### DEFINITIONS

Cyclical flagging of the male sailfin blenny consists of bursts of activity separated by periods of inactivity during which the male either remains completely inside its shelter or protrudes with its head and anterior body in an attitude of vigilance (fig. 9). Each burst of activity consists of one or more "episodes" during which the male emerges and raises and lowers its dorsal, anal, and pelvic fins one or more times. We refer to each individual cycle of raising and lowering the fins as a "fin lift."

Signals were classified as "low flags" if the fish emerged less than an estimated two

or three full body lengths out of the hole, "high flags" if they emerged more than three full body lengths. If the fish left its hole without raising the dorsal fin, it was recorded as an "excursion." Computer programs were used to compute the intervals between the episodes and to calculate the rate of flagging as measured by the number of episodes during a given interval (usually 10 min). The maximum flagging rate by one male was 85 episodes in 10 min on 7 June 1988 at 05:10.

During both low and high flagging the pelvic fins move forward as the dorsal fin is raised and backward as the dorsal fin is lowered (fig. 10, low flagging). Synchronization is not absolute; usually the pelvic fins move slightly after the dorsal fin, reaching their forward limit after the dorsal fin has started backward. The raising (forward) movement of the dorsal and pelvic fins would tend to

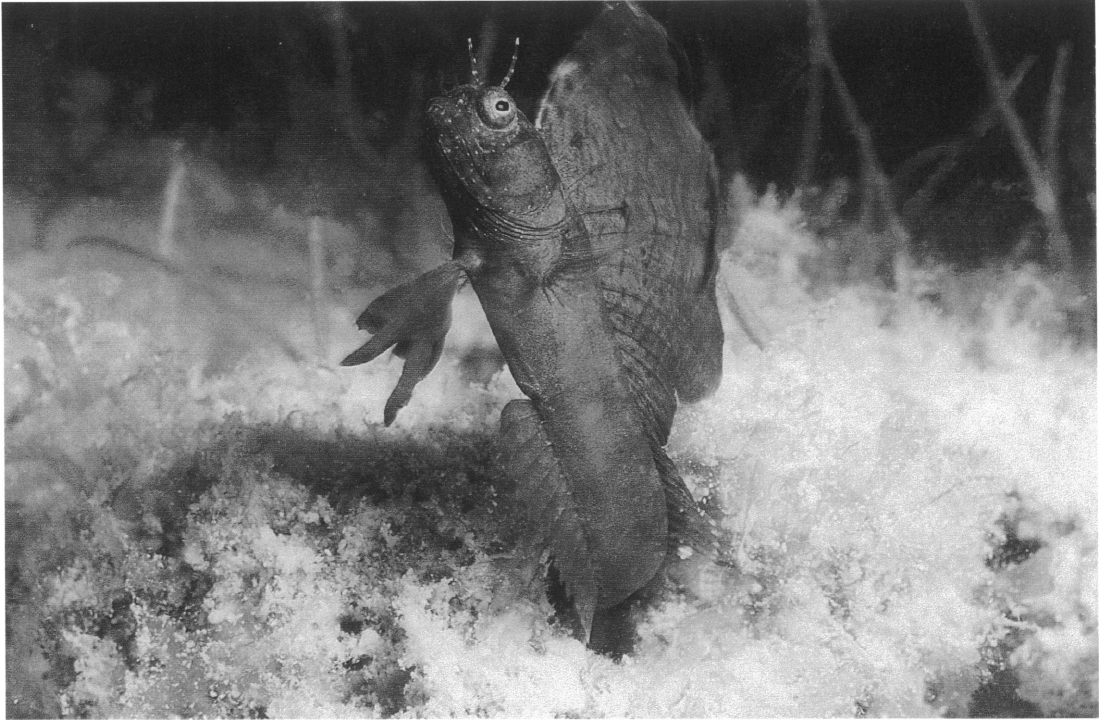


Fig. 10. Closeup of flagging male sailfin blenny at the height of a fin lift showing fully extended dorsal, anal, and pelvic fins (photo by Carl Hansen, USNM).

push the body backward, and the lowering of the fins would drive the fish forward. These movements are probably counteracted by opposing movements of the pectoral fin, which is at right angles to the body as the dorsal and anal fins are lowered (visible in figure 10). Because the pectoral fin is nearly transparent, we have not been able to determine its precise movements from videotapes.

#### LOW FLAG

We recorded the number of fin lifts and the duration of a sample of low flag episodes from real-time videotapes made in the field in March 1991 (table 4). Differences in mean duration and mean number of fin lifts during different time periods, by two individual males, on three different dates, were statistically significant at the 0.01 level (ANOVA and t-tests), but, because there was no obviously consistent pattern, we pooled the results.

In this pooled sample, the number of fin lifts per episode ranged from 1 to 19 (mean

= 6.7 lifts, SD = 3.5, CI = 6.5–7.1, N = 421). The duration of episodes ranged from 0.5 to 7 sec (mean = 1.73 sec, SD = 1.01, CI = 1.5 – 1.6, N = 422) (table 4). In figure 11 the duration of and number of lifts during low and high flag episodes are summarized as frequency histograms.

#### HIGH FLAG

A smaller proportion, usually less than 15% of the episodes were high flags, during which the fish emerged as much as one-half meter or so from the burrow. High flags start with the fish emerging part way from the burrow and raising and lowering the fin as in low flag episodes, but then the male moves up in the water column and continues to raise and lower the fins (fig. 12). High flag episodes typically included 5 to 24 lifts (mean = 14.3 lifts, SD = 3.77, CI = 13.1–15.5, N = 36). Comparison of 25 high flag episodes from 26 and 27 March 1988 and 11 from 16 to 18 March 1991 with the low flag episodes discussed above showed that high flags in-

TABLE 4  
Number of Fin Lifts and Duration of Low Flag Episodes

Subject, date, time of day	Number of lifts			Duration (sec) of episodes		
	N	Mean	SD	N	Mean	SD
Male A						
16 Mar 91, AM	85	5.9	2.7	85	1.49	0.66
16 Mar 91, PM	28	7.8	2.5	28	1.34	0.79
Male A1						
18 Mar 91, AM	87	8.4	3.5	88	1.96	0.80
18 Mar 91, PM	83	7.1	3.6	83	1.39	0.65
19 Mar 91, AM	138	5.9	3.2	138	1.46	0.98

cluded more lifts per episode ( $t = 12.46$ ,  $DF = 456$ ,  $P < 0.001$ ). Durations of high flag episodes were also greater (mean = 3.0 sec,  $SD = 1.04$ ,  $CI = 2.7\text{--}3.3$ ,  $N = 36$ ,  $t = 7.2$ ,  $DF = 456$ ,  $P < 0.001$ ). Figure 11 shows frequency histograms for number of lifts and duration of high flag episodes.

FLAGGING EFFORT

Males flag whether or not there are eggs in their shelters. Some shelters collected in the field contained no eggs and Andreyko (MS) found that captive males also flagged when there were no eggs in the shelter.

Sixteen full-day records, each covering approximately 11 hours with interruptions of less than 15 min were analyzed to provide an indication of the “normal” amount of cyclical flagging effort by males (table 5). These records included nine individuals and nine separate days. There were no significant differences in numbers of high flags, low flags, excursions, or total number of flagging episodes between days, and only the number of high flags was significantly different between individuals.

Full-day records from 33 additional days were excluded because of experiments conducted in the colony on those days, but it is of interest that the greatest number of episodes by one individual, 1160, occurred on a day when the colony was covered by a translucent plastic sheet.

FLAGGING PERIODICITY

Males have a rigorous regimen of intense flagging activity around sunrise and again in

the late afternoon (fig. 13). In the morning, flagging was usually in progress by the time there was enough light for the camera to record an image, but the signaling was at a low rate. As the light increased, the rate of flagging increased until shortly after sunrise, then flagging started to decline. By about 2 hours after sunrise, when the sun reached an average altitude of 31.9° ( $SD = 12.54$ ,  $N = 28$ ), flagging slowed to sporadic episodes and continued at a low rate until afternoon, when the pattern was reversed. Beginning about 3 hours before sunset, when the sun had dropped to an average altitude of about 43° ( $SD = 15.03$ ,  $N = 20$ ), the flagging rate increased and reached a peak about 45 min before sunset, thereafter declining until the blennies were essentially inactive by the time the camera could no longer pick up an image. Although this pattern was consistent, there were pronounced fluctuations in intensity within the peak periods. Often there was a period of intense flagging in the early afternoon followed by a period of flagging at a lower rate before the late afternoon peak. In figure 14 flagging rates are plotted against calculated altitude of the sun for 12 representative days. Although there is a great deal of scatter, there is a definite pattern of decreased flagging when the sun is high in the sky.

The numbers of flagging episodes by individual fish before and after midday (12:00 hours) were compared for days with essentially complete records. There was no significant difference between the number of low flag episodes in the morning and afternoon (morning average 242.6, range 22–559; af-

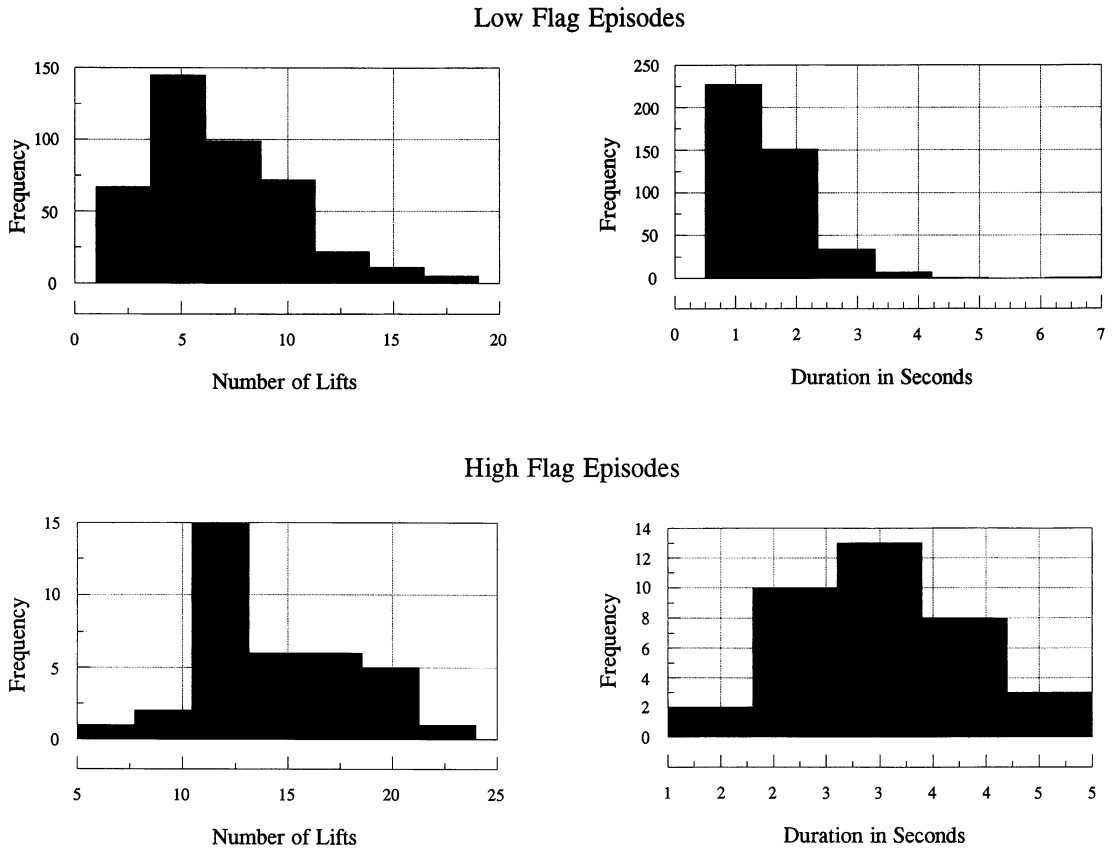


Fig. 11. Frequency histograms of number of fin lifts and duration of (top) low and (bottom) high flagging episodes.

ternoon average 239.9, range 36–478,  $N = 19$ , paired  $t$ -test,  $t = 0.08$ , 18 DF = 18,  $P = 0.933$ ). High flags, however, occur more frequently in the afternoon. In the same sample the morning average was 12.0 (range 0–35), and the afternoon average 26.1 (range 4–85); a paired  $t$ -test indicated this difference was highly significant ( $t = 3.28$ , DF = 17,  $P = 0.005$ ).

We were unable to find any indication of nocturnal flagging activity. All individuals were essentially quiescent at the lowest light levels our equipment could detect, and captive individuals held at Carrie Bow Cay did not flag at night nor did we detect flagging when we snorkeled over the colony at night.

#### FACTORS AFFECTING CYCLICAL FLAGGING

##### Relation to the Position of the Sun

There is a strong correlation between the altitude of the sun and the rate of signaling

by males (fig. 13). A summary of the relationship between flagging and the altitude of the sun is given in table 6. This general pattern was present even on days when the colony was manipulated experimentally (see for example figs. 18, 21, 22). A comparison of the daily flagging cycle with a plot of the azimuth of the sun revealed no correlation with flagging intensity. In fact, azimuth changes most rapidly when the sun is near the meridian, the time when flagging is minimal. Thus, direction of the sun does not affect flagging behavior.

**RIPPLE SHADOWS:** The morning decline in signaling rate also coincides with the onset of distinct ripple shadows on the bottom, which is, in turn, determined by the altitude of the sun. When the sun is high enough and not obscured by clouds, ripples and wavelets on the surface focus the light into bright lines and pronounced broader shadows, producing

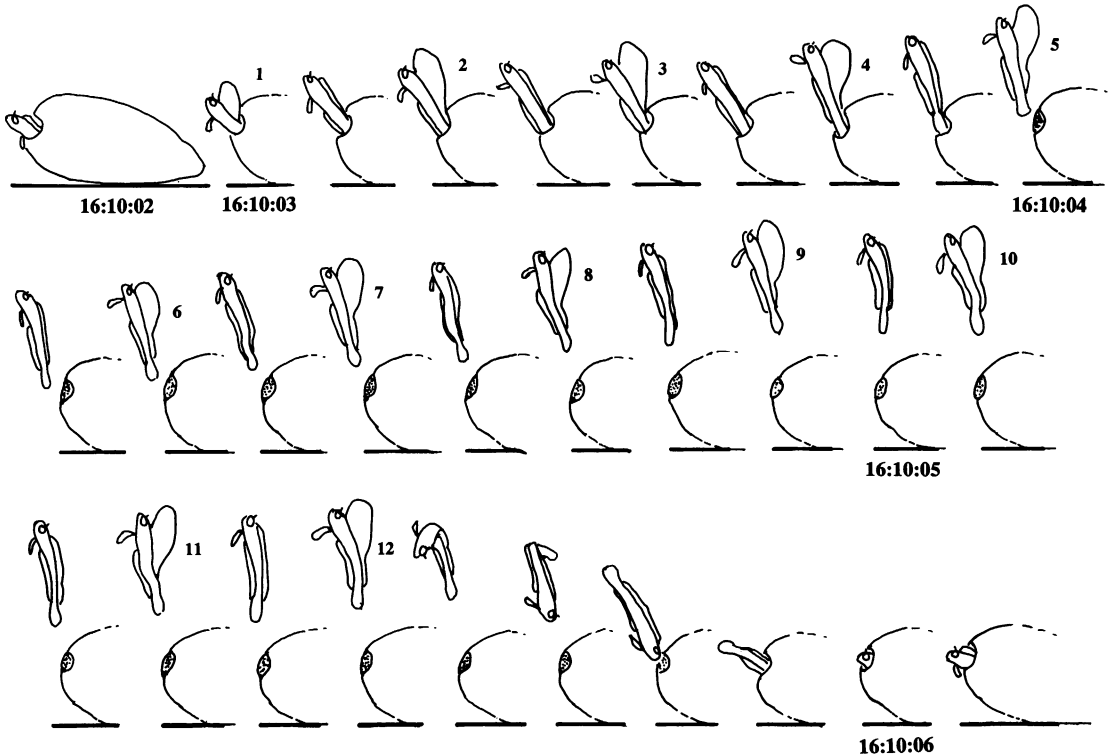


Fig. 12. Sequence of fin lifts during a high flag episode. Sketches from video tape recorded in the field at Carrie Bow Cay on 27 March 1988. The episode began at ten minutes and two seconds after 4 PM (16:10:02, last frame) and concluded approximately 3 seconds later (16:10:06, first frame). The episode consisted of 12 lifts (numbered), the first four occurred as the fish was emerging; the last eight while the fish was fully out of the shelter hole.

a moving mottled pattern on the bottom. The difference in light intensity and rapidity of movement between the light and dark areas is at times great enough to make it difficult to read the tapes. When a cloud passes in front of the sun, these ripple patterns disappear, and the light becomes more uniform.

Frequently, disappearance of the ripple patterns seemed to trigger flagging episodes. We tested this relationship in two ways: by examining the videotapes from shallow and deep-water colonies and by conducting field experiments. We assigned the degree of ripple shadows on the videotapes from 4 June

TABLE 5  
Male Blenny Activities<sup>a</sup>

Activity	N	Mean number of episodes	SD	Range	CI
Total flagging episodes	16	449.9	285.6	137-964	297-603
High flags	15	61.7	74.4	13-293	20-102
Low flags	15	395.9	288.7	91-994	236-556
Excursions	15	14.3	12.4	1-41	7-21

<sup>a</sup> Data from 16 full-day video tape records representing nine individuals on nine separate days. N represents the number of record segments studied.

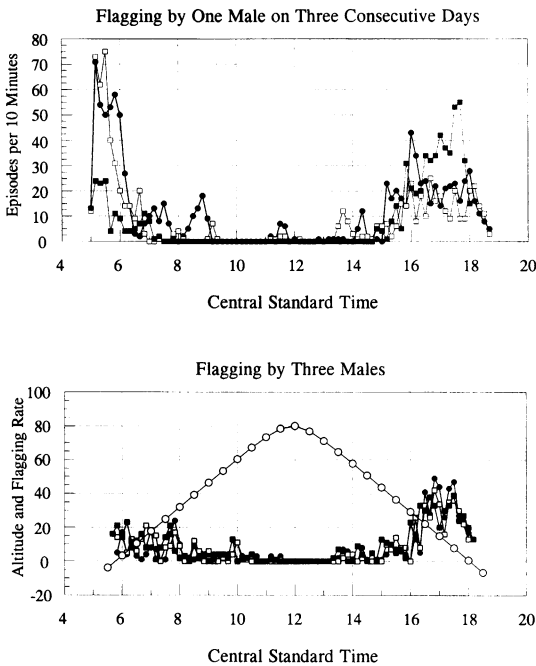


Fig. 13. Normal daily flagging cycle. Top, flagging rates by a single male on 4 consecutive days, 4–7 June 1988. Bottom, cyclical flagging patterns of three males recorded on 7 April 1988. Circles indicate calculated altitude of the sun (in degrees). Flagging rates given as number of episodes per 10-min interval.

1988 into three arbitrary categories, 0 for no visible shadows, 10 for slight shadows, and 20 for intense shadows. Linear regression analysis yielded a correlation coefficient of 0.37 and the following regression equation:

$$\text{Signal rate} = 16.0 - 0.56 \text{ ripple state.}$$

The slope is highly significant (ANOVA,  $F = 12.75$ ,  $P < 0.001$ ).

Ripple states were also plotted with the signaling rates for each of 81 10-min periods during the day (fig. 15). Decline in the flagging rate during the morning period follows the onset of ripple patterns rather closely, but the afternoon flagging often begins before the ripple effects disappear. Bursts of flagging episodes during midday are roughly correlated with clouds passing in front of the sun and moderating or eliminating ripple patterns.

**WATER DEPTH:** In deeper water the ripple patterns are much less pronounced, although

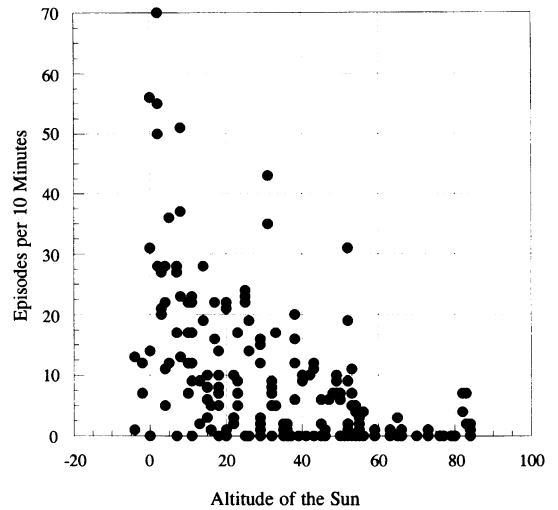


Fig. 14. Flagging rates plotted against altitude of the sun over 12 representative days.

there is some change in light intensity as waves pass overhead. The 2-hour limitation of the camcorder at the 10-m site did not allow us to tape continuously for an entire day. Therefore, we compiled composite records covering 2 days in April 1989 and three days in November 1989, with only

TABLE 6  
Normal Flagging Cycle

Event	N	Mean (SD)
Morning peak (minutes after sunrise)	30	8.97 (16.02)
Altitude of sun at morning peak (degrees)	29	0.82 (2.76)
End of morning activity period (minutes after sunrise)	30	132.4 (54.66)
Altitude of sun at end of morning activity period (degrees)	28	31.93 (12.54)
Beginning afternoon activity period (minutes before sunset)	29	190.31 (59.77)
Altitude of sun at beginning of afternoon activity period (degrees)	28	42.85 (15.03)
Evening peak (minutes before sunset)	30	48.3 (40.88)
Altitude of sun at evening peak (degrees)	29	9.22 (9.14)

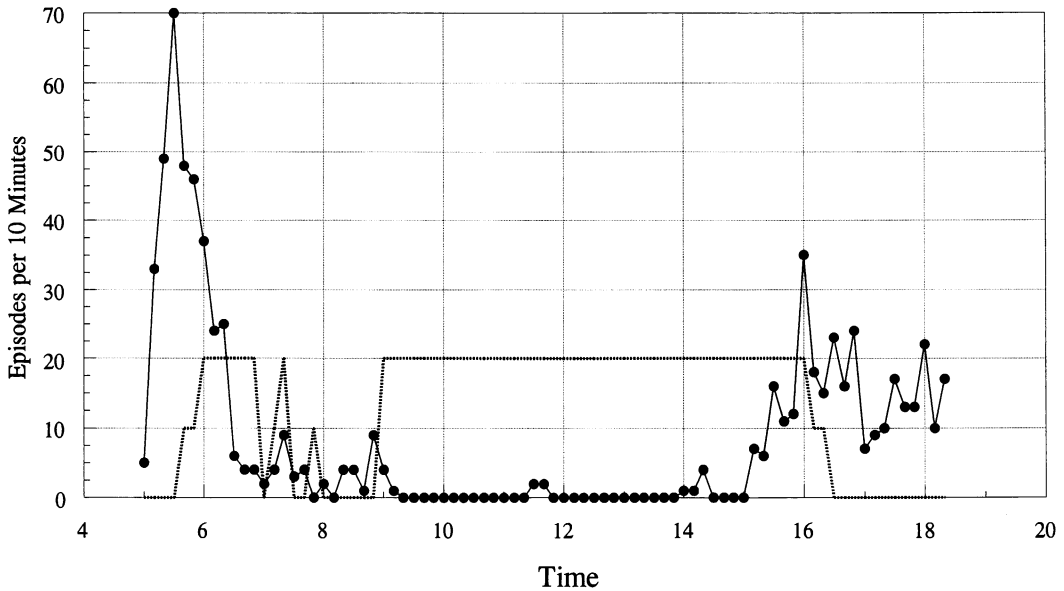


Fig. 15. Effect of ripple shadows. Smooth line represents flagging rates; dotted line is an estimate of intensity of ripple shadows.

short gaps as the camera was brought to the surface to change tapes and was then replaced. In general the cyclical activity pattern of the blennies with peaks in the morning and afternoon, is present as in the shallow-water blennies, but at the deepwater site there is more flagging in the middle part of the day. This further supports the hypothesis that strong ripple patterns inhibit flagging. The flagging activity of representative deepwater males is shown in figure 16.

**EXPERIMENTAL SHADING:** To test further the effects of shading, we floated a translucent blue plastic tarpaulin over the site to suppress the ripple shadows (fig. 17). The tarp was deployed for part to all of the day on 5–11 April 1989 and 10–14 November 1989. This reduction in illumination triggered flagging during the part of the day when flagging usually would have been minimal or absent. Results for representative males on 2 days in April 1989 are shown in figure 18. The basic pattern of more intense flagging in the early morning and late afternoon remains, but there is considerable flagging activity during the middle of the day. To eliminate the possibility that the tarpaulin was having some effect in addition to shading the area, we repeated the experiment with a clear plastic

sheet. This control had little effect on the signaling pattern, although there were brief periods of flagging activity at the time the tarp was placed in position and again when it was removed in the afternoon (fig. 18).

**ARTIFICIAL ILLUMINATION:** We also placed a bright light over the site in order to create ripple shadows during of the morning and afternoon activity peaks. There was no discernible effect on the flagging rate even though the artificial light produced prominent ripple shadows on the bottom. Apparently ripple shadows by themselves are not sufficient to inhibit flagging when the total light levels are low.

### Wave Surge

Whenever the wind was from the northwest, there was a surge effect in the study area that was at times strong enough to disturb the camera mounting. This could be detected on the tapes by the movement of fragments of sea grasses and other debris in the field of view. Although we made no attempt to quantify the effect of surge, it is apparent that flagging activity was much reduced on days when there was a strong surge.



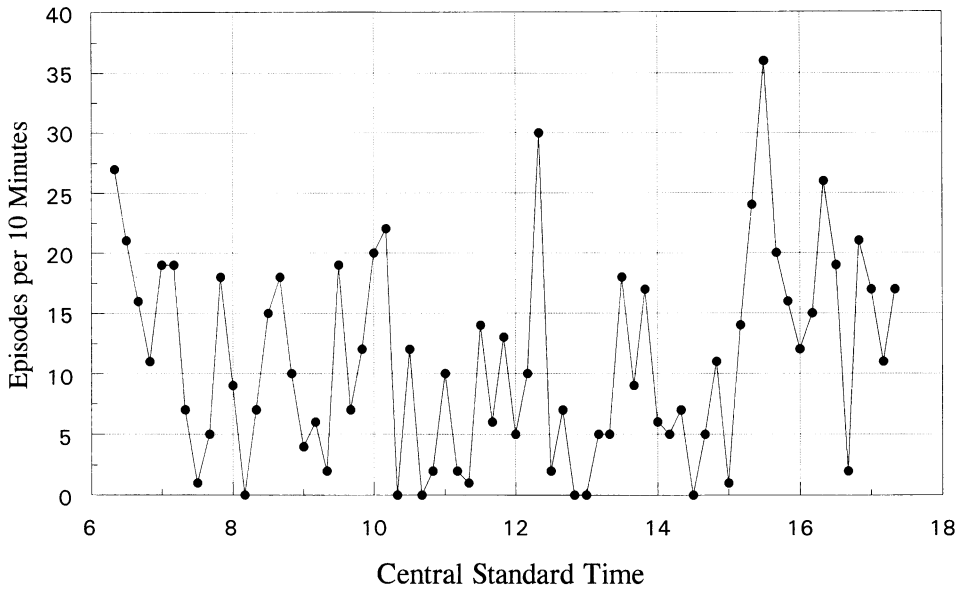


Fig. 16. Signaling at deepwater colony of sailfin blennies on 13 November 1989. Composite from several 2-hour recordings. Morning and afternoon activity peaks are present, but there is more flagging during the middle of the day, indicating that there is less midday inhibition of signaling by ripple shadows.

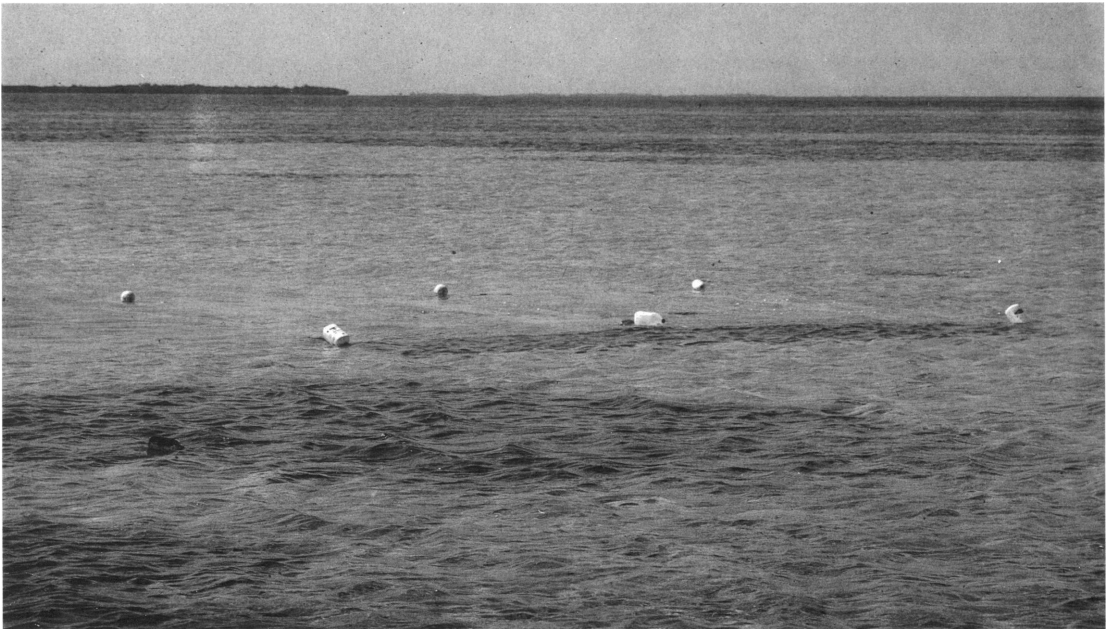


Fig. 17. Blue tarp shading part of the study area.

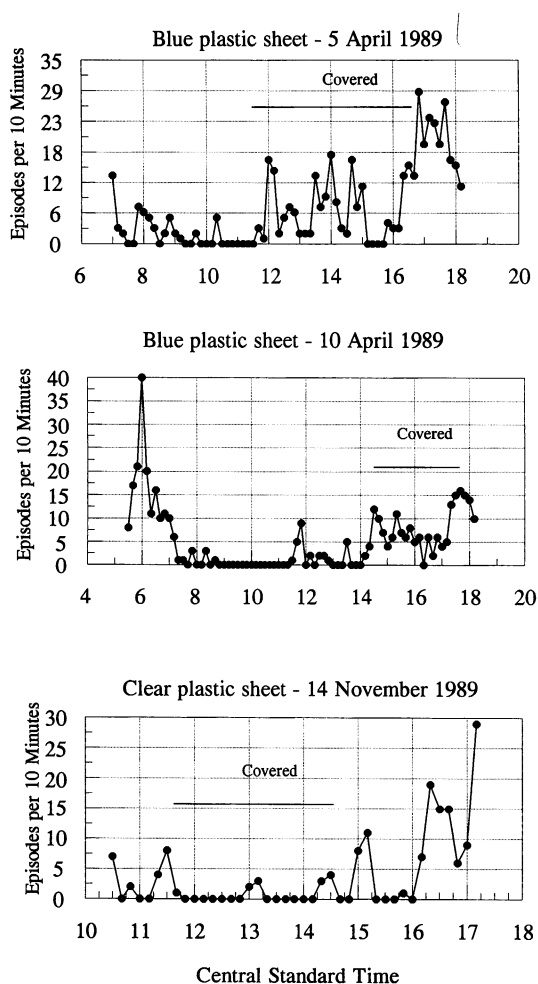


Fig. 18. Effect of shading on flagging periodicity of representative males. Top and middle, flagging activity is increased while blue plastic sheet is in position. Bottom, clear plastic has no effect on flagging rate. Increased signaling intensity at 11:30 and 15:15 is apparently in response to waders deploying and removing the clear plastic sheet.

#### NONCYCLICAL FLAGGING

At times when there would be little flagging activity, flagging also can be triggered by identifiable perturbations such as the approach of a diver or another blenny.

#### Synchronization between Individual Males

Most of our recordings were made with the camera positioned so that two or more males were in the field of view. Observations of the nearest fish were the most accurate,

whereas it is likely that we missed some of the signals made by more distant individuals. Analysis of the data reveals that the flagging episodes of adjacent individuals are highly correlated. This was seen on all graphic plots and tested statistically by comparing the signaling of three males recorded on 7 April 1989 by means of a repeated measure ANOVA ( $F = 1.83$ ,  $P = 0.163$ ). However, there does not seem to be a direct one-to-one relationship between signals and responses (fig. 13, bottom). The observation that the peaks of signaling intensity for two or more individuals are synchronized suggests that males are responding to some common stimuli.

We examined our records to determine if there was a "leader"—that is, a dominant individual who consistently initiated periods of intense flagging—and found no obvious pattern. To test the hypothesis that flagging was random, that is, that the signaling of each individual male was not influenced by the signaling of others, we performed a Markov analysis, recording the number of times flagging by each individual male was followed by flagging by each of the other males. If there was no other influence we expected that responses would be proportional to the total numbers of signals by each. We did this for 5–8 June 1988, when there were three fish in view of the camera. During this period the colony was left essentially undisturbed although blenny number 3 was moved with respect to blenny number 2 several times (blenny numbers as in table 7). Cross tabulations with  $\chi^2$  tests revealed that the resulting patterns were highly significant ( $P = 0.001$ ) and similar for the 4 days. In table 7 the observed responses are given as a percent of the expected responses. Male number 1 was followed by itself, that is, it signaled again before any other blenny signaled, fewer times than expected on all four days, and by number 2 more times than expected on 3 days out of 4. Individual 2 was followed by 1 and 3 more than expected and by itself less than expected. On all four days individual 3 was followed by 2 more than expected and by itself less than expected. Similar patterns and levels of significance were noted when we moved additional males into view of the camera: 5 males were in view on 5 June, 7

TABLE 7  
**Signaling Sequence by Three Males**  
 (plus and minus signs indicate cells where the observed responses<sup>a</sup> are greater or less than the expected numbers by  $\chi^2$  analysis)

Initiating male	Responding male	5 Jun 88	6 Jun 88	7 Jun 88	8 Jun 88
1	1	58.3 (-)	45.1 (-)	73.8 (-)	67.2 (-)
	2	89.0 (-)	108.9 (+)	123.5 (+)	20.9 (-)
	3	112.9 (+)	117.9 (+)	89.4 (-)	93.5 (-)
2	1	112.9 (+)	121.8 (+)	114.2 (+)	122.2 (+)
	2	51.6 (-)	78.0 (-)	48.1 (-)	75.2 (-)
	3	123.6 (+)	117.5 (+)	115.6 (+)	118.2 (+)
3	1	101.2 (=)	100.7 (=)	100.4 (=)	91.8 (-)
	2	126.7 (+)	124.6 (+)	109.5 (+)	118.5 (+)
	3	86.2 (-)	66.7 (-)	88.4 (-)	81.6 (-)

<sup>a</sup> Observed responses are given as percentage of expected responses.

on 10 June, 9 on 11 and 12 June, 11 on 13 June, and 6 on 14 June. We also tabulated the number of times each fish was the second, third, and so on, to flag after each male flagged. These patterns in all cases were not random, but there were no clear leaders, and we are unable to account for the observed patterns.

#### Response to Mechanical Models

A series of experiments made use of mechanical models that simulated the motion of the dorsal and anal fins of males. These models were operated remotely through a bicycle brake cable so that their motion could be controlled by the experimenter (fig. 19). One model was presented on 18 and 19 November 1988 after the morning activity peaks when normally there would have been little flagging activity. The model was nearly twice the length of the largest males (60 mm long with "dorsal spines" 30 mm long), and its presence seemed to stimulate increased flagging activity by the live blenny. The results of mechanical model experiments on 18 November 1988 are shown in figure 20. The model was positioned at 08:53 and operated to produce a series of flagging episodes during which the investigator attempted to duplicate the normal flagging pattern of a real blenny. During the first 10-min period, the real blenny responded by increasing its flagging rate to 10 episodes. After this initial burst of flagging activity, flagging decreased despite of continuing signaling by the exper-

imenter until 09:30. Because the flagging rate when the model was presented was well below the maximum rate during morning and afternoon peaks, we attribute the cessation of reaction to habituation rather than fatigue.

The model was then left in place but not operated until 10:40, when it was again used to present a series of flagging episodes. This elicited another increase in signaling by the real blenny to a maximum of 16 episodes between 11:10 and 11:20. The model was removed at 11:48, and soon afterward the signaling rate of the real blenny dropped to 0 and then returned to background levels. Presentation of the model from 15:50 to 16:34, during the afternoon flagging peak, seemed to have little or no effect that we could detect. It appears that the resident male was responding to the presence of the model and to its activation, but in view of the fact that the response was no more intense than the response to the presence of experimenters as they placed the tarps over the colony, it is uncertain that the blenny recognized the model as a sailfin blenny male.

#### Response to Other Stimuli

In another series of experiments, we placed a series of objects 20 cm from a resident male. Presentation of inanimate objects (empty 1-quart clear jar with black lid; clear plastic bag weighted with a small stone; orange, green, and brown soda bottles) all caused a slight increase in signaling rate of about the same magnitude as the increase as-

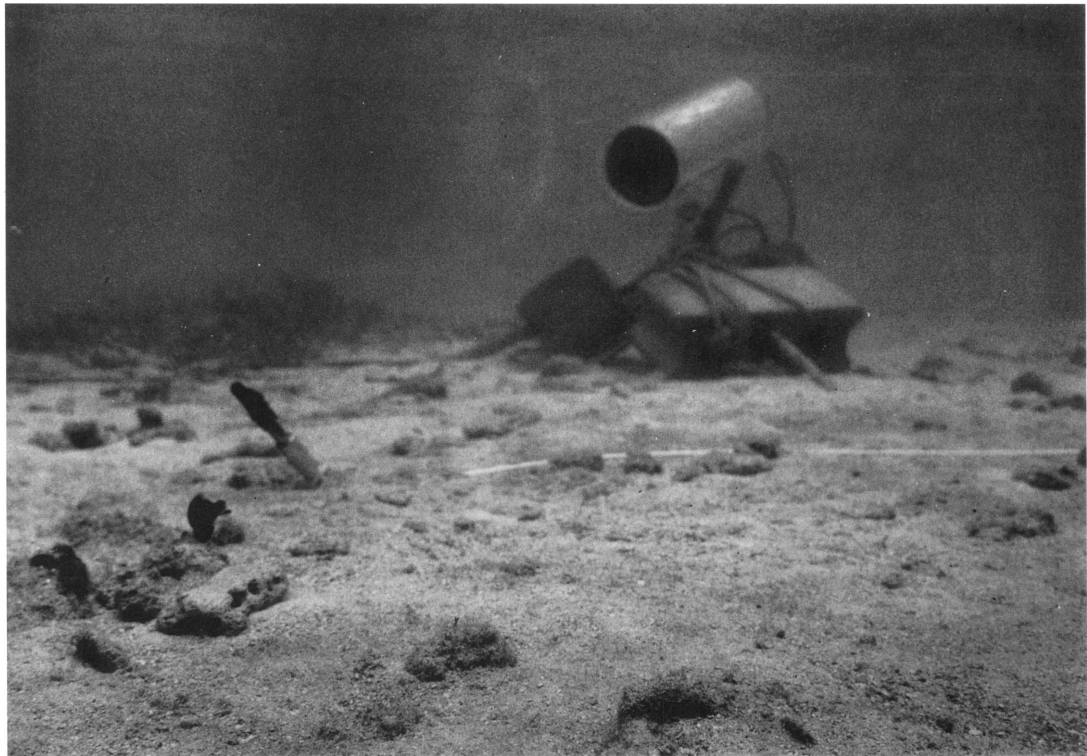


Fig. 19. Mechanical male deployed at site (photo by Chip Clark, USNM).

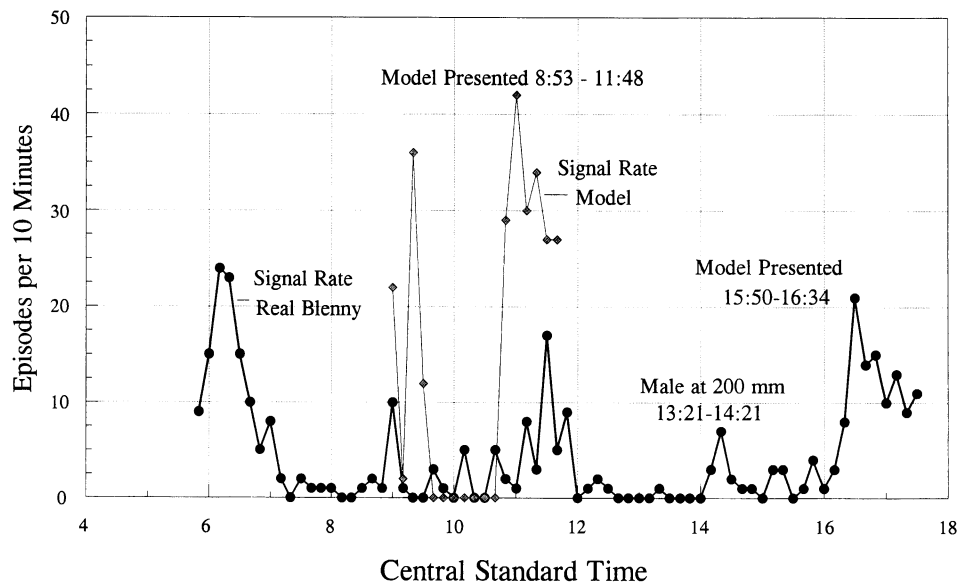


Fig. 20. Results of mechanical model experiment, 18 November 1988. Flagging of the model was followed by an increase in flagging rate of the real blenny.

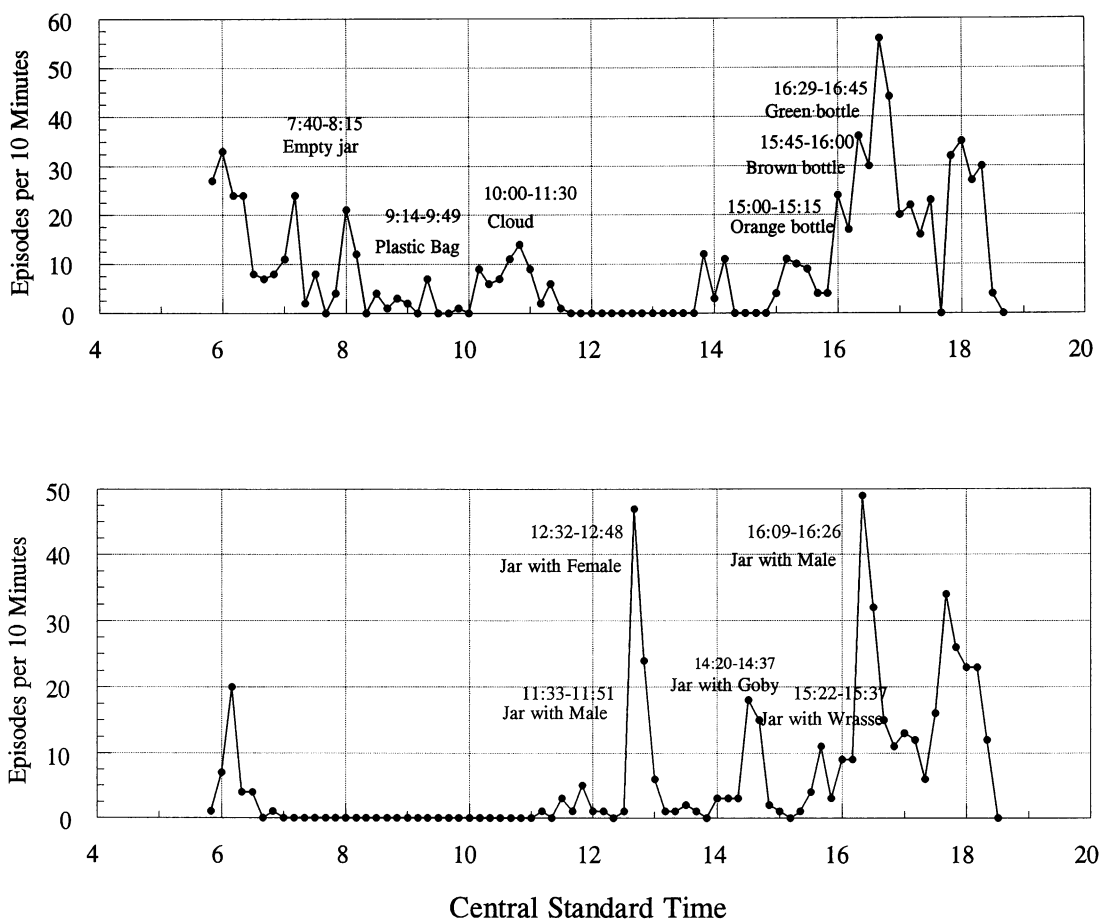


Fig. 21. Presentation of a series of objects, 20-21 March 1991. Presentation of a jar with a captive female sailfin blenny resulted in greatly increased flagging by the male blenny.

sociated with a cloud passing in front of the sun. Glass jars with captive female sailfin blennies usually elicited a strong response, jars with captive individuals of other species of small reef fishes a moderate response, and jars with captive male sailfin blennies elicited highly variable responses (fig. 21).

#### Lone Male Experiments

As an additional test of whether the flagging episodes are, in fact, signals, we attempted to remove all females and males with their shelters, except one male, from the immediate vicinity of the camera in the expectation that without a response there would be a decrease in signaling effort. Recolonization is quite rapid because females and displaced males, as well as occasional resident

males, move around the colony area. Therefore, there is no assurance that females were not present, nor can we be certain that there were not other males nearby but out of view of the camera. Nevertheless, it appears that signaling does continue in the absence of other males (fig. 22). All males that we could find within approximately 10 m from the camera except one were removed on the morning of 17 November 1989. An afternoon flagging peak by the remaining male was present but less intense than normal, the maximum rate reaching only 14 episodes per 10 min (the normal rate is two to four times as high). A rather low morning peak was present the next day (18 November). During that morning divers removed 60 more blennies from the grid area, not all of which were

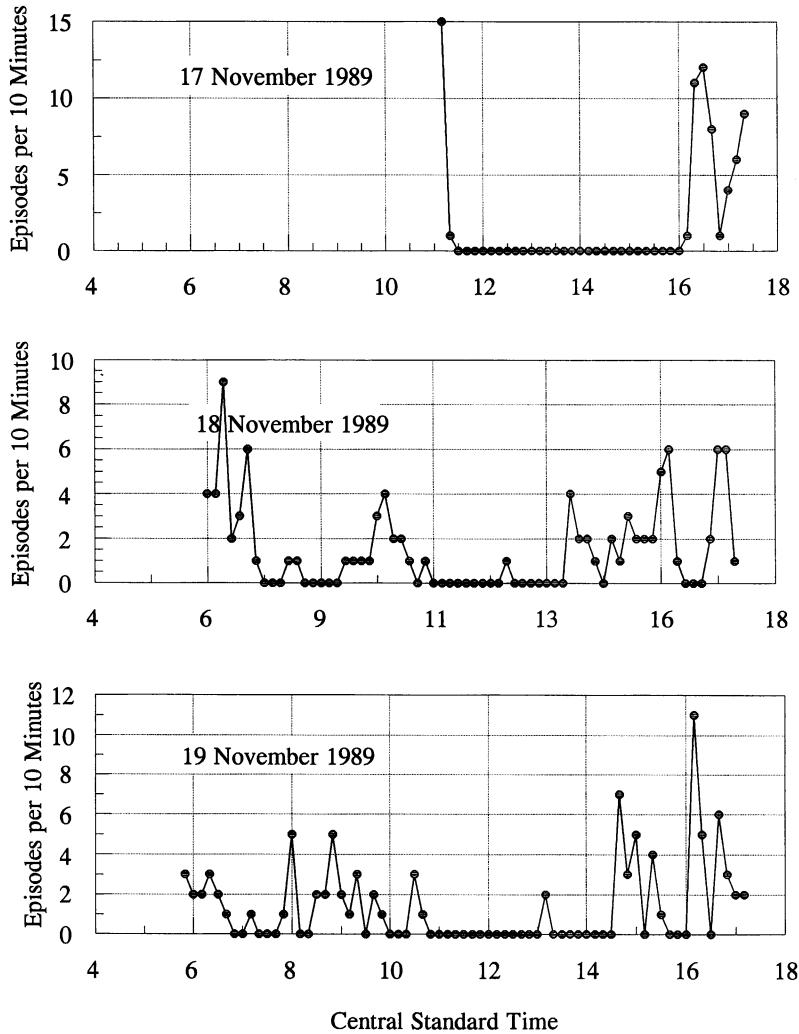


Fig. 22. Lone male experiment, 17–19 November 1989. With removal of surrounding blennies, cyclical flagging by the lone male continued but at a reduced rate. Peaks at 10:00 on 18 November and 8–9:00 on 19 November are associated with the investigator removing additional males.

necessarily within sight of the remaining male. The evening peak was very low. The following morning (19 November), 2 days after our attempt to leave only one male, we removed three more males and 29 additional females from the grid area. The morning peak was again low, with a maximum rate of three episodes per 10-min period, and the afternoon peak reached only 11 episodes per 10 min. A northwest wind on 18 and 19 November caused enough wave action to loosen the camera on its mounting, and this wave

disturbance may account for the low rates of signaling during the morning and evening peaks of those days.

Another male comparably isolated on 25 March 1991 appeared to have a normal morning peak the next day, before additional males were added in the afternoon of 26 March.

Thus, removal of surrounding males appears to depress the rate of flagging but does not completely eliminate the cyclical flagging morning and afternoon peaks.

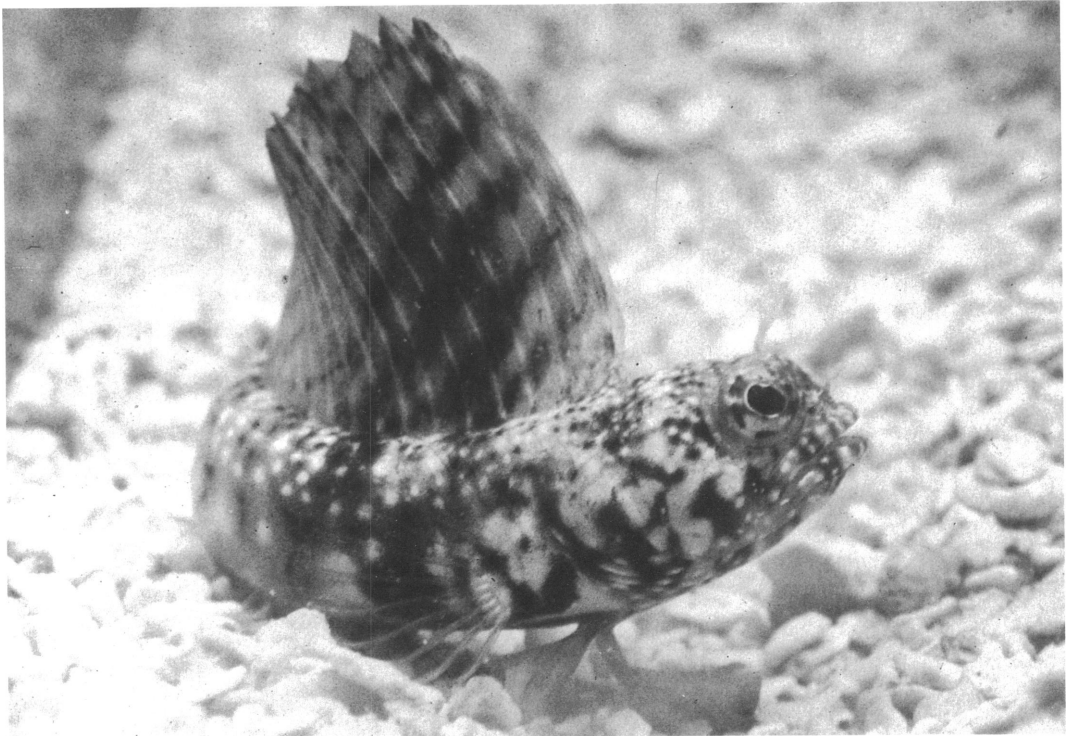


Fig. 23. Male in aggressive display with the dorsal fin fully erect (photo by Chip Clark, USNM).

#### AGGRESSIVE DISPLAYS AND COMBAT

In addition to flagging, males will present an aggressive display if another male approaches or is moved close. The aggressive display consists of emerging from the hole, blanching so that the color pattern breaks up into a complex array of spots and lines, erecting the dorsal fin, and turning laterally so that the surface presented to the intruder is maximized. This behavior can be elicited by placing a mirror close to a male or even by the reflection in the lens of a camera (fig. 23). Or it can be triggered by physically moving the shelter stones close together (fig. 24). By moving males and their home rocks to within varying distances of other males we conducted a series of experiments on signaling responses. Moving the entire rock seemed to have little effect on the occupant, and most males resumed signaling within minutes, often within a few seconds, after their homes were repositioned.

The aggressive display can be followed by

an actual physical attack, and sometimes the attack occurs without being preceded by a display. Wickler (1963) has photographed the combat in aquarium situations. In nature we observed that the subordinate male usually abandons its shelter and leaves the area, but in the confines of our aquarium there was often considerable damage, including torn fins and, in one case, loss of an eye.

On 27 March 1988 we moved a small male to within 43 cm of an established male. Within seconds the resident male left his shelter and rushed to the shelter of the new male, which had retreated into its hole. Several other attacks by the resident male followed, but apparently they were not successful in driving the intruder away, and eventually both males began to flag normally. Later, we collected both males and determined that the standard length of the resident was 44.9 mm and that of the intruder was 30.6 mm. One explanation for the ability of the smaller intruder to withstand the attack



Fig. 24. Two males in combat attitude after their stones have been moved close together (photo by Carl Hansen, USNM).

of the larger resident male might be that the opening of the intruder's hole was small enough to exclude the defender.

On 14 March 1996 intruder males were introduced into the territories of five established males in the field. Each of the intruders was shaken out of its own home into a plastic bag and placed approximately 20 cm away from the resident in its burrow. Because of the variation in how the intruders left the bags, the actual distance ranged from 5 to 20 cm. All of the intruder males were in the mottled color phase when introduced. Two of the resident males responded to the intruder by flagging episodes, without blanching, until the intruder moved away from the resident's burrow. Two of the resident males blanched to the mottled pattern, at first remained partly within their burrows, and then moved out and turned laterally toward the intruder, which soon left the area. The remaining resident male left its hole and bit the intruder, then withdrew, blanched, and turned broadside for a few seconds before returning to its own hole. About 40 sec later

it repeated the attack, the two remaining side by side for a few seconds before the intruder swam away. The resident returned to its hole and assumed its normal color pattern.

In all cases the combat was experimentally induced. We have not observed combat or even aggressive posturing on our many hours of taped observations of undisturbed blennies. We conclude that under normal circumstances aggressive displays and perhaps normal cyclical signaling discourage males from moving into holes that are within the territory of another male.

#### COURTSHIP FLAGGING

Andreyko (MS) described in detail the courtship of sailfin blennies brought from Carrie Bow Cay to aquaria at the AMNH and confirmed that spawning had occurred by recovering fertile eggs from the nests. The courtship displays by males as observed in the aquaria have been confirmed by us in field tapes. These displays are distinctly different from the routine low and high flags



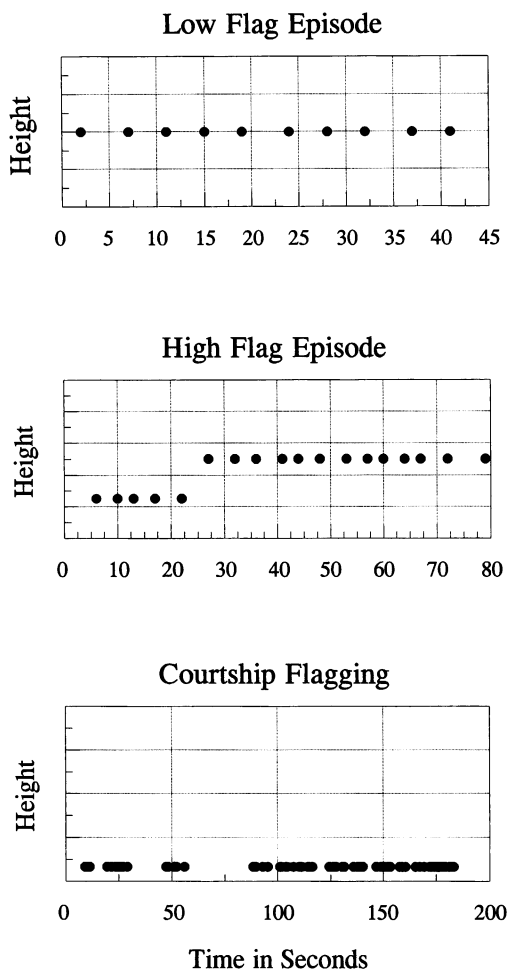


Fig. 25. Timing of fin lifts and relative height above the bottom during high flags, low flags, and courtship flagging. Height scale is relative only, 0 to about 10 cm during low flags, and 0 to about 10 cm during the first part of the high flag episodes and 15 to 25 cm during the later part of high flag episodes. By contrast, courtship displays are made with the male close to or in contact with the bottom.

and are stimulated by the presence of females and obviously directed at them. The male responds to the approach of the female by a special signal that consists of emerging part way from the burrow and raising the dorsal fin in a series of short episodes of one or two lifts each, separated by short intervals. In figure 25 the sequence of fin lifts during courtship signaling are compared with low and high flags. The lifts during low and high

flags are regularly spaced, whereas the lifts during courtship are sporadic and much more frequent. If the female responds by entering the shelter, the male follows her and turns so that his head protrudes from the burrow opening. Visible vibration and head bobbing by the male follows, which is apparently the time of fertilization. After courtship had been witnessed repeatedly in the laboratory, we recognized spawning behavior on the field tape for 24 March 1991 at 05:50. In that case the female entered the male's shelter after only a single episode of two lifts. The female remained in the shelter for 3 min and then left. The male signaled with a burst of two quick lifts of the dorsal fin as she moved away. In both laboratory and field observations, spawning appears to occur shortly after sunrise, about the time of the morning peak cyclical flagging in the field.

#### COLONY STRUCTURE AND DYNAMICS NUMBERS AND DENSITY

The main colony was sharply delimited on three sides by beds of sea grasses, but there was no defined limit to the northern boundary of the colony; males were simply more widely spaced to the north. We estimate that the census grid represented about half of the area occupied by the colony; that is, that the total area of the colony was approximately 750 m<sup>2</sup>. When we moved males in their shelter pieces of rubble from the area of the camera (see below) to a region more than 10 m beyond the limits of the grid, we soon found additional pieces of rubble in the grid area occupied by males and most of the old fragments that had been moved outside of the grid area were abandoned. Apparently the grid area represented prime habitat. We did not attempt to study this apparent homing behavior.

#### Accuracy and Consistency of Censuses

In 1988 we counted males and females (or immatures) in the grids. On the first census, 2 June, we located 22 males and 13 females; on 3 June we found 29 males and 56 females; and on 4 June we found 32 males and 88 females. Females are difficult to locate, and the increase probably reflects improvement

TABLE 8  
**Population Density**  
(numbers of individuals in grid study area)

	Males	Females
June 1988	31	93
November 1988	32	41
April 1989	46	57
November 1989	61	98

in our ability to find them. Ten days later, on 14 June, we located 31 males and 93 females. The final count included 6 females that were not counted earlier (no marker stones next to their holes), 83 reconfirmed females (or immatures), and 4 females in holes previously marked as having been occupied by males. Twenty-three males were in holes previously marked, seven were in unmarked holes, and one was in a hole that was marked earlier as containing a female or immature. Because we could not distinguish individuals, there may have been additional movements. Recognizing the difficulty of locating individuals, especially females, we made at least two counts on each sampling date and took the highest count as the most likely to be the most accurate.

#### Year-to-Year Variation in Population Density

The number of males guarding shelters ranged within the grid area from 31 in June 1988 to 61 in November 1989 (table 8). The location of the colony had shifted by about 20 m in 1987, and it appears that the population was increasing as it became established in the new area, although the second highest count (93) for females and immatures was in June 1988. Over the next three observation periods, from November 1988 to November 1989, there was a steady increase. After the conclusion of our field observations in 1993, the center of the colony shifted again about 50 m to the north in 1994–1996.

#### Clumping

Clumping was measured as the ratio of the variance to the mean number of shelters per 25-m<sup>2</sup> quadrat. If the shelters are randomly distributed, this ratio should be close to 1 (a Poisson distribution); the higher the ratio, the

TABLE 9  
**Clumping of Shelter Sites**  
(number of shelters in 25 m<sup>2</sup> quadrat)

	Males	Females
June 1988		
N	31	93
Mean	2.067	6.200
Variance	2.067	26.734
V/M ratio <sup>a</sup>	1.000	4.312
November 1988		
N	31	41
Mean	2.133	2.733
Variance	2.124	9.924
V/M ratio <sup>a</sup>	0.996	3.631
April 1989		
N	46	5
Mean	3.067	3.800
Variance	3.638	6.171
V/M ratio <sup>a</sup>	1.186	1.624
November 1989		
N	61	98
Mean	4.067	6.533
Variance	5.532	12.552
V/M ratio <sup>a</sup>	1.316	1.921

<sup>a</sup> The V/M ratio equals the variance divided by the mean and is a measure of clumping.

greater the clumping (Pielou, 1977). There is a pronounced difference between the sexes in the amount of clumping (table 9). Males (V/M ratio = 0.9 to 1.3) are close to randomly distributed; females are highly clumped (V/M ratio = 1.6 to 4.3). Further interpretations of these data are discussed later.

#### FACTORS LIMITING THE POPULATION

##### Availability of Sheltering Sites

It does not appear that all of the acceptable sheltering sites are occupied, even at the highest observed population levels. Table 3 indicates that, on average, each square meter contains more than 30 coral fragments larger than 5 cm in diameter, hence the grid area of 375 m<sup>2</sup> would have in excess of 11,000 fragments. Even if only 5% of these fragments had an appropriate cavity to be a potential shelter site, the capacity of the grid area would be more than 560 individuals. Our highest count (61 males and 98 females) was 159. Some of the potential shelter sites were

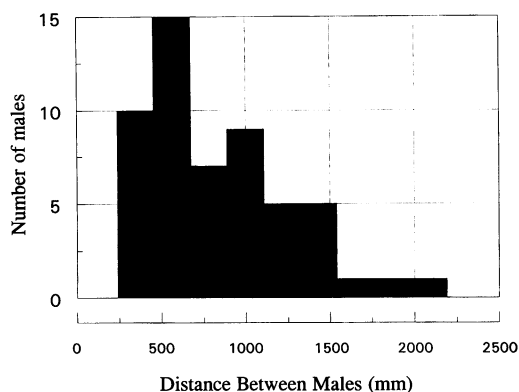


Fig. 26. Histogram of intermale distances for 89 males; plotted by 500 mm intervals.

occupied by mantis shrimps (stomatopods), but these did not seem abundant enough to limit the population of blennies. Therefore, it is unlikely that the population is limited by the availability of sheltering sites.

#### Spacing of Males

Males actively defend their shelter sites, and this would seem to be the major factor limiting the population within the colony. On 14 March 1991 we measured the distances between 35 males inside the grid area and 54 males outside the grid area. Within the grid area, the males were significantly farther apart (mean = 154 cm, SD = 82.4); outside the grid the mean intermale distance was 83.4 cm (SD = 43.1) ( $t = 46.7$ , DF = 46,  $P < 0.001$ ). The minimum distance in the study site was 36 cm; in the extralimital area it was 34 cm. This may be due to sampling error, or possibly the grid area was in prime habitat that the males defended more assiduously. The mean nearest-neighbor distance in the combined sample was 111.2 cm, the median 90 cm, and the range 19 to 318 cm. A histogram (fig. 26) of the combined samples indicates a peak frequency near 50 cm and secondary peak about 100 cm. Occasionally we found individuals even closer together; in one case two males occupied holes on opposite sides of the same coral fragment about 10 cm in diameter (24 March 1991). We did not determine if there is a correlation between size of male and size of the territory.

There is a question as to what minimum intermale distances represent. If the territo-

ries are areas within which no other males are permitted, then the intermale distance is the sum of the radii of adjacent territories. If, however, they are the limits of the area within which a male will permit approach but not sheltering by another male, then the minimum distance is slightly more than the radius of the territory of the most effective male, and most of the area can be shared for feeding and other activities, such as signaling. High flag episodes may, in fact, require use of most of the area.

Not all of the grid quadrats were occupied during every census and the highest average number of males per 25 m<sup>2</sup> quadrat (November 1989) was 4.1. The greatest number of males in a single quadrat was 8 (0.32/m<sup>2</sup>). The minimum distance between males is approximately 40 cm, indicating that each square meter could support at least two and that the 375 m<sup>2</sup> grid area could support approximately 750 males. Clearly, the population of males was well below these levels.

#### ATTRACTION EXPERIMENTS

In an effort to test the hypothesis that the signaling of males serves to attract individuals of both sexes, we removed all of the potential shelter rocks from the experimental area at the end of the grid censuses. On 14 September 1990 we cleared the area of large fragments, then set out two grids near the western part of the study area. In each grid we replaced approximately 50 fragments that appeared to us to be potential shelter rocks. These were arranged in squares, each consisting of approximately seven rows with seven fragments in each row. One grid was seeded with five males in their shelter fragments and the other was left vacant. The next day, two additional grids were established at the other end of the study area, one with five males and one without. On 22 September we retrieved each rock individually and washed it in weak formalin to drive any fish from their burrows. The results were as follows.

On 14 September 1990, five males were added to experimental plot number 1. Retrieved on 22 September were 10 male, 5 female, and 4 juvenile sailfin blennies, 1 juvenile grunt, *Haemulon* sp. In control plot number 2 no fish were added. Retrieved were

1 male, 7 female, and 3 juvenile sailfin blennies, 1 goldspot goby, *Gnatholepis thompsoni*, and 2 blackfin cardinalfish, *Astrapogon puncticulatus*.

On 15 September 1990, 5 males were added to experimental plot number 3. Retrieved on 22 September were 7 male and 5 female and juvenile sailfin blennies, 1 pugnose pipefish, *Bryx dunckeri*, 2 blackfin cardinalfish, and 1 juvenile mahogany snapper, *Lutjanus mahogoni*. In control plot number 4 no fish were added. Retrieved were 2 female sailfin blennies, 2 blackfin cardinalfish, and 1 juvenile bluehead, *Thalassoma bifasciatum*.

The two experimental plots together gained a total of 7 males, 14 females and immatures, and 5 other fishes. The control plots gained 1 male, 12 females, and 6 other fishes. The numbers of female and immature sailfin blennies and other fishes was approximately the same in the control and experimental plots, but substantially more males were attracted to the plots to which males had been added. A  $3 \times 2 \chi^2$  test indicates that these data are not adequate to reject the null hypothesis that there is no difference between the control and experimental plots at the 0.05 level ( $\chi^2 = 3.747$ ,  $DF = 2$ ,  $P = 0.115$ ). However, the observation that substantially more males are recruited to areas where males are already present supports the idea that signaling attracts more males to the area. That the control plot in which a male became established attracted many more females also supports the idea that signaling males attract both sexes.

We suggest that for this kind of experiment the length of time between the introduction of the pioneer males and the recovery census is critical. If the recovery is carried out too soon, the recruits will not have had enough time to colonize the area in response to the pioneer males. If the recovery census is delayed too long, the results may be masked by normal random movement of adults of both sexes.

## REPRODUCTION

The mating of the sailfin blenny is clearly a female choice system. Males maintain territories around their shelter holes, and females move to the male of their choice.

## EGG DEPOSITION

The demersal, adhesive eggs are deposited on the walls of the shelter cavity by the female and guarded by the male. Andreyko (MS) observed spawning by captive fish in holes that were lined by glass vials. Eggs were deposited in small groups in a regular pattern. In nests collected in the field, these patterns are indicated by clumps of eggs in the same stage of development within the single layer of eggs on the wall of the cavity.

Shelters were collected in the vicinity of the study site in November 1989. The males were removed and each rock was scored with a hacksaw along the estimated longitudinal axis of the shelter hole and split with a chisel. The opened shelters were then placed in small containers with a low flow of seawater. Samples of about 10 eggs were then removed each day until the eggs hatched in approximately 7 days. Ambient water temperature was approximately 27° C. In the laboratory Andreyko (MS) found that hatching occurred in 6 to 9 days. Because spawning occurred only in the early morning, the eggs in a given nest were separable into groups differing in age by approximately 24 hours and recognizable by their stage of development (Andreyko, MS).

## Sizes of Rubble Fragments Occupied

The shelter "stones" (e.g., coral fragments and remains of mollusc shells) of 37 individuals collected 28 February and 1 March 1992 were measured to determine if there was any difference in the size of fragments selected by males and females. Three measurements—greatest length, width, and height—were taken on each fragment. Although the shelter stones are irregular, these dimensions provide an approximation of the overall size of the shelter fragments (table 10). In general, larger fish select larger fragments ( $r^2 = 0.27$  for the smallest of the dimensions plotted against standard length), but Newman-Keuls tests revealed that differences in size of stones selected by males, females, and immatures were not significant at the 0.05 level.

## Nest Cavities and Their Openings

Some of the shelter cavities appeared to be recently vacated holes made by boring

TABLE 10  
**Sizes of Rubble Fragments Occupied by Males and Females**  
 (measurements in millimeters)

Dimension	Males (N = 17)	Females (N = 15)	Juveniles (N = 5)
Mean length (SD)	97.8 (34.1)	78.7 (25.0)	79.0 (24.8)
Mean width (SD)	58.5 (16.2)	53.7 (17.4)	51.0 (12.9)
Mean height (SD)	37.4 (12.5)	30.3 (9.7)	24.0 (8.2)

clams (*Lithophaga*). They had rather smooth walls and were round in cross section. One shelter was in what appeared to be the tube of either a polychaete worm or a vermetiform mollusc. Most of the shelters, however, were in irregular cavities of undetermined origin. It is clear that sailfin blennies occupy a wide variety of cavities, whatever their origin.

The shape of the individual cavities ranged from tubular to nearly spherical (fig. 27). The openings to the burrows were circular to elliptical and smaller than the chamber inside. Table 11 summarizes the dimensions of 22 shelter cavities that had been occupied by males. The openings averaged 5.4 mm  $\times$  6.7 mm and the chambers averaged 9.0 mm  $\times$  13.4 mm in cross section and 31.5 mm in length. Chamber opening dimensions, and chamber height and width were not significantly correlated with standard length but length of the chamber was correlated with the standard length of the occupant ( $r^2 = 0.37$ ).

#### FREQUENCY OF SPAWNING

One measure of male reproductive success is the number of developmental stages pres-

TABLE 11  
**Dimensions of Shelter Cavities Occupied by Males**  
 (measurements in millimeters)

Measurement	N	Mean	SD	Range
Opening diameter				
Maximum	22	5.61	1.71	3–11
Minimum	18	6.68	1.64	5–11
Chamber diameter				
Maximum	23	9.00	2.61	5–14
Minimum	23	13.44	4.04	6–22
Chamber length	23	31.50	9.11	13–15

ent in the nest. Fewer stages indicate less frequent spawning; more stages indicate a higher level of reproductive activity. Shelters of 67 males were collected in March and April of 1987 and 1988 and in June 1988 at Carrie Bow Cay. Eleven (16.4%) had no eggs and the remaining 56 nests contained from one to six stages of developing eggs. Only one male shelter contained all six stages; the average number of stages was 2.6. Table 12 shows the percentage of shelters containing each stage during two periods, March–April and June. Stages 5 and 6 are about twice as frequent as stages 1 through 4 and each probably represents more than one age cohort that are indistinguishable because of the slight morphological changes late in development. Of the 56 shelters containing eggs, 9 (16.1%) had only one stage, and 16 (28.6%) had two stages. Of those with two stages, 11 (68.8%) had consecutive stages, indicating that the eggs had been spawned on successive days. Nineteen (33.9%) of the shelters had three stages; 5 of these shelters had consecutive stages, 12 had one stage missing between spawnings, and 2 had spawnings from alternate days. Nine shelters (16.1%) had four stages, none of which were consecutive; and two shelters (3.6%) had five stages, both with 1 day missing from the sequence; and only one shelter (1.8%) had a full sequence of six stages. While some individual males spawn every day (often more than once a day), most males spawn on one to three consecutive days and then skip one or more days.

Regression analysis of numbers of eggs and numbers of stages against male size (SL) and against relative length of the dorsal-fin spines showed no statistically significant trends. Although our data do not address this point, it seems possible that reproductive success is more related to flagging behavior

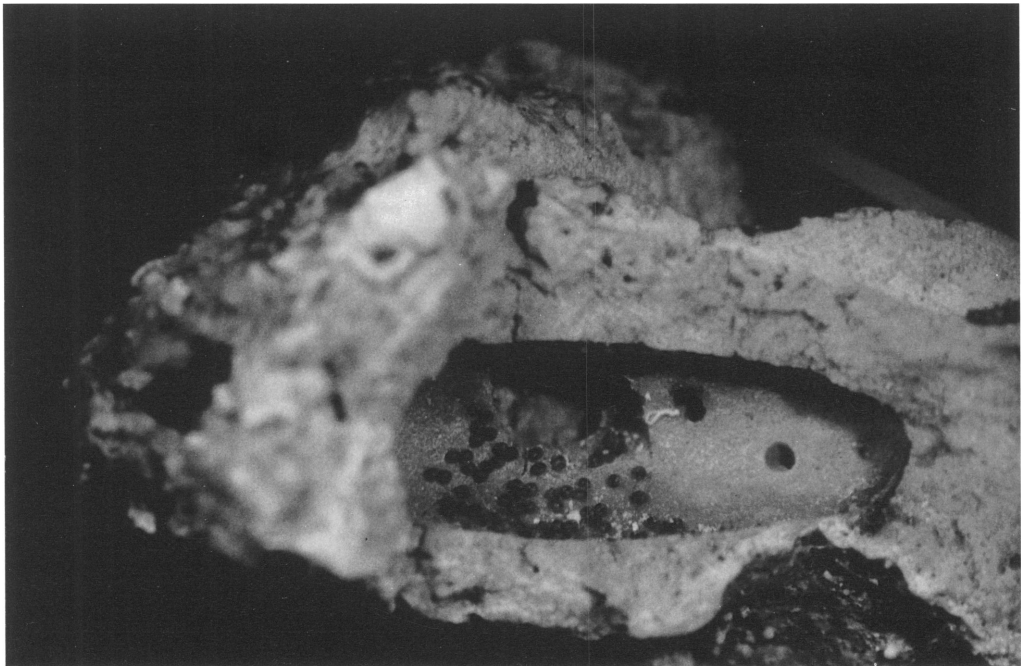


Fig. 27. Typical nest cavities in limestone rubble, probably remains of conch shells or coral fragments.

TABLE 12  
Egg Stages Present in 67 Shelters<sup>a</sup>

Stage number	March–April (N = 47)		June (N = 15)	
	Number	Percent	Number	Percent
1	12	25.5	2	13.3
2	13	27.7	4	26.7
3	12	25.5	3	20.0
4	14	29.8	5	33.3
5	26	55.3	9	60.0
6	23	48.9	8	53.3

<sup>a</sup> Eleven shelters contained no eggs.

than to size (body length) or dorsal-fin development.

#### SPAWNING PERIODICITY

We have found males guarding shelters with eggs in February, March, April, June, September, and November (table 13). Although there was some variation in the percentage of burrows that contained eggs, there was no indication that the species does not spawn throughout the year. In the laboratory, however, individuals stopped spawning for periods of a few days to a few weeks (Andreyko, MS). Presumably this explains why not all of the shelters guarded by males contained eggs.

#### NUMBER OF EGGS

Male reproductive success can also be measured by the number of eggs in the shelters. The number of eggs in a nest varied from 26 to 509 (mean = 167.9, SD = 112.2), and individual cohorts varied from two or three eggs to a maximum of 268 (table 14). Andreyko (MS) determined that females in aquaria deposit 60 to 150 eggs per spawning, suggesting that occasionally more than one female deposits eggs in the same nest on the same day. A regression of the average number of eggs of each stage against age (equals stage number) showed a negative slope (mean number of eggs =  $831.32 - 4.29 \times \text{age}$ ,  $r^2 = 0.1768$ ), but this slope is not significantly different from 0 ( $t = 0.93$  with 4 DF,  $P = 0.36$ ). Once the eggs have been fertilized, there seems to be no consistent pattern of attrition, although some attrition occurs.

TABLE 13  
Seasonal Reproductive Rate of Males

Month	Nests examined	Nests with eggs (percent)
March/April	47	37 (79)
June	14	13 (93)
September	4	3 (75)
February	18	11 (61)

#### REPRODUCTIVE POTENTIAL

At any given time, approximately 51% of the nests guarded by males contained stage 6 eggs, and the average number of stage 6 eggs was 38.9 (SD = 31.8). Therefore, if all stage 6 eggs in each nest hatch on the same day, with an average population of 42 males in the grid area, 21 males would release approximately 817 hatchlings each day, nearly 300,000 per year.

#### SUMMARY AND DISCUSSION

Clearly, courtship displays by males are aimed at females and lateral aggressive displays, which can be elicited by presentation of a mirror or by an intruder male, are directed at males. The function of the routine high and low flags, however, is enigmatic. Such conspicuous behavior patterns immediately suggest a function in courtship or territorial defense, but it is possible that the routine periodic flagging serves some function other than, or in addition to, communication. Possible functions include the following.

**Feeding**—It is unlikely that the flagging episodes are related to food capture. There is no indication that the blennies actually pursue anything during flagging, and there are far fewer individual food items in the stomachs than would be expected even if a small fraction of the flagging forays were successful feeding incidents.

**Temperature control**—The large surface area of the expanded dorsal fin would make an excellent heat exchange organ, but, because the blennies are constantly immersed in seawater, it is unlikely that dissipation of heat is a problem. Furthermore, the muscle activity associated with flagging would probably produce more heat than would be disbursed through the dorsal fin even if it were highly vascularized.

TABLE 14  
Egg Number and Numbers of Shelters in Which Eggs Are Present by Stage

Egg stage	March and April		June	
	Mean number of eggs (SD)	Number of shelters (percent)	Mean number of eggs (SD)	Number of shelters (percent)
1	60.4 (59.5)	11 (30.5)	63.7 (15.0)	3 (20.0)
2	85.2 (51.7)	13 (36.1)	79.8 (24.7)	4 (26.7)
3	68.8 (57.1)	12 (33.3)	99.3 (100.3)	4 (26.7)
4	68.3 (53.0)	14 (38.9)	68.2 (58.1)	5 (33.3)
5	71.3 (48.3)	26 (72.2)	71.3 (46.0)	9 (60.0)
6	34.7 (31.2)	23 (63.9)	41.5 (29.9)	8 (53.3)
Totals	168.2 (112.5)	36	148.4 (91.0)	15

Surveillance—Moving up in the water column would increase the distance over which the blenny could see. Although we know nothing of the visual powers of the blenny, the advantage conferred by the added sight distance would probably be more than offset by the increased exposure to predation.

Nest grooming—Longley (*in* Longley and Hildebrand, 1941) suggested that the body of the blenny as it moved in and out of the shelter hole would act as a piston to force water in and out of the nest. If this were important, we would expect the blennies to be active at approximately the same intensity throughout the day and night.

Waste disposal—Release of feces and urine out of the nest would, of course, prevent contamination to which the eggs might be especially sensitive, but the frequency of flagging and the lack of nocturnal activity makes it unlikely that this is a major function of flagging behavior.

It is possible that flagging serves some other purpose that we have not considered, but none of the above hypotheses seems viable, and we conclude that flagging is a form of communication, that is, a method of transferring information from one individual to another. We must then consider whether the signals are directed toward conspecifics or heterospecifics.

Throughout our review of the videotapes we kept records of any interactions with other species, looking especially for cases in which the approach of another species appeared to trigger an episode of signaling by the blenny. The only case that we were able

to find was one in which the blenny was approached by a sand tilefish, *Malacanthus plumieri*, at the deep site. Because tilefishes collect coral fragments for their nests, they may be more of a threat to the blennies than other species that merely graze on algae growing on the rocks. However, careful examination of other tapes with sand tilefishes in view failed to confirm this reaction to sand tilefishes, and we can only conclude that the isolated case was a coincidence of a routine flagging that happened to occur simultaneously with the approach of the tilefish.

We have been unable to demonstrate conclusively that the approach of another species inhibits signaling by the sailfin blenny males, but because cyclical signaling is normally sporadic and apparently unpredictable within its normal periodicity, it is difficult to be certain that the cessation of signaling when another fish approaches briefly is other than a normal interval between episodes. We were also unable to identify any cases in which the behavior of another species appeared to be influenced by the signaling of the sailfin males.

Longley (*in* Longley and Hildebrand, 1941) commented that the approach of mantis shrimps “greatly provoked” male sailfin blennies, but we did not observe this kind of interaction, although mantis shrimps around Carrie Bow Cay do occupy holes similar to those selected by blennies.

We found no evidence that signaling by the sailfin blenny alters the behavior of a member of another fish species, and, finally, the observation that signaling continues



when no other species are close by supports the hypothesis that signaling is directed only at other sailfin blennies and not at other species of fishes.

Only male blennies have greatly expanded dorsal fins and dark coloration and only males guard eggs in nest holes for protracted periods. Females, on the other hand, are cryptically colored, have lower dorsal fins, and move about freely. Thus, signaling is associated with restricted mobility of males. We suggest that flagging serves the function of attracting conspecifics of both sexes and is of major importance for maintaining the integrity of the colony structure. When we removed all males but one, that male continued to signal, and the area was quickly repopulated by males and females. Males guarding nests continue to court approaching females and entice them to add more eggs to the shelters. Spawning apparently continues throughout the year. Because the males are more or less static, it is essential that females be attracted to the area of the colony. It must also be advantageous for there to be abundant other males present since females are also promiscuous (Andreyko, MS).

The periodicity of the signaling, intense in the early morning and late afternoon, appears to be subject to modification by changes in light intensity and severe water motion. The apparent advantage of this cycle is that the most intense signaling effort coincides with the best viewing conditions. Although predation does not appear to be intense at any time, many predators are most active and probably move to parts of the reef complex where prey is more abundant during the period when the blennies are signaling most intensely in habitats that are relatively distant from the reefs.

It is not clear to us what determines when and why the males exhibit high or low flags. Possibly low flags are aimed at nearby individuals and high flags are directed at those farther away, but we were unable to confirm this. High flags, which last longer and occur farther from the shelter of the nest, would seem to expose the blennies to greater risk of predation and perhaps the low flag is a compromise—less effective but much safer.

We conclude that male sailfin blennies use

their large dorsal fins to present the following kinds of signals.

**Courtship:** A series of individual lifts close to the bottom, triggered by the approach of a female and ending when the female enters the nest or leaves the area. Clearly, this variety of flagging serves as an aspect of communication during courtship. The flagging can be modified by the response of the female, indicating that there is an exchange of information in both directions.

**Aggressive display:** With the fish remaining on the bottom, the dorsal fin is raised and remains erect as the fish blanches and turns to present its flank thus making itself more visible to an intruder. Male spacing keeps habitat open for females. If all suitable nest holes were occupied by males, the females could only approach those males at the periphery of the colony. The size of territory that can be defended is a balance between the need for more females and food, exposure to combat (competition), and risk of predation.

**Cyclical low and high flagging episodes:** Each episode consists of a series of lifts, usually with the fish well above the bottom. This signaling is most frequent in the early morning and late afternoon. Cyclical flagging is subject to modification by external conditions such as strong ripple shadows or intense wave action. Usually the episodes appear to be spontaneous, not triggered by any obvious outside factor, but they may also appear as a general "greeting" or "curiosity" signal given at the approach of another sailfin blenny, a swimmer, or presentation of an inanimate object. Flagging is synchronized among males, but there does not appear to be an individual male that initiates a series of episodes to which other males respond. Probably the synchronization is the result of individual males reacting to the same stimulus or to each other. Low and high flags may be equivalent and merely represent different levels of intensity, or they may convey different information. We have not been able to determine what triggers the flagging episodes, nor have we been able to discover what determines whether the episodes will be low flags or high flags.

Hastings and Springer (1994) recognize the subfamily Chaenopsinae with three clades:

the *Acanthemblemaria* clade, the *Chaenopsis* clade (which includes *Emblemaria*), and the *Coralliozetus* clade. Many aspects of life history are known for representatives of all three clades. Members of this subfamily are united by peculiarities of the male reproductive system, including a single testis on one side and an accessory organ on the other side that is similar to the testis except that it lacks seminiferous tissue. (In *Coralliozetus angelica* the testis is on the left side and there are two accessory organs on the right side [Patzner, 1992]). The Chaenopsinae also share derived osteological features, including dorsal-fin spines that are ossified basally and change distally to tissue, probably collagen, that stains with alcian blue.

The Caribbean species of *Acanthemblemaria* tend to live in holes in solid limestone and other firm bottom, including artificial structures. Clarke (1989, 1992, 1996), in a study of *A. spinosa* and *A. aspera* in the Virgin Islands, showed that both species preferred the higher parts of dead coral colonies, but *A. spinosa* displaces *A. aspera* when they occur together. Johnson and Brothers (1989) described a small species, *A. paula*, that lives in burrows in dead coral on both sides of the reef crest and in rocky pavement areas of the reef flat. Clarke (1994) found that species of *Acanthemblemaria* and *Emblemaria* showed clear-cut spatial separation although certain species overlapped. Among the factors that determined the distribution of the species were depth, hole size, hole orientation, food availability, and height above the prevalent bottom.

The species of *Acanthemblemaria* show varying degrees of signaling, sometimes by displaying the white lining of the mouth and sometimes by moving their head from side to side or in and out of the burrow opening. Courtship signals have been described for the Eastern Pacific species *A. macrospilus* as consisting of a series of movements in which the anterior half of the body is projected outward and immediately withdrawn (Stephens et al., 1966). Females respond by entering the male's nest and depositing eggs, after which they leave and sometimes move immediately to the nest of a nearby signaling male.

Hastings (1988a) studied the factors affecting male success in *Acanthemblemaria*

*crockeri* in the Gulf of California and found that females select males on the basis of several criteria, including size of the male, quality of the shelter, time of residence by the male, whether the male was already guarding eggs, and his coloration and intensity of signaling. Interestingly, intensity of signaling was negatively correlated with the number of eggs received.

Hastings (1986, 1988a, 1991a) also has intensively studied the behavioral ecology of *Coralliozetus angelica* in the Gulf of California. That species lives in vacant barnacle tests in areas where there is strong wave action. Males court females with a bobbing and weaving motion while partly out of the barnacle shells. The most successful males were larger, but this was offset by the fact that larger males require larger holes (barnacles), which tended to be fouled with algal growth. Females preferred clean shelters.

Members of the genus *Chaenopsis* occupy holes in rocks and tubes of annelid worms. Robins et al. (1959) described threat and attack behavior of *Chaenopsis ocellata*. Hastings (1991a) has described reactions to predators by the signal blenny, *Emblemaria hypacanthus*, in the Gulf of California, where the males use empty gastropod shells as shelter sites. He found that males and females spent less time out of their shells in areas where the number of predators was high than they did in areas where there were fewer predators. Courtship consisted of a series of fin lifts while the male was close to the entrance to the shelter, similar to the courtship signals of the sailfin blenny.

Apparently all chaenopsids that have been studied are paternal species with the males guarding the eggs in holes in coral, rocks, worm tubes, barnacle tests, or mollusc shells. In the *Acanthemblemaria* and *Coralliozetus* clades the shelter sites are in massive, immovable structures, often in areas with strong wave action. In the *Chaenopsis* clade, some species of *Chaenopsis* live in sandy areas in worm tubes, and at least two species of *Emblemaria* live in small fragments of corals or gastropod shells that can be moved by animals and wave surge. In effect, the water currents bring food to the blennies and reduce the need for them to expose themselves to predation while they are seeking food. This

is balanced against the possibility of disruption of the nests during violent weather. The chaenopsids that live in holes in solid rock or in worm tubes in sand are limited as to where they can live by the availability of habitat. The sailfin blenny, however, has an abundance of fragments available to it, and therefore signaling appears to us to be a way of attracting conspecifics to the colony and maintaining the integrity of the colony.

All of the chaenopsids studied so far have female choice mating systems, in which males signal approaching females, and aggressive displays toward intruder males. Cyclical flagging as described here, that is, not directly related to courtship, however, has not been reported for any species except the sailfin blenny.

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## APPENDIX

### List of Additional Fish Species Seen at the Study Site [arranged in phylogenetic order]

Yellow stingray, *Urolophus jamaicensis*  
Dwarf herring, *Jenkinsia* sp.  
Lizardfish, *Synodus* sp.  
Redfin needlefish, *Strongylura notata*  
Sand tilefish, *Malacanthus plumieri*  
Yellowfin mojarra, *Gerres cinereus*  
Mojarra, *Eucinostomus* sp.  
Porgy, *Calamus* sp.  
Foureye butterflyfish, *Chaetodon capistratus*  
Banded butterflyfish, *Chaetodon striatus*  
Spotfin butterflyfish, *Chaetodon ocellatus*  
Bluehead, *Thalassoma bifasciatum*  
Slippery dick, *Halichoeres bivittatus*  
Stoplight parrotfish, *Sparisoma viride*  
Redtail parrotfish, *Sparisoma chrysoternum*  
Beaugregory, *Stegastes leucostictus*  
Great barracuda, *Syngnathus barracuda*  
Blue tang, *Acanthurus coeruleus*  
Ocean sturgeon, *Acanthurus bahianus*  
Doctorfish, *Acanthurus chirurgus*  
Orangespotted filefish, *Cantherhines pullus*  
Sharpnose puffer, *Canthigaster rostrata*  
Smooth trunkfish, *Lactophrys triqueter*