

Reproductive Behavior of the Anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan

Jack T. Moyer and Lori J. Bell

(Received February 16, 1976)

Abstract The reproductive behavior of the anemonefish, *Amphiprion clarkii* (Bennett) is described from the island of Miyake-jima, Japan. Host anemones of the genus *Parasicyonis* provide nesting habitats which vary considerably in size, resulting in differences in social behavior. Agonistic behavior is more pronounced in large, crowded colonies than in small ones with a single dominant pair and 2~3 subdominant fish. Only dominant fish are sexually active. Courtship behavior is initiated by the male and consists merely of nest cleaning, sometimes with bodies touching, and nipping at the tentacles of the anemones. Head-shaking, dorsal and ventral leanings, and jaw-clicking, often described as courtship displays, are considered here as agonistic behavior, occurring more regularly in newly established pairs where the pair bond is weak than in established "veterans". Spawning takes place between 9 AM~3 PM. The male assumes most of the responsibility for egg-care, the female only rarely fanning eggs. Nocturnal egg care is lacking except on the night of hatching. Eggs hatch between 34~70 min after sunset.

Introduction

The anemonefishes of the genus *Amphiprion* Bloch et Schneider have received considerable attention in the literature, with most research being focused on the symbiotic relationships between various *Amphiprion* spp. and their host anemones (Verway, 1930; Gohar, 1948; Davenport and Norris, 1958; Fishelson, 1965; Mariscal, 1970 a, 1970 b, 1970 c, 1972). In recent years, attention has turned increasingly to more general studies of anemonefish behavior, encompassing various aspects of their life history (Namba, 1964; Allen, 1972; Fricke, 1974; Moyer, 1976).

Studies of the pomacentrid fish, *Amphiprion clarkii* (Bennett) commenced in the waters of Miyake-jima, Japan (34°05'N, 139°30'E) in the summer of 1969, continuing through December, 1975. Some findings have been reported. Moyer and Sawyers (1973) discussed territoriality and Bell (1976) examined fecundity and nesting success. In this paper we will concentrate on courtship behavior and spawning.

Methods and materials

SCUBA was used for all observations in the sea, amounting to more than 400 hours. During

1974~75, 2~4 dives were made daily throughout most of the breeding seasons. Prior to 1974, and during winter throughout the study, underwater observations were made 2~5 times weekly, with few exceptions. Specimens were collected for identification and meristic studies using screen and hand nets.

Observations were made while lying motionless a few meters from host anemones or floating quietly 2~3 m above anemones. Fish soon became accustomed to us, and some individuals could actually be handled. Frequently, the A-2 female at Igaya had to be gently lifted from the nesting hole to permit examination of eggs.

Nests were identified by either numbers or letters, e. g., Toga A, Sabigahama 1; Igaya A-1, A-2, etc. Individual fish were not marked, but could be easily identified by location, color patterns, individual behavior, or combinations of all three.

Depths and temperatures were read from commercial diving gauges and recorded along with field notes on plastic tablets. Eggs and larvae under study in the laboratory at the Tatsuo Tanaka Memorial Biological Station (TMBS) were maintained in a 26 liter aquarium. Adult and juvenile fish were kept in 63 liter aquaria for studies of agonistic postures.

Results

Habitat and anemone hosts

A total of 68 nests and more than 140 adult fish were under observation at 61 anemone colonies at five separate locations around the island of Miyake. Nests and fish at Toga Bay, Sabigahama, Abe, and Okubo were studied whenever possible, but only at Igaya were oceanographic conditions suitable for daily observations (Bell, 1976). The Igaya site has been described by Moyer (1974, 1975) and Moyer and Shepard (1975). The site at Toga Bay was described in detail by Moyer and Sawyers (1973); however, populations under observation there have increased from 18 to 34 since that study. The study areas at Okubo, Sabigahama, and Abe are located on submerged lava flows, with only minimal outcroppings of *Acropora* corals as compared to rather extensive coral plateaus at Igaya and Toga Bay. Host anemones in Miyake waters include *Parasicyonis maxima* (Wassilieff), combined colonies of *P. maxima* and *P. actinostoloides* (Wassilieff), and, rarely, *Stoichactis haddoni* (Saville-Kent) (Moyer, 1976).

Territory and agonistic behavior

Moyer and Sawyers (1973) described territoriality in Miyake populations of *A. clarkii*, limiting their discussion primarily to the large Colony C at Toga Bay, an extensive mixed anemone colony of *Parasicyonis maxima* and *P. actinostoloides* that shelters more than 20 anemonefish. Other large colonies, such as the Toga Bay colonies E, F, M, U, and Z, exhibit territorial situations similar to Toga C, i. e. relatively small male territories centering around nest sites and an intensification of agonistic behavior.

More frequently, *A. clarkii* occupies small colonies of *Parasicyonis* anemones or *Stoichactis haddoni*. In these habitats, a single pair of dominant nesting fish occupies the site. In small colonies, as many as four subdominant individuals may share the site, usually easily distinguished from dominant fish by more orange on the body and distinctive caudal fin markings (Moyer, 1976). Subdominant fish are seldom seen with nesting fish at isolated single anemone sites, although juveniles may be present. Agonistic encounters are infrequent in small anemone colonies and single anemones, and are usually observed only within 2~3 days of spawnings. At such times,

agonism may occasionally be directed at the mate, depending upon the strength of the pair bond. Old, established pairs rarely show agonistic postures towards their mates. More often, subdominant fish are chased until aggression is inhibited by convulsive, jerking appeasement displays.

In these small populations, a clearly defined pecking order exists, agonistic displays are brief and of low intensity, and we have only rarely observed fighting, although biting is occasionally seen. An exception occurred at a small anemone in Toga Bay on July 24, 1974. Two small sub-adult *A. clarkii*, one orange and one dark-phased, were engaged in a dramatic struggle, apparently for control of the small *P. actinostoloides* anemone. They repeatedly rushed directly toward each other, leaning slightly to one side (the "dorsal leaning" of Allen, 1972), dorsal and anal fins extended, and jaws clicking. Frequently, sudden, swift biting attacks were made by either or both fish, both turning quickly to one side after each brief attack. At one point, they locked jaws and thrashed around violently for at least five seconds. From time to time the orange-phased fish jerked his body in appeasement, and seemed to be slightly at a disadvantage. Time did not permit us to watch the outcome, but two days later, the orange fish was in control of the anemone and his dark opponent was never seen again.

At isolated colonies, where no subdominant fish occur, pre-spawning aggression is often directed at *Thalassoma cupido* (Temminck et Schlegel) or *Dascyllus trimaculatus* (Rüppell). At each spawning, the male at an Igaya nest aggressively chased a sub-adult *Pomacentrus nagasakiensis* Tanaka that occupied the ledge by the anemone colony. We never observed this fish being chased between spawnings or when eggs were in the nest, but only after the substrate-biting courtship activities had commenced. On the other hand, the egg-eating *T. cupido* and other *Thalassoma* spp. are frequently chased from nest sites when eggs are in the nest. With the exception of the *Thalassoma* species, inter-specific aggression is rather rare at sites where subdominant *A. clarkii* are present, probably because conspecifics serve as a more natural outlet for aggression (Lorenz, 1966).

Large colonies show less stable dominance pat-

terns, and are useful locations for studying various intensities of agonistic behavior. Social interactions are intense and complex. Early morning watches in the breeding season show almost no agonistic behavior, as most fish feed on drifting plankton. Territorial males stay at their nests. At Toga Colony C, between 8:30~9:00 AM, the mood of the colony changes dramatically, and chasing, dorsal and ventral leanings, clicks, staccato rattles, and quivering appeasements continue almost uninterrupted until mid-afternoon, particularly at times of spawning. The apparent synchronous nature of spawnings in *A. clarkii* populations seems to greatly increase tension within the large colony at such times, resulting in intensive agonistic behavior. Dominant males at nests "c", "g", and "h", (Moyer and Sawyers, 1973: fig. 2) all jerk convulsively in appeasement at the approach of their mates, even though dominance among nesting fish has not changed in two years. Unlike situations in small anemone colonies, familiarity with the mate does not lead to decreased agonism. Female "a" (Moyer and Sawyers, 1973) repeatedly visits both nests "h" and "g", both males appeasing with the quivering display. Nesting males frequently chase smaller subdominant and juvenile fish from their territories, uttering rapid staccato rattles, apparently produced by rapid movements of the jaw. The convulsive, shaking appeasement display inhibits aggression immediately, and the aggressor turns toward his territory only to suddenly be pursued by the smaller fish, who turns to flee the renewed attack by the dominant fish. These encounters rage back-and-forth for several seconds at a time, gradually drawing further and further from the nest of the dominant fish, until he returns to his nest.

The agonistic vocabulary is varied and complicated, with different levels of intensity. Dorsal leaning seems to be a low intensity threat posture, with ventral leaning the corresponding appeasement. However, not infrequently, ventral leaning elicits a quivering appeasement. Jaw-clicking is a higher intensity threat signal (possibly the "threatening sounds" of Schneider, 1964). A corresponding appeasement is convulsive body-jerking ("head-shaking", Allen, 1972: 208). The highest intensity threat display is the

staccato rattling, produced while chasing the opponent. High intensity appeasement is shown by rapid body-shaking while drifting upward, either head up or head down, accompanied by clicking sounds.

Courtship behavior

Reproductive activity of *A. clarkii* at Miyakejima begins with the full moon of mid- to late May. Cold winter waters (13~16°C) inhibit activity from January to early April, during which time males stay within shelter holes close to their nesting sites of the previous summer. As winter approaches, females usually move off from nesting sites to find shelter holes in crevices under nearby anemones or coral, within 2~3 m from the nest site. With the warming waters of spring, females return to their nest site of the previous year, or occasionally to another site. For example, the female at Igaya A-1 developed the grey caudal fin of old age during the 1974 summer and failed to survive the cold February waters in 1975. By late April, her place had been taken by the female from A-2, 10 m away. A formerly subdominant female at A-2 mated with the A-2 male, losing the orange border on her caudal fin as the season progressed.

Courtship begins with substrate biting by the male. In newly established pairs, some agonism may be exhibited during courtship. The male seems to defend the nest site even from the female at first, seldom leaving the vicinity of the nest. He rushes back toward the nest, his sudden dash frequently eliciting first a quivering appeasement and then an aggressive chase or jaw clicking by the female. Except in the large anemone colonies, the intensity of these agonistic encounters decreases with time, soon becoming the dorsal and ventral leaning described by Allen (1972: 207~211) and others. By late summer, in old, established pairs, agonism is almost nonexistent.

Substrate biting appears to be the major form of courtship. Invariably, the male begins the substrate biting, tearing away algae from the nesting surface. The female only rarely takes part early in the courtship, although her swollen abdomen almost certainly elicits his nest cleaning behavior. Within one day of spawning, the female assists in substrate biting, but only rarely leads the male to the nest. On the spawning day, both

fish usually enter the nest together to bite the substrate, and often the female leads the male to the nest. For example, on July 2, 1975, the A-1 male was observed biting the substrate 13 times in a 30 min watch. During that time, the female joined him for 14 additional substrate bitings, 12 of which were initiated by the male. The female led the male to the nest only twice. Only two low-intensity agonistic postures were observed in the 30 min watch, e. g., dorsal leaning by the male, and mutual ventral leaning. The male, however, seemed somewhat defensive of the nesting area, rushing to beat the female to the nest on many occasions. A 30 min watch on July 3 was quite different. Mutual substrate biting continued for almost the entire period, with the female frequently leading the male to the nest, with no apparent concern by the male. No agonistic postures were observed. Substrate biting continued for 60~180 sec or longer each time. Often the bodies of the two fish touched in the nest. Both individuals frequently pulled at the tentacles of the anemones or carried tentacles away from the nesting surface. Spawning occurred later that day. Numerous observations at other nests are similar.

Biting of the anemone tentacles directly precedes spawning. Intensive tentacle-biting causes the anemones to withdraw, exposing the nest surface for spawning. The shrunken tentacles are a good signal to the observer that spawning will soon follow.

Males typically initiate pre-spawning activities, as described. The pair at Igaya B provided an interesting exception. The female is a large veteran of more than 100 mm S. L. The 1975 male was a small newcomer who replaced the 1974 male late in that summer, after the former defender disappeared. At Igaya B, throughout the entire 1975 breeding season, the female initiated substrate biting and almost always led the male into the nest. Early in the season the male rarely defended the nest, but by October, he often led the female in attacking intruders.

Substrate biting is not always an action associated with courtship. It is frequently seen on the morning following the hatching of eggs, as the male cleans egg cases from the nest site. Substrate biting is also a displacement activity brought about by agonistic approaches by the female. These are normally caused by "food

disputes", coincidental meetings of male and female as both pursue the same planktonic organism. Such meetings usually result in aggressive jaw-clicking or chasing by the larger female. The male often responds by rushing to the nest and biting the substrate.

Spawning

Spawning takes place from 6~8 times a season between mid-May and early October (Bell, 1976). Spawning usually occurs between about 9:00 AM~3:00 PM, with the majority taking place in mid- to late morning. Our latest observation was at a nest in Toga Bay, July 18, 1975, where spawning occurred between 2~3 PM. We have several records of spawnings between 9~10 AM. The entire spawning sequence was observed only once (July 19, 1975). We staggered observation times to permit renewal of our air supplies one at a time, allowing continuous observation for 3.5 hours. Since, to our knowledge, spawnings of *Amphiprion* species in nature have never been described through the entire sequence, we will discuss it in detail.

We arrived at the Igaya site at 9:15 AM, finding both fish at the entrance of the nest. The male turned away from the nest and the female bit him twice on the side. He immediately went into the nest and bit at the nest surface. She bit him again moments later.

There was considerable mutual substrate biting mixed with feeding. The female's abdomen was large. Twice the male chased *Thalassoma cupido*, the female leading him back to the nest to bite the substrate. Four times the female bit the nest surface by herself, once because the male was preoccupied with a subdominant fish. He chased it, ending the chase with the rapid staccato rattle so common in agonistic encounters at Toga C and other big colonies. For the next 30 min they mixed substrate biting with feeding. Not infrequently, subdominant conspecifics were chased. Both fish nipped at anemone tentacles, which became shrunken and withdrawn. At 9:58 AM, the female entered the nest and settled on the nest surface, moving her pectoral fins as if spawning, but her body did not move, and no eggs were laid. After a second trip to the nest surface, her ovipositor was visible, but still no eggs had been laid. The male bit the substrate while the female was in

the nest, and skimmed over the nest surface with rapid movements of the pectoral fins, as if fertilizing eggs, when she was not in the nest. The third time the female entered the nest, she settled on the surface, remaining stationary for a moment, except for movement of her pectoral fins. When she left the nest, 7~10 orange eggs remained. For the first two minutes, she laid eggs while remaining stationary, but at 10:04 AM, she began moving around the nest surface, propelling herself with alternate beats of her pectoral fins.

The male continued substrate biting. Spawning continued in slowly increasing circles, the diameter of the egg-patch increasing from about 4 cm at 10:19 AM to 6 cm by 10:30 AM. As the egg patch increased in size, the male entered the nest with the female, both skimming over the nest surface, propelled by alternate pectoral beats. Both left the nest for 1~3 sec intervals. They frequently mouthed the anemone tentacles, which remained shrivelled and discolored. At 11:05 AM, the female left the nest for 10 sec. Trips from the nest increased in time and frequency. By 11:30 AM, her ovipositor was partially withdrawn. She extended it again and again to lay more eggs, but with longer trips away from the nest. The last spawning pass was at 12:04 PM, two hours and six min after her first dry pass. The male made his last fertilizing pass over the nest surface at 12:24 PM. His genital papilla was nearly totally withdrawn by 12:30 PM. The female was feeding over coral 4 m away when the male stopped fertilizing.

Unlike other pomacentrids for which data is available, no elaborate displays accompany spawning. Substrate biting gradually increases in frequency and intensity and with no apparent signal, spawning begins. No color changes are noticeable in either male or female. There is often considerable wastage of eggs during spawning. Both male and female may have eggs stuck to the pelvic and anal fins, and many are laid on top of others, only to be removed later by the mouthing of the male.

On rare occasions, a male may spawn with more than one female in a season. A dark-colored male at Toga usually spawned with a melanistic female that normally shared the *Stoichactis haddoni* anemone. However, in

June, 1975, one clutch of eggs was spawned by a female showing much orange on her body, including anal and pelvic fins. She remained in the vicinity of the anemone until after the eggs hatched, when she was replaced by the dark-phased female, who had not been seen during the interval in which eggs were in the nest.

A more unusual situation occurred in late July, 1975, at Sabigahama Nest 9. Two patches of eggs were laid in the same nest, one patch covering about 2/3 of the other. The first were spawned on about July 17, with the second spawning occurring about three days later. Only the fringes of each patch hatched, and a heavy growth of fungus appeared on the overlapped eggs. These patches were almost certainly spawned by different females. Visits to the nest at that time showed only the male in the vicinity of the nest site. Moyer and Sawyers (1973) reported polygamous behavior in *A. clarkii*.

Spawning may take place at more than one nest site during a single season. The Igaya A-1 pair used two nest holes during the 1974 season, as did the 1972 Toga C "a-b" male. Usually, however, the same nest is used for several years.

Eggs are large, new eggs measuring 2.7×0.9 mm. Egg patches contain 1,000~2,500 eggs which hatch in $6(1/2) \sim 13(1/2)$ days (Bell, 1976). Bell (1976) estimated annual fecundity at 10,000~16,000 eggs.

Care of eggs

Although the female occasionally fans eggs and guards the nest, the male is far more active. For example, 98% of all egg-fanning during daily observations over one entire $7(1/2)$ day incubation period at Igaya A-2 was performed by the male. Observations at other locations were similar. An exception was at Igaya B, where the female fanned 43% of the time in a one hour observation on the first day after spawning, but fanned only rarely after that. Fanning of eggs is usually frequent on the day after spawning, diminishing mid-way in the incubation period, and increasing to a peak on the day of hatching (Fig. 1).

Fanning is performed primarily with the pectoral fins and occasionally the caudal fin. Eggs are frequently mouthed, apparently to remove dead eggs.

Agonistic behavior is minimal during periods when eggs are in the nest. Various species of

Thalassoma are chased by both sexes, but intra-specific encounters and chasing of other species are seldom observed. *Thalassoma cupido* has

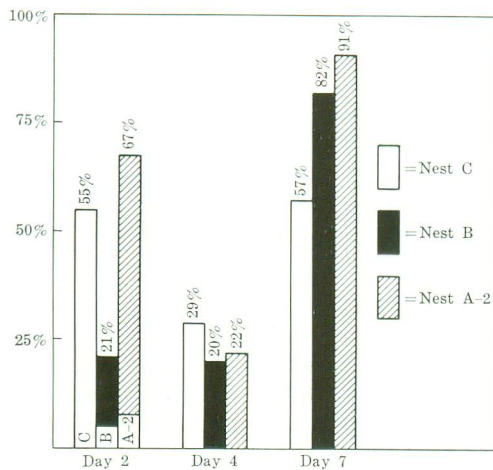


Fig. 1. Comparative nest care at three nests in Igaya Bay, showing % of time spent in nest fanning or cleaning egg patch during one hour watches.

been observed eating eggs of *A. clarkii* (Bell, 1976).

Hatching

In July, 1975, the eggs from Toga E-3, and the small nesting rock on which they were laid, were brought to the laboratory and allowed to hatch in a 26 liter aquarium. An airstone was placed beneath the nest surface to allow continuous movement of the eggs. A few eggs hatched at dusk on July 19. None hatched during the following day, but by 6 PM, that evening, eggs began hatching at a slow pace. The first rapid flurry of hatching was at 7:30 PM, 35 min after sunset, which was at 6:55 PM on July 20. By 8:10 PM, 2/3 of the approximately 1,500 eggs had hatched. The remainder were fungoused and dead.

Results in nature were similar. At Igaya A-2, July 10, 1975, all eggs had hatched by 9:05 PM. On July 14, at Igaya B, all but 5~6 eggs had hatched by 7:50 PM, 52 min after the 6:58 PM sunset of that date. The remaining 1/2 dozen eggs had hatched by 8:05 PM.

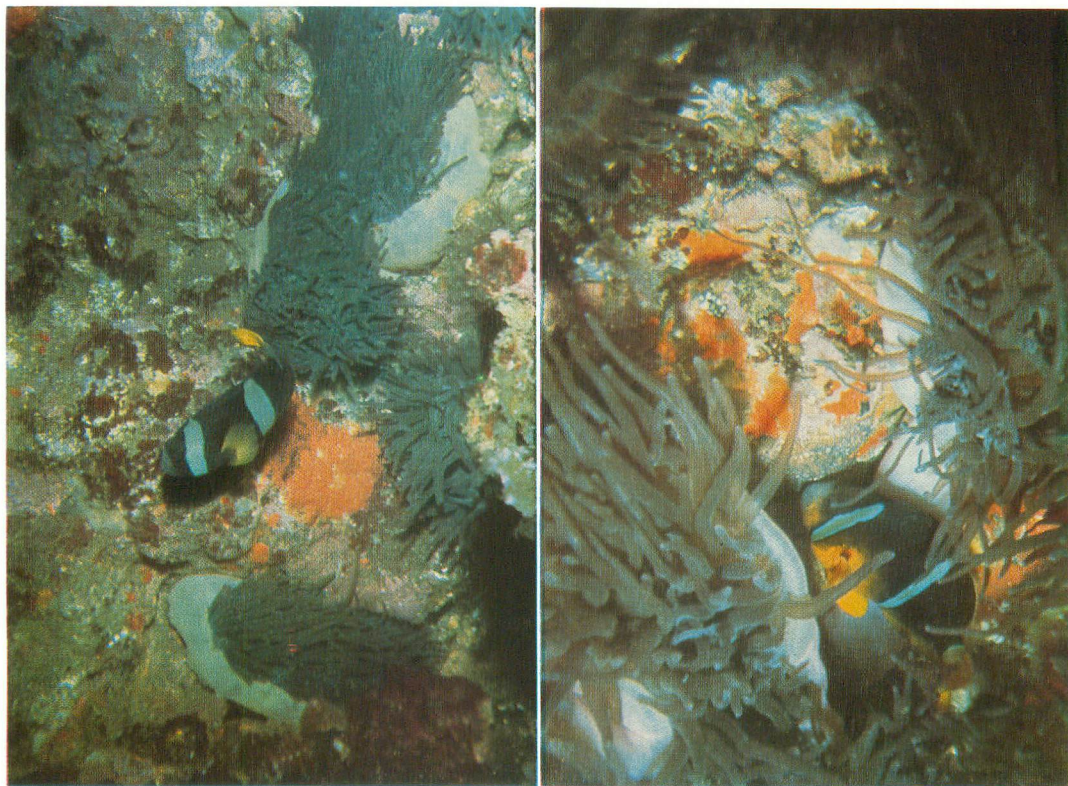


Fig. 2. A. Igaya A-1 male fans one day old eggs. (Left)
B. Sabigahama No. 6 male mouthing eggs on day of hatching. (Right)

At Igaya A-1, July 24, 1975, the first eggs hatched at 7:00 PM, eight min after the 6:52 PM sunset. The first major hatching flurry came 36 min after sunset, at 7:28 PM. Hatching was stimulated by rapid fanning of eggs by the male, rarely the female. Flurries of eggs hatched after each fanning. The male fanned almost continuously, leaving for 3~4 sec intervals when the hatching flurries took place. He was not intimidated by our lights. Female fanning and mouthing of eggs occurred only when the lights were turned off, and then only infrequently. Hatching slackened at 7:45 PM, stopping by 8:00 PM. Only about 1/2 of the eggs hatched. The remainder hatched the following night.

Hatching at Igaya C and Igaya B on July 26, 1975, began at 7:34 PM and 7:25 PM respectively, with the first hatching flurry coming 46 min after the 6:51 PM sunset at Nest C and 39 min after sunset at Nest B. Eggs stopped hatching by 7:50 PM at both sites, again with hatching incomplete. The remaining eggs at both sites hatched the following night.

Another clutch of eggs hatched at Igaya B on Aug. 19, 1975. We arrived at the nest in time to watch the final eggs hatch at 7:15 PM, 48 min after sunset, which was at 6:27 PM.

From our observations, it is clear that, although some hatching takes place before dark, the first major flurry of hatching begins between about 35~45 min after sunset, and continues until 48 min to more than one hour after the setting sun. Longer examples probably resulted from the negative effect of our lights. Hatching flurries were induced by egg fanning, usually by the male. Near the end of the hatching period, fanning decreased and mouthing of eggs increased in frequency. When hatching was observed from the beginning, large numbers of eggs remained to hatch the next night. However, when nests were visited after the normal hatching hour or not at all, all eggs hatched in a single night, i. e., were not in the nest the following morning, suggesting that lights inhibit hatching to a considerable extent. It is not known whether the initial hatching flurry was delayed by our lights.

Larvae were attracted to our lights in the field and to aquarium lights in the laboratory. Those measured at the laboratory 12 hrs after hatching showed a remarkable variation in size, ranging

from 3.3 mm~5.2 mm.

Discussion

1. Courtship and spawning

Unlike many pomacentrids, there seems to be no elaborate courtship display (Reese, 1964; Ehrlich, 1975; Moyer, 1975). Just prior to spawning, substrate biting and nest cleaning increase in frequency and anemone tentacles are nipped causing them to shrink away from the nesting surface. Mutual substrate biting often results in the bodies touching, but we have never observed body-shaking at such times. Body-shaking accompanying mutual substrate biting is considered an important sexual behavior in *Amphiprion bicinctus* Rüppell (Fricke, 1974). Fricke (1974) has shown substrate biting to function strictly as ritualized signalling, pointing out that actual cleaning of the nest surface is minimal. This is probably true in Miyake waters as well in mid-summer. However, substrate biting accompanying the first spawning in May, after a six month rest period, also functions to clean the nesting surface, as evidenced by white scar tissue and ripped flesh on the lips of nesting fish at that time.

In a veteran pair, in which the pair-bond is long-established, there is little fear-motivated appeasement (i. e., ventral leaning, body shaking). In new pairs, various amounts of agonism are observed. In such pairs, females seem to be dominant over males in most cases, and may often rush towards the male, who leans in appeasement. Such agonism by females and appeasement postures by males led Allen (1972: 209~216) and Moyer and Sawyers (1973) to conclude that the female initiates courtship behavior and spawning. The situation is complicated by the fact that occasionally the male responds to aggressive approaches by his mate by rushing to the nest to bite the substrate, an act usually associated with courtship. That these are displacement activities (i. e., behavior occurring under conflict situations and apparently irrelevant to the immediate situation) is evident by the fact that they are isolated instances, occurring only very seldom in a given watch and often several days before true nest cleaning begins. Allen (1972: 238) noted substrate biting as a displacement activity in captive *Amphiprion melanopus* Bleeker.

In "established" or "veteran" pairs, appeasement postures are minimal, except in the large colonies, eliciting either no noticeable response or only a low-intensity appeasement, i. e., a slight ventral leaning, usually by the smaller male. However, during the early stages of substrate biting, the male rushes to the nest at the approach of the female, as if defending it from her. This often leads to mutual substrate biting. We have rarely noticed *A. clarkii* taking particularly aggressive roles in courtship and spawning in veteran pairs, except at Toga Colony C, and in our opinion, the leanings, body-shaking, and jaw-clicking often associated with courtship by many authors are, in fact, expressions of agonism between fish in which the pair bond is still relatively weak and fear of close approach remains. The male seems to initiate courtship and spawning by substrate biting, although this is almost certainly elicited by the swollen abdomen of the female.

Morris (1956) describes three types of mating behavior: (1) situations in which one partner is attacked during the mating period, which he designates with the abbreviation fAM; (2) situations in which one partner tries to flee during the mating period (FaM); and (3) situations in which the partners neither flee nor attack (faM). Fricke (1974) found neither aggression nor flight associated with the mating and spawning of *A. bicinctus* in the Red Sea, and classified it as faM-behavior. Among Miyake populations of *A. clarkii*, aggressive approaches by females in the large colonies cause the male to rush to the nest surface to bite the substrate. Even in so-called established pairs in isolated anemones, approach by the female in the early stages of courtship leads to what we have interpreted as a defensive rush to the nesting surface by the male, similar in some ways to male behavior in the large colonies. *A. clarkii* mating behavior at Miyake, therefore, resembles FaM-behavior in some respects, differing from that of *A. bicinctus*.

In Miyake populations of *A. clarkii* we have never observed the "up-down dance" described by Fishelson (1965) in courtship and spawning of *Amphiprion bicinctus*. Likewise, we have never observed signal jumps nor enticement behavior so common in other pomacentrids (Abel, 1961; Myrberg et al., 1967; Moyer, 1975, etc.) pre-

sumably because pair bonds tend to be permanent unlike the lek-type social systems of many pomacentrids in which males must actively compete for spawning mates (Ehrlich, 1975, and others).

2. Care of eggs

Nest care by *A. clarkii* is similar to that described by Allen (1972: 216~224) for *A. chrysopterus* Cuvier. The male assumes primary responsibility for fanning and mouthing of eggs and the female only rarely takes part. Agonistic activity is minimal, with various species of the labrid genus *Thalassoma* receiving most attention. As in *A. chrysopterus*, egg-care decreases mid-way through the incubation period, increasing again to reach a peak on the day of hatching. Various reasons for increased egg care as the eggs near the hatching hour have been suggested by Reese (1964) and Allen (1972: 236~238); e. g., visual cues elicited by silver eyes of the embryos or lower oxygen tension of water in the nest due to increased metabolic activity of the embryos. Our observations show considerable movement of embryos within the eggs on the day of hatching, which might also contribute to increased fanning behavior.

Albrecht (1969) observed increased egg-fanning at night in *Abudefduf saxatilis* Linneaus throughout the incubation period. Nocturnal egg care could result from decreased oxygen at night in particular habitats. Our studies of *A. clarkii* showed nocturnal egg care only on the night of hatching. During initial stages of incubation, fish remained in the tentacles of the anemones in nocturnal colors. Observations of *Pomacentrus nagasakiensis* Tanaka, *Chromis flavomaculata* Kamohara, and *C. miyakeensis* Moyer et Ida are similar.

3. Hatching

Hackinger (1967) and Neugebauer (1969) found hatching to occur within one half to one hour after the onset of darkness in aquarium studies of *Amphiprion akallopisos* Bleeker, *A. bicinctus*, and *A. ephippium* (Bloch). In their aquarium study, Tanase and Araga (1975) reported the hatching of *A. clarkii* eggs "just after sunset". Our numerous Miyake records of the hatching of *A. clarkii* eggs in nature, beginning between 35 and 45 min after sunset, support the laboratory findings of the above authors and are in agreement with the findings of Fricke (1974) concerning *A. bicinctus* in nature.

Acknowledgments

Gratitude is expressed to John Shepard, Kathy Meyer and Claire Sawyers of TMBS for contributing to this study. A special thanks to Dr. Gerald R. Allen, Western Australian Museum, for critical review of the manuscript. Thanks to Dr. Hitoshi Ida, Kitasato University, Dr. Yoshiaki Tominaga, Tokyo University, and Dr. Teruya Uyeno, Luther Shingaku Dai-gaku, for helpful advice, and to Mr. Hajime Masuda, Tokai University, who kindly photographed Igaya Nest A-1 and Sabigahama Nest 6 for Fig. 2.

Literature cited

- Abel, E. F. 1961. Freiwasserstudien über das Fortpflanzungsverhalten des Monchfisches *Chromis chromis* Linne, einem Vertuiter der Pomacentriden in Mittelmeer. Z. Tierpsychol., 18 (4): 441~449, figs. 1~7.
- Albrecht, H. 1969. Behavior of four species of Atlantic damselfishes from Columbia, South America, (*Abudefduf saxatilis*, *A. taurus*, *Chromis multilineata*, *C. cyanea*: Pisces Pomacentridae). Z. Tierpsychol., 26: 662~686, figs. 1~5.
- Allen, G. R. 1972. The anemonefishes: their classification and biology. TFH Publications, Inc., Neptune City, N. J.: 1~288, figs. 1~140, tabs. 1~23.
- Bell, L. J. 1976. Notes on the nesting success and fecundity of the anemonefish, *Amphiprion clarkii*, at Miyake-jima, Japan. Japan. J. Ichthyol., 22 (4): 207~211, 1 fig., 1 tab.
- Davenport, D. and K. S. Norris. 1958. Observations on the symbiosis of the sea anemone *Stoichactis* and the pomacentrid fish, *Amphiprion percula*. Biol. Bull. Woods Hole, 115 (3): 397~410, 1 fig., 1 tab.
- Ehrlich, P. R. 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst., 6: 211~247.
- Fishelson, L. 1965. Observations and experiments on the Red Sea anemones and their symbiotic fish *Amphiprion bicinctus*. Bull. Sea Fish. Res. Stat. Haifa, 39: 1~14, figs. 1~7.
- Fricke, H. W. 1974. Öko-ethologie des monogamen Anemonenfisches *Amphiprion bicinctus* (Freiwasseruntersuchung aus dem Roten Meer). Z. Tierpsychol., 36: 429~512, figs. 1~41, tabs. 1~16.
- Gohar, H. A. F. 1948. Commensalism between fish and anemone. (With a description of the eggs of *Amphiprion bicinctus* Rüppell). Fouad I. Univ. Publ. Mar. Biol. Sta. Ghardaga (Red Sea), 6: 35~44, 1 fig.
- Hackinger, A. 1967. Anemonenfische-im Aquarium gezuchtet. Die aufzucht von *Amphiprion bicinctus* in Aquarium. Aquarien Magazin, Stuttgart: 137~141, figs. 1~14.
- Lorenz, K. 1966. On aggression. Harcourt, Brace, and World, Inc., New York: 1~306.
- Mariscal, R. N. 1970 a. An experimental analysis of the protection of *Amphiprion xanthurus* Cuvier and Valenciennes and some other anemonefishes from sea anemones. J. Exp. Mar. Biol. Ecol., 4: 134~149, figs. 1~8, tabs. 1~6.
- Mariscal, R. N. 1970 b. The nature of the symbiosis between Indo-Pacific anemonefishes and sea anemones. Mar. Biol., 6 (1): 58~65, figs. 1~5.
- Mariscal, R. N. 1970 c. A field and laboratory study of the symbiotic behavior of fishes and sea anemones from the tropical Indo-Pacific. Univ. California Publ. Zool., 91: 1~33, figs. 1~16, tabs. 1~3.
- Mariscal, R. N. 1972. Behavior of symbiotic fishes and sea anemones. In H. E. Winn and B. L. Olla, ed. "Behavior of marine animals: current perspectives in research. Vol. 2, Plenum Press, London-New York," 327~360, figs. 1~4.
- Morris, D. 1956. The function and causation of courtship ceremonies. In "Collected papers by Desmond Morris. Patterns of reproductive behavior. Panther Books, London," 128~152, figs. 1~16.
- Moyer, J. T. 1974. Notes on the reproductive behavior of the wrasse, *Thalassoma cupido*. Japan. J. Ichthyol., 21 (1): 34~36.
- Moyer, J. T. 1975. Reproductive behavior of the damselfish *Pomacentrus nagasakiensis* at Miyake-jima, Japan. Japan. J. Ichthyol., 22 (3): 151~163, figs. 1~5.
- Moyer, J. T. 1976. Geographical variation and social dominance in Japanese populations of the anemonefish *Amphiprion clarkii*. Japan. J. Ichthyol., 23 (1): 12~22, 2 figs., tabs. 1~4.
- Moyer, J. T. and C. E. Sawyers. 1973. Territorial behavior of the anemonefish, *Amphiprion xanthurus*, with notes on the life history. Japan. J. Ichthyol., 20 (2): 85~93, figs. 1~2.
- Moyer, J. T. and J. W. Shepard. 1975. Notes on the spawning of the wrasse, *Cirrhitilabrus temminckii*. Japan. J. Ichthyol., 22 (1): 40~42.
- Myrberg, A. A., B. D. Brahy, and A. R. Emery. 1967. Field observations on the reproduction of the damselfish, *Chromis multilineata* (Pomacentridae) with additional notes on general behavior. Copeia, 1967 (4): 819~827, figs. 1~7.
- Namba, T. 1964. Kumanomi-rui no isoginchaku ni taisuru hanno ni tsuite. Graduate thesis,

- Tokyo Univ. Fisher., 1~74, many figs. In Japanese.
- Neugebauer, W. 1969. So zuchten wir Korallenfische. Aquarien Magazin, Stuttgart (Dec. 1969): 483~488, figs. 1~14.
- Reese, E. S. 1964. Ethology and marine zoology. Oceanogr. Mar. Biol. Ann. Rev., 2: 455~488, figs. 1~2.
- Schneider, H. 1964. Biokustische Untersuchungen an Anemonenfischen der Gattung *Amphiprion* (Pisces). Z. Morphol. Ökol. Tiere, 53: 454~474, figs. 1~14.
- Tanase, H. and C. Araga. 1975. Observations of breeding and taxonomy of the anemonefish, *Amphiprion clarkii* (Bennett). Dobutsuen-Suizokukan Zasshi, 17 (1): 16~21, figs. 1~2. In Japanese.
- Verway, J. 1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. Treubia, 12 (3-4): 350~366, figs. 1~5.
- (Tatsuo Tanaka Memorial Biological Station, Toga

Farm, Ako, Miyake-jima, Tokyo, 100-12, Japan. Present address of LJB: 5473 Honors Drive, San Diego, Calif. 92122, USA)

三宅島におけるクマノミの生殖行動

Jack T. Moyer and Lori J. Bell

クマノミの社会行動は、サンゴイソギンチャクの群落の大きさによって異なり、大きく密な群落において威嚇行動はより顕著である。優占ペアのみが性行動を行なう。求愛行動（卵床の清掃、時々体を触れ合うこと、イソギンチャクの触手を噛むこと）は、雄によって始められる。頭を振る行動、背腹にそり返る行動、顎で発音する行動は、新しい不安定なペアで多く見られ、定着した古いペアでは弱く求愛行動でなく威嚇行動と思われる。産卵は午前9時から午後3時の間に行なわれる。卵は主に雄が保護する。夜間の保護行動は、孵化の夜以外は見られない。卵は日没後34~70分後に孵化する。

(100-12, 東京都三宅村阿古 富賀農園 田中達男記念生物実験所)