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Monogamous mating system and spawning cycle in the gobiid fish, Amblygobius phalaena (Gobiidae)

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Key words: reproduction, pair bond, feeding, burrowing, semilunar spawning cycle.

Synopsis

Reproductive ecology and mating system of the gobiid fish, Amblygobius phalaena, were studied on the coral reef at Sesoko Island, Okinawa, Japan. This goby usually lives in pairs, and maintains territories with several burrows for shelter and spawning. Although a few paired individuals changed partners, most pairs remained together over successive rounds of reproduction. Mate guarding by females appeared to prevent males from mating with other females. Spawnings were synchronous with semilunar periods. Several expected spawnings failed to occur (12%). These may have been caused by the delays in spawning preparation of the paired females or by the disturbance caused by a typhoon. A pair spawned in one of the several burrows within their home ranges. Eggs were deposited on the ceiling of the burrow, and were tended by the paired male for 3-4 days until hatching. The males tended eggs at the expense of their feeding. Aggression toward fishes approaching their burrows were exhibited by the males as well as the females. Because of its low frequency in females, this behavior did not limit their ability to feed.

Introduction

Most gobiid fishes appear to spawn polygamously or promiscuously (Breder & Rosen 1966, Thresher 1984), but monogamous mating has been suggested for some species because of their pairing behavior (Barlow 1984, Thresher 1984, Reavis 1997, Takegaki & Nakazono 1999a).   Such a pairing, however, does not always mean that those species are monogamous because extra-pair matings have been reported: e.g., harlequin bass, Serranus tigrinus (Pressley 1981) and longnose filefish, Oxymonacanthus longirostris (Barlow 1987, Kokita & Nakazono 1998).   Therefore, long-term field observations are needed to clarify the monogamous mating system; at least one reproductive event as defined by Barlow (1984).

Amblygobius phalaena (Gobiidae) is distributed in the Indo-Pacific Ocean, including the Ryukyu Islands, being found in shallow sandy areas (Akihito 1984). This goby feeds mainly on filamentous algae and harpacticoid copepods hiding in the sand (Sano et al. 1984).   Thus far, reproductive ecology and mating system in the genus Amblygobius have not been studied.   Although Reavis & Barlow (1998) reported that A. phalaena lives in polygynous groups, no evidence of polygynous mating was shown.   On the other hand, Paulson (1978) reported that A. phalaena usually lives in pairs.   I investigated the reproductive ecology and mating system of A. phalaena on a coral reef at Okinawa, Japan, and, in this paper, I describe pairing behavior, feeding and burrowing behavior, spawning cycle and parental care in A. phalaena.

Materials and methods

Underwater observations were carried out by snorkel on the coral reefs along the Nagahama Beach on the northern coast of Motobu Peninsula (26° 42′ N, 127° 57′ E), Okinawa, Japan during 24 July - 19 October 1996.   The study area of about 100 x 100 m was set in the nearshore moat, 2.0-3.0 m below sea level.   The substratum was composed mainly of sand and dead coral fragments, with scattered coral colonies and rocks.   Water temperature on the sea bottom varied between 22.7 and 30.7 °C during the study period.

All of the adult Amblygobius phalaena (>110 mm in TL) in the study area were captured with a barrier net and hand net, and the body lengths measured (mm TL) and sexes determined.   Gobies with a swollen abdomen had short thick papillae and a single spot on upper caudal fin near base, and were regarded as females. Their male

partners had long tapered papillae and one or more spots on the end of caudal fin in addition to a spot on upper caudal fin near base.   The number of spots of each fish did not change during the study period.   The captured fish were marked by sewing a ribbon tag (3.0 cm long, 0.3 cm in width) with sewing needle into the dorsal musculature anteriorly to the dorsal fin.   After marking, the fish were returned to their respective collection sites.   Sixteen males and 19 females were marked.

To determine pair bonds of A. phalaena, I surveyed the study area for 2-3 hours almost every day and recorded the presence of marked fish and their partners.   A pair was defined as a male and female which were swimming or feeding close together. Although weather or poor water conditions sometimes prevented observations, I considered that the social state of each individual did not change during those days and treated the data analyses accordingly.

After spawning, the female's abdomen was always deflated.   I therefore checked the degree of abdominal swelling to determine the date or time of spawning. For estimating the period of preparation for the next clutch, the degree of abdominal swelling was classified by eye into five categories: stage 1, abdomen deflated, just after spawning; stage 2, abdomen flat as in the non-breeding season; stage 3, abdomen in the incipient stage of swelling; stage 4, abdomen moderately expanded; stage 5, abdomen fully expanded.

To determine pair home ranges, a substrate map was prepared for a 35 x 30 m quadrat within the study area.   To record locations and swimming routes of 5 pairs, I conducted 10 minutes of observations in the daytime (12:24-16:00h), 3-4 times for each pair from 9-19 October in 1996.

To examine the cost of egg care, the behavior of both sexes of pairs was compared between egg-tending period and non-egg-tending period.   I conducted 5 minutes of observations in the daytime (12:03-17:45h), 1-6 times for 7 males and 6 females during the egg-tending periods and 1-2 times for them during the non-egg-tending periods.   I recorded the numbers of feeding bites and burrowing behavior, and the time spent in the burrow by males during the egg-tending periods.   I was usually able to observe both fishes of a pair simultaneously, but when separated, I observed each fish alternatively at intervals of one minute.

To observe egg-tending behavior in a burrow, a male (114 mm in TL) and female (132 mm) were captured far from the study area on 14 May 1996, and kept in an aquarium (60 x 30 x 35 cm) with running sea water (26.5-27.5 ℃).   An artificial burrow (50 x 10 x 10 cm) was constructed with bricks along the front-glass of the aquarium, all sides of which were covered with black vinyl-sheet so as not to disturb the

fish.   After spawning, male egg-tending behavior was observed for about 5 minutes, 2-3 times every day until hatching.   The body sizes (TL) of newly-hatched embryos (n=12) were measured under a binocular microscope.

In the study area, two egg masses were collected on the day of spawning (26 August and 10 September) by breaking down the burrow with a hammer.   The egg mass attached to a broken piece of burrow substrate was put into plastic container underwater and transported to the laboratory where the total wet weight of each egg mass was measured, as well as the wet weight and egg number of 10 sub samples.   The total number of eggs per clutch was then calculated from the average weight-number ratio of 10 samples.   The egg size (mm in diameter, n=12) was measured by micrometer under a binocular microscope.

Results

Pairing and home range

In each pair of A.phalaena, male (mean TL ± SD=132.9 ± 7.0 mm, range=121-147 mm, n=16, unmeasured 6 pairs were not included) and female (126.4 ± 6.9 mm, range=116-136 mm, n=16) sizes were significantly correlated (Pearson's correlation coefficient, r=0.54, p<0.05, n=16).   Males were usually larger than their mates (13 of 16 pairs; paired t test, t=4.03, p<0.01).   Six solitary males (mean TL ± SD=127.8 ± 7.3 mm, range=121-137 mm; mean solitary period ± SD=4.3 ± 4.6 days, range=1-13 days) and 3 solitary females (121.7 ± 4.0 mm, range=117-124 mm; 4.3 ± 3.5 days,1-8 days) were also found in the study area.   Two of the 6 solitary males intruded from outside of the study area and the other solitary individuals had lost their partners within the study area.   The mean daily sex ratio (males : females) ranged from 0.91-1.18 in the study area (mean ratio ± SD=1.02 ± 0.05, n=88 days).

Each pair and solitary individual had one or more burrows within their home ranges   (Figure 1).   The burrows were used for shelters and spawning sites.   Both sexes of a pair usually swam and foraged together, at a distance of 0.3-2.0 m.   Home ranges of all pairs, including 5 pairs as shown in Figure 1 (33.6-101.0 m2), did not overlap with each other.

Pair bonds were maintained for 3 to at least 88 days (mean ± SD=45.7 ± 33.9 days, n=22 pairs) during the study period (88 days).   Ten pairs (45%) remained together without changing partner and four pairs (18%) disappeared together from study area.   In five pairs (23%), one of the mates (3 males and 2 females) disappeared.   The

pair bonds of the other three pairs (14%) were broken by the intrusions of solitary individuals (2 males and 1 female).   Both of the two intruding males (137 and 138 mm TL) were larger than the original paired males (121 and 130 mm).   There was no difference in body size between the intruding female and original paired female.   In case of the female intrusion, the original paired male (136 mm) had a chance to mate with both the original paired female (124 mm) and the intruding solitary female (124 mm).   But the competition between those females was so intense that the paired male could not control them.

Intrusions by the solitary individuals into pairs' home range were observed five times during the study period, and always resulted in intraspecific aggression. Fighting individuals placed themselves side by side, spreading their all fins and bending their bodies into a sideways s-shape.   At this time, the partner of the winner also occasionally assisted in driving off the loser (twice in females).

Feeding and burrowing behavior

Amblygobius phalaena mouthed the thin layer of sand, and then sifted out food from sand through its gill rakers.   They also fed upon benthic algae.   Male feeding frequency during the egg-tending periods (median=4.0 bites, range=0-7.0 bites, n=7) were significantly lower than those during non-egg-tending periods (17.0 bites, range=0-33.0 bites, n=7; Wilcoxon signed-ranks test, T=2.0, p<0.05), while female feeding frequency did not differ between them (egg-tending periods: 26.5 bites, range=23.3-28.8 bites, n=6; non-egg-tending periods: 30.0 bites, range=23.0-43.0 bites, n=6; Wilcoxon signed-ranks test, T=4.5, p>0.05).   Females fed more than males during both egg-tending periods (Mann-Whitney U test, U=42.0, p<0.01) and non-egg-tending periods (U=35.0, p<0.05).

Among pairs, only males constructed burrows.   The male used his mouth to dig into substratum (coral pavement), carrying away sand, dead coral-fragments, rubble and shells out of the burrow.   The male dug burrows not only during the non-egg-tending period (mean ± SD=6.7 ± 10.2 times, range=0-25.0 times, n=7), but also during the egg-tending period (1.2 ± 1.3 times, range=0-4.0 times, n=7).   There were 3 L burrows with one opening (dimension of one burrow: 40-65 mm inside diameter, 300 mm in horizontal length, 190 mm in depth) and 8 U shaped burrows with two openings (dimension of two burrows: 50-70 and 40-90 mm inside diameter, 210 and 230 mm in horizontal length, 175 and 100 mm in depth, respectively).   The frequency of male burrowing behavior was negatively correlated with that of feeding

bites (r= - 0.80, p<0.05, n=7).

Reproduction and spawning cycle

During the study periods, 37 spawnings of 13 pairs were recorded (Figure 2). The 13 pairs spawned an average of 2.8 times (SD=1.3, range=1-5 times over 88 days). Spawning intervals of multiple-spawning pairs (11 pairs) ranged 9 to 30 days (mean period ± SD=17.7 ± 6.1 days, n=23). All recorded spawnings took place between tagged pairs. The pair spawned in one of the several burrows within their home ranges. Eggs were deposited on the ceiling of the burrow. All eggs in a burrow (n=10 including collected 2 clutches) were uniform in texture and color. There was only one clutch in each burrow. Clutch sizes collected on the day of spawning were 37, 665 (male 129 mm TL, female 124 mm) and 38, 443 eggs (male 137 mm, female 121 mm). Eggs were ovoidal in shape (major axis, mean ± SD=1.64 ± 0.04 mm; minor axis, 0.50 ± 0.01 mm, n=13), being connected to each other with adhesive filaments. The egg bunches hung down from the ceiling of the burrow (about 1-3 cm).

Spawning occurred approximately 3 days (mean ± SD=3.1 ± 1.6 days, range=1-7 days, n=37) before new and full moon (i.e., semilunar spawning cycle; Figure 2). Egg guarding periods lasted 3 or 4 days after spawning (3.1 ± 0.3 days, n=34), and then, hatching occurred synchronously at either the new or full moon phases. But, at least, five expected spawnings by five different pairs were canceled (shown as thick lines in Figure 2). Body size of those pairs (male: median=134.5 mm, range=123-142 mm; female: 125.0 mm, range=118-136 mm, n=5) did not differ from that of the other breeding pairs (male: 136.0 mm, range=127-145 mm; female: 123.0 mm, range=116-135 mm, n=8; Mann-Whitney U test, U=18.5 and 20.0, respectively, both p>0.05). Although, most females (29 of 32 females, unobserved 5 females were not included) spawned stages 4 or 5 of abdominal swelling, three females of the five canceled pairs had not reached stage 4 until new or full moon (stage 2, 3 and 3). The other 2 females had reached stage 5.

Parental care

Fanning of eggs was performed only by the male parent. During the brooding periods, the male stayed in the burrow in total 41.7% (range=19.4-66.8%, n=5 males) of the time. In 9.8% (range=1.7-57.1%) of the time , the male fanned at the burrow entrance in an upward posture probably to provide oxygenated sea water into the

burrow.   The total time allocated to these two behavior patterns increased with development of the eggs (Friedman test, X_2=7.3, df=2, p<0.05, n=5).   The rest of time was spent burrowing, feeding (around the burrow, 0.1-5.0 m) and attacking (median=39.1%, range=0-71.3%).   In the aquarium, the male intermittently fanned the eggs with its pectoral fins while shaking its body beneath the eggs.   Occasionally, the male gently held a part of the eggs in its mouth, before immediately spitting it out. The newly-hatched embryos, 2.48-2.64 mm TL (mean ± SD=2.59 ± 0.05 mm, n=12) were observed in the aquarium after sunset (20:20).

Twelve attacks against 6 fish species approaching their burrows were observed: four times on Parapercis cylindrica, three times on Valenciennea longipinnis, twice on Halichoeres trimaculatus and once on Parupeneus multifasciatus, Thalassoma lutescens and solitary A. phalaena.   Paired females also attacked those intruders (twice), but she never came into the egg-tending burrow.   No predation on eggs was observed.

Discussion

This study revealed that Amblygobius phalaena is monogamous in my study area.   Although a few paired individuals changed partners, most pairs remained together over successive rounds of reproduction until the end of the study period or until the one or both mates disappeared.   This result fits the definition of monogamy applied to fishes by Barlow (1984).   The mate changes were caused by the intrusions of solitary individuals into the home range of the paired fish.   Because larger A.phalaena had an advantage in intraspecific aggression, larger solitary individuals could take a partner from smaller paired individuals.   The missing individuals may have been eaten by predators: I observed that two A.phalaena (one adult and one juvenile) were predated by Synodus dermatogenys (Takegaki, unpublished data).

Reavis & Barlow (1998) reported that A.phalaena live in polygynous groups consisting of a single large male that maintains a burrow, and multiple females that shelter in shallow depressions under the coral head.   These females did not exhibit agonistic interactions regardless of their close proximity.   They suggested that the potential benefit of a burrow exists for female A.phalaena, and the coexistence of females is due to limited burrow substrate and reproductive males.   In my study area, however, the sex ratio was almost even, and all males, including solitary males, maintained one or several burrows in their home ranges.   Thus, it appears to be difficult for a male to monopolize multiple females by resource defence in the study area.   Barlow (1986) suggested that monogamy in gobiid fishes is associated with

shared burrows and mate guarding, and hypothesized that an abundance of nest sites allows all males to breed, and given a balanced sex ratio, females would be able to guard a monogamous mate. I observed that some A.phalaena males had opportunities to mate with both resident female and intruded female, but were prevented from doing so by the intense guarding exhibited by resident females. Barlow's hypothesis also suggests that the guarding sex gains a selective advantage by monopolizing a mate. The female A.phalaena would probably suffer in polygyny through the loss of male help, such as egg-care or burrow construction. The abundance of available burrows for spawning and intense mate guarding by females may be important factor for monogamy in this species, as has been reported in related gobies: Valenciennea strigata (Reavis, 1997) and V. longipinnis (Takegaki & Nakazono, 1999a).

Most A. phalaena had a semilunar spawning cycle, but five expected spawnings did not occur. There was no influence of female size or male size on the spawning-cancel. In 3 of these, the abdominal swelling of paired females had not reached stage 4 before full or new moon, while greater than 90% of semilunar spawning females had reached stage 4 or 5 (probably just before or after ovulation) until the day before spawning. Have those spawning-canceled females been ready for spawning? The delayed spawning has been reported in Nile tilapia Oreochromis niloticus, in relation to low dietary protein level of females (Gunasekera et al. 1996). Higher feeding rate of paired female A. phalaena compared to paired males appears to be closely related with egg production. Thus, the spawning-canceled females may not have garnered enough energy through food to produce eggs every spring tide. On the other hand, the remaining 2 spawning-canceled females had reached stage 5 on 3 and 4 days before the new moon (14 August), respectively. These cancels appeared to be disturbed by a typhoon (12-13 August): their burrows had been buried under the sand completely.

Although all five spawning-canceled pairs had already reached stage 4 five days after the full or new moon, they did not spawn until the next spring tide. Lunar and semilunar spawning cycles occur commonly in reef fishes, and are considered to contribute to the propagule dispersal and survival (Robertson 1991). Also, if they spawn after the full or new moon, their young may not be properly dispersed. If spawning-canceled pairs spawn irrespective of lunar phase, they can do so without decreasing the number of spawnings. However, their next spawning will be late for the following tide, because semilunar-spawning pairs needed an average 10.6 days (SD=1.8 days, range=8-13 days, n=16) to reach stage 4. Thus, spawning-canceled pairs may prefer to synchronize spawning to lunar phase rather than to increase the

number of spawnings.

In pairs, burrows were maintained only by the males, and the female did not join in burrow construction. As reported in some monogamous fishes, to increase female fecundity through the reduction in energy consumption or the promotion of feeding, paired males take on the greater part of the burden of work; e.g., territorial defense (surgeonfish, Robertson et al. 1979, butterflyfish, Hourigan 1989), burrow construction (goby, Takegaki & Nakazono 1999b) and parental care (cichlid, Yanagisawa 1986, Rogers 1988). The burrow construction of A. phalaena males limited their feeding, but, as a result, both sexes in a pair may be able to have higher reproductive success. Paired females of related gobies Valenciennea strigata (Reavis 1997) and V. longipinnis (Takegaki & Nakazono 1999b) burrowed at 33.7% (4.1 of 12.2 times per 5 minutes in average) and 22.2% (2.6 of 11.7 times) of total frequency, respectively. To reduce the burrowing burden, they preferred to mate with larger males with higher burrowing ability (Reavis & Barlow, 1998; Takegaki & Nakazono, 1999b). In A. phalaena, relatively low frequency of burrowing behavior (6.7 times) may allow no female's participation in the burrowing work due to the simple burrow structure and construction.

Although parental care of eggs was performed mainly by the males, paired females also exhibited egg-guarding behavior against fishes approaching their burrow. Egg care by females is rare in gobiid fish (see Blumer 1982, Thresher 1984). The egg-care by female A.phalaena was infrequent, suggesting no reduction in energy consumption occurred. On the other hand, males tended eggs at the expense of their feeding. Increase of time spent egg care with the development of eggs seems to be a response to increase of oxygen requirement of the eggs, as has been reported for some gobiid fishes (Torricelli et al. 1985, Lindström & Wennström 1994, Takegaki & Nakazono 1999c) and stickleback fishes (van Iersel 1953, Sevenster 1961, Reebs et al. 1984).

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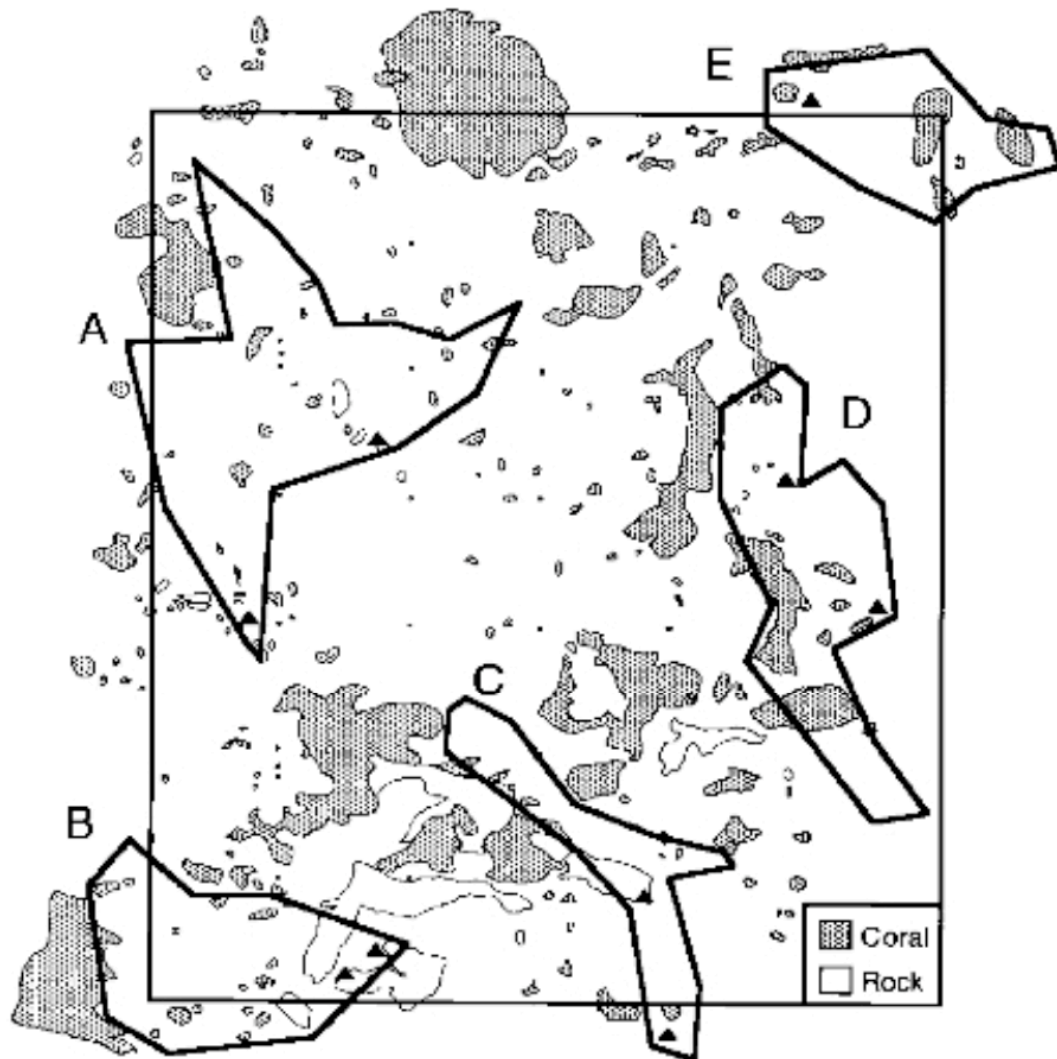
Figure 1. Home ranges of five pairs of *Amblygobius phalaena* (A = male 142 mm SL, female 133 = mm; B = male 127 mm, female 116 mm; C = male 136 mm, female 124 mm; D = male 133 mm, female 124 mm; E = male 130 mm, female 136 mm). The distribution of corals and rocks on the sandy floor is also shown. Triangles indicate burrows.
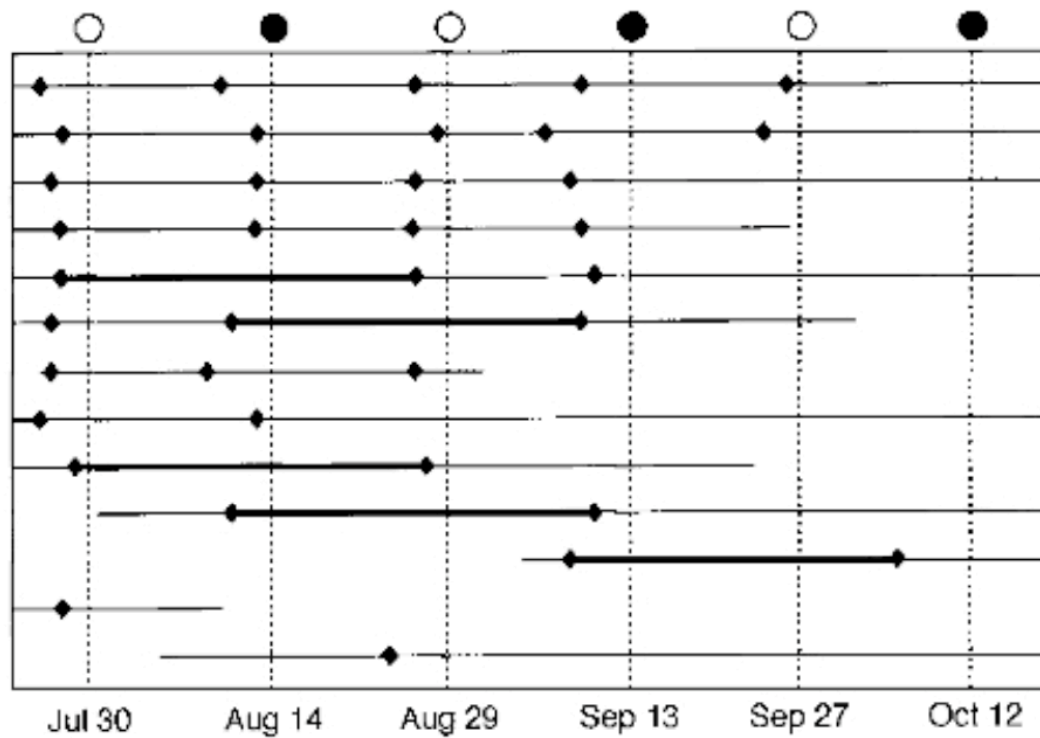
Figure 2. Relationship between lunar phase and 37 spawings (diamonds) of 13 *Amblygobius phalaena* pairs. Solid thin and thick lines indicate the pairing period and the periods when each pair should have spawed, respectively. Solid and open circles indicate new and full moon, respectively.