Geographical Variation and Social Dominance in Japanese Populations of the Anemonefish Amphiprion clarkii

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Abstract Geographic variation between populations of the anemonefish, Amphiprion clarkii (Bennett) from the Bonin Islands, Yaeyama Islands, Okinawa, and Miyake-jima, Japan, is described, and relationships between color patterns and social dominance of the species at Miyake-jima are discussed. Yaeyama populations show the greatest degree of variation in color, but sexual dichromatism is not always pronounced. In Okinawan populations, adult males can be consistently recognized by orange borders on the caudal fin, compared to uniformly yellow caudal fins in adult females. Populations from Kyushu to Miyake-jima show subdominant fish of both sexes displaying orange caudal borders, similar in appearance to Okinawan males. Dominant males have solid orange or nearly solid orange caudal fins, whereas dominant females show pale yellow caudal fins. Anal and pelvic fins darken with dominace. Miyake fish are slightly larger than those from Okinawa, with slightly greater meristic counts and narrower body bars. Variations in color patterns appear to be related to selective pressures imposed by differences in habitat. A melanistic form occurs in the Bonin Islands. Sexual dichromatism is not present in populations from the Bonin Islands. Melanistic individuals from the Bonin Islands inhabit Radianthus anemones. Fish inhabiting the anemone, Stoichactis haddoni, at Okinawa and Miyake-jima are of the dark phase.

Introduction

Considerable variation in color and meristics can be found in populations of *Amphiprion clarkii* (Bennett) over its wide geographical range. This variation has led to taxonomic confusion resulting in a long list of synonyms. In Japan, two distinct forms have been recognized: *Amphiprion snyderi* Ishikawa from the Bonin Islands and *A. japonicus* Temminck et Schlegel from Nagasaki (Ishikawa, 1904; Temminck and Schlegel, 1842). Both are now considered junior synonyms of *A. clarkii* (Allen, 1972: 114).

Recent investigations in pomacentrid behavior have shown that variations in local habitats may be reflected in differences in behavior between geographically isolated populations within a single species (Fricke, 1975 a, 1975 b).

From 1973 to 1975, local populations of *Amphiprion clarkii* were examined at Miyake Island (34°05′N, 139°30′E), the Bonin Islands (26°38′N, 142°09′E), Okinawa (26°05′N, 128°00′E) and the Yaeyama Islands (24°25′N, 124°10′E) (Fig. 1). Findings concerning variations in color, meristics, and certain aspects of

social behavior are reported below.

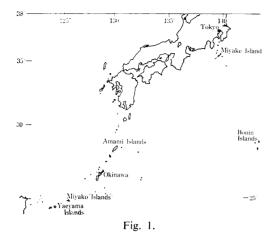
Methods and materials

SCUBA was used for all research, amounting to more than 100 hours under water. Specimens were collected using screen and hand nets. All specimens are deposited at the Tatsuo Tanaka Memorial Biological Station (TMBS). Behavioral studies were conducted while lying motionless near sea anemones for periods of from 15~60 min. Observations were recorded on plastic tablets.

Results

Habitat and anemone hosts

As Allen (1972; 165) and others have pointed out, anemonefish species are never encountered without a sea anemone, although sea anemones without anemonefish are not uncommon. By far the most common host anemones for *Amphiprion clarkii* in Miyake waters are *Parasicyonis maxima* (Wassilieff) or mixed colonies of *P. maxima* and *P. actinostoloides* (Wassilieff). More rarely, colonies of only *P. actinostoloides* are inhabited by anemonefish, but in all of our records, only juveniles and



subadults occur with this species, and we have never found a nest associated with it except in mixed colonies with *P. maxima*.

Both *P. maxima* and *P. actinostoloides* have been synonymized by many authors under the name *P. actinostoloides*. Uchida et al. (1975) have clarified this confusion and have provided complete descriptions and photographs of both species. Both usually occur in colonies, attaching their pedal discs to rocks or stony corals. Some colonies are quite extensive. Colony C at Toga Bay is inhabited by 20~24 fish and protects four active nests.

In addition to the preceding species, two of 68 nests under observation at Miyake were located under the tentacles of Stoichactis haddoni (Saville-Kent). This species, incorrectly identified as S. kenti (Haddon et Shackleton) by Moyer and Sawyers (1973), is rare in Miyake waters. A preference for Parasicyonis anemones is suggested by the fact that only two of four S. haddoni anemones under observation were occupied by adult fish, although all were located within 20 m of successful Amphiprion populations. A third sheltered three juveniles for a short time in August, 1974, but none survived. A juvenile survived for two days in one S. haddoni site in Toga Bay in July, 1974, but we have never observed young fish sheltered in the other Toga Bay S. haddoni anemone.

Two other anemone species have been recorded as hosts for *Amphiprion clarkii* juveniles at Miyake. *Radianthus malu* Haddon et Shackleton at Igaya sheltered two small juveniles for about a month in June~July, 1973, and a single juvenile in 1975 which survived until

winter, reaching approximately 60 mm T. L.

Radianthus papillosa (Kwietniewski)?, in Igaya Bay, sheltered three 15~20 mm juveniles for more than a week in 1974. These were frequently swept 30~40 cm from the anemone by relatively strong surge, and were destroyed by Typhoon No. 14 in late August. No other Amphiprion have been observed at any of four other individuals of this anemone at Igaya Bay, Sabigahama, and Toga Bay, and Uchida (personal communication) has never seen anemone-fish associated with this species at Kushimoto.

At Okinawa, Radianthus kuekenthali (Kwietniewski) is the most commonly observed host for A. clarkii, although R. malu and R. gelam (Haddon et Shackleton)? are sometimes encountered with anemonefish. Stoichactis haddoni also shelters A. clarkii. Juveniles have been found in Radianthus simplex (Haddon et Shackleton).

Our findings in the Yaeyama Islands are similar, except that *R. gelam*? appears to be the most common anemone host in deep waters outside the barrier reef. *Stoichactis haddoni* and *R. malu* are often encountered with *A. clarkii* in shallow waters on the reef and in the lagoon, and juvenile anemonefish are sometimes found associated with *R. simplex*.

All of our observations of *A. clarkii* in the Bonin Islands have been in association with an unidentified *Radianthus* anemone.

Distinction of A. clarkii populations in Japanese Waters

Four distinct forms of *Amphiprion clarkii* occur in Japanese waters. Each can easily be distinguished by combinations of color and size. In the discussion below, each form is named after the geographical area in which it is found.

1. Yaeyama-type (Fig. 2 A~C). Materials: TMBS 750614–01 (1), June, 1975, Taketomijima, TMBS 750614–02 (1), June 1975, Taketomijima, TMBS 75–0617 (2), Taketomi-jima, TMBS 751223–01 (1), December, 1975, Kuroshima, TMBS 751224–01 (1), December, 1975, Kuroshima, TMBS 751225–01 (2), December, 1975, Kuroshima, 67~92 mm in S. L.

This form is described first because it seems most typical of the species as described by Allen (1972: 110~117). There is much variability in coloration and size of adult specimens. Our eight examples range from 67~92 mm in

standard length. Specimens taken from the lagoon are small (67~72 mm) while examples from deep water outside the barrier reef are large (89~92 mm). Frequent field observations verify this trend. Fin colors are variable. Dorsal fin colors are grey, black, or combinations of both. Sexual dichromatism is difficult to discern, although there is a tendency toward orange caudal fin borders in males. However, we have collected females with orange caudal borders and males with uniformly creamywhite caudal fins. A. clarkii is not common in these islands, and host anemones are rather isolated from each other. A single anemone normally shelters a pair of adult anemonefish and occasionally one or two juveniles.

2. **Bonin Islands-type** (Fig. 2 L) Materials: TMBS 740624 (2), June, 1974, Chichijima. 96.5~104 mm in S. L.

This is a relatively large, melanistic form, occurring in the Bonin Islands. Two TMBS specimens from Chichijima measure 104 mm and 96.5 mm respectively, and six others observed by us at Chichijima and Ototojima appeared equally large. Except for the three white bars on the body, a creamy-white caudal fin, and a pale yellow pectoral fin, the entire fish is black. Sexual dichromatism is not present in this form. Juveniles are dusky orange, noticeably different in shade than juveniles of A. clarkii we have observed elsewhere. This anemonefish is rather rare, apparently due to the scarcity of anemones in the Bonin Islands. All of our observations have shown this fish to be associated with an anemone of the genus, Radianthus. In every case, a single pair of adults shared the sea anemone with 8~10 juveniles.

3. Okinawa-type (Fig. 2 D~F). Materials: TMBS 751116–01 (4), November, 1975, Sesoko-jima, TMBS 751116–02 (5), November, 1975, Sesoko-jima, TMBS 751117–01 (2), November, 1975, Sesoko-jima. 63~88 mm in S. L.

This form ranges from Miyako-jima (25°00′N, 125°02′E) to the Amami Islands (28°04′N, 129°05′E) in the Ryukyu Islands. Our 11 adult specimens average 80.6 mm S. L. Considerable variability occurs in color, especially of the pelvic and anal fins, which may be either orange, black, or combinations of both. Dorsal fins are usually either black or grey, but occasionally orange. Pectoral fins are orange except in specimens

associated with the anemone, Stoichactis haddoni, in which case they are dark grey or pale yellow (see discussion). The color of the caudal fin of adults is indicative of the sex. Detailed field data on 55 specimens show that males invariably display orange borders on an otherwise creamy-white caudal fin. The width of the orange border varies somewhat, but is usually quite thin, i. e. $1\sim2$ mm in width. We have never seen a solid orange caudal fin in Okinawan populations. Female caudal fins are a solid creamy-white. Okinawan fish live mainly in the anemone, Radianthus kuekenthali, or occasionally R. malu. ?R. gelam, or Stoichactis haddoni. A single adult pair inhabits each anemone, frequently sharing the host with 1~2 juveniles and perhaps 2~3 Amphiprion perideraion Bleeker. Host anemones are abundant; neighboring Amphiprion pairs may be found within 8~10 m of each other. Yasuda (personal communication) reports a particularly dense population at Miyakojima.

4. Japan-type (Kyushu, Shikoku, Kii Peninsula, Izu Islands, etc.) (Fig. 2 G~I). Materials: TMBS 740718–01 (1), July, 1974, Miyake-jima, TMBS 750620–01 (2), June, 1975, Miyake-jima, TMBS 750623–01 (3), June, 1975, Miyake-jima, TMBS 750714–01 (4), July, 1975, Miyake-jima, TMBS 751129–01 (1), November, 1975, Miyake-jima, 78.5~106 mm in S. L.

This fish is very similar to the preceding type, but differs in several important respects. It appears to be somewhat larger than the Okinawan form. Our 11 specimens (all nesting, dominant fish) average 88.1 mm S. L. The bars on the body are considerably narrower than those on Okinawan specimens (Table 4), and dorsal, anal, and pectoral ray counts are higher (Table 1).

Populations of several adult fish often inhabit the same colony of *Parasicyonis* anemones, resulting in clearly defined patterns of social hierarchy. Detailed field records on 183 fish indicate that dominant nesting males display solid or nearly solid orange caudal fins (Fig. 2 G). Caudal fins of nesting females are usually a solid creamy-white, but occasionally a trace of orange may appear at the border of either or both lobes, near the base (Imai, 1972; Moyer and Sawyers, 1973; Tanase and Araga, 1975). Female caudal fins darken with old age, turning greyish-black (Fig. 2 J). This is accompanied by a lightening

Table 1. Fin ray counts for Japanese populations of Amphiprion clarkii.

| | Dorsal fin | | | | | | Anal rays | | | | Pectoral rays | | | | | | | |
|--------------|------------|---|----|----|----|----|-----------|----|---|---|---------------|----|----|----|----|----|----|----|
| Type | IX | X | ΧI | 14 | 15 | 16 | 17 | 18 | 1 | 2 | 13 | 14 | 15 | 17 | 18 | 19 | 20 | 21 |
| Japan-Type | 4 | 6 | 1 | _ | _ | 5 | 5 | 1 | | 1 | _ | 6 | 4 | - | _ | _ | 9 | 2 |
| Okinawa-Type | _ | 9 | 2 | _ | 2 | 9 | | — | - | _ | 2 | 9 | | _ | _ | 6 | 5 | _ |
| Yaeyama-Type | _ | 8 | _ | | 1 | 6 | 1 | _ | _ | _ | 4 | 2 | 2 | _ | | 3 | 2 | 3 |
| Bonin-Type | _ | 1 | 1 | _ | 1 | 1 | _ | | _ | _ | 1 | 1 | | _ | _ | 1 | 1 | |

Table 2. Comparison of sexual dichromatism in nesting (dominant) and non-nesting (subdominant) *A. clarkii* from Miyake Island.

| | No. of fish in which identifica- tion of sex is clear | No. of fish in which identi- fication of sex is not clear |
|------------------|--|--|
| Nesting fish | 96 (92%) | 8 (8%) |
| Subdominant fish | 8 (13 %) | 55 (87%) |

Table 3. Anal and pelvic fin colors and percentages of nesting *Amphiprion clarkii* at four sites at Miyake Island.

| | Anal | fin | Pelvic fin | | | |
|------------|-----------|----------|------------|-----------|--|--|
| Site | Black | Orange | Black | Orange | | |
| Toga Bay | 53 (85%) | 9 (15%) | 37 (59%) | 25 (41 %) | | |
| Sabigahama | 18 (90%) | 2 (10%) | 11 55%) | 9 (45%) | | |
| Igaya | 10 (100%) | 0 (0%) | 6 (60%) | 4 (40%) | | |
| Okubo | 6 (50%) | 6 (50%) | 1 (8%) | 11 (92%) | | |
| Total | 87 (84%) | 17 (16%) | 55 (53%) | 49 (47%) | | |

Table 4. Comparison of Width of 1st and 2nd Bars of *Amphiprion clarkii* adult specimens from Sesoko Island, Okinawa, and Miyake Island.

| Location | Fish No. | Standard length in mm | Width of 1st bar in % of S. L. | Width of 2nd bar in % of S.L. | | |
|-----------|------------|-----------------------|--------------------------------|-------------------------------|--|--|
| Okinawa | 751116–01a | 88 | 11 | 11 | | |
| | 751117–01b | 87 | 10 | 11 | | |
| | 751116-02a | 85 | 8 | 11 | | |
| | 751116-01b | 82 | 11 | 12 | | |
| | 751116-01c | 82 | 7 | 12 | | |
| | 751117-01a | 82 | 13 | 15 | | |
| | 751116-02b | 81 | 15 | 17 | | |
| | 751116-02d | 80 | 10 | 12.5 | | |
| | 751116-02e | 80 | 12.5 | 15 | | |
| | 751116-02c | 76.5 | 12 | 14 | | |
| | 751116-01d | 63 | 13 | 17 | | |
| Miyake I. | 751129-01a | 106 | 7 | 6 | | |
| | 750620-01a | 102.1 | 10 | 10 | | |
| | 750623-01a | 101.5 | 9 | 9 | | |
| | 750718-01a | 96 | 6 | 8 | | |
| | 750623-01b | 87 | 8 | 8 | | |
| | 750620-01b | 84.5 | 8 | 8 | | |
| | 750623-01c | 82.5 | 8 | 8 | | |
| | 750714-01c | 79 | 6 | 8 | | |
| | 750714-01d | 79 | 6 | 8 | | |
| | 750714-01a | 78.5 | 8 | 8 | | |
| | 750714-01b | 69.5 | 7 | 7 | | |

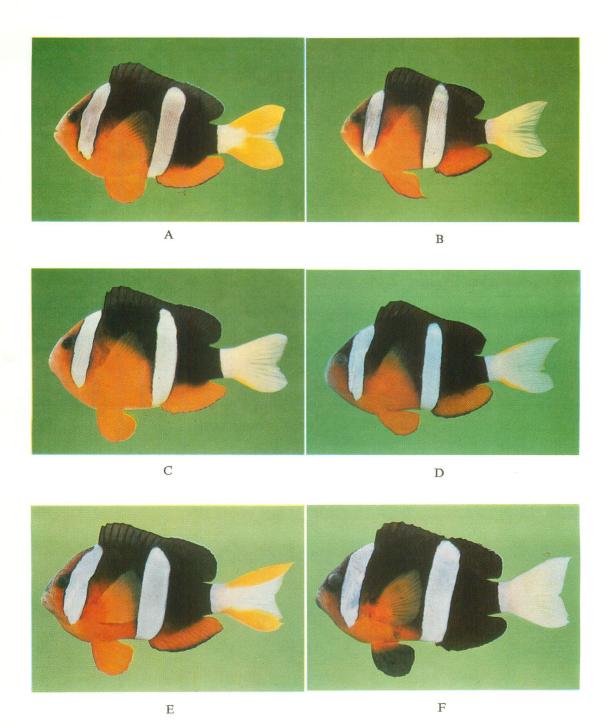
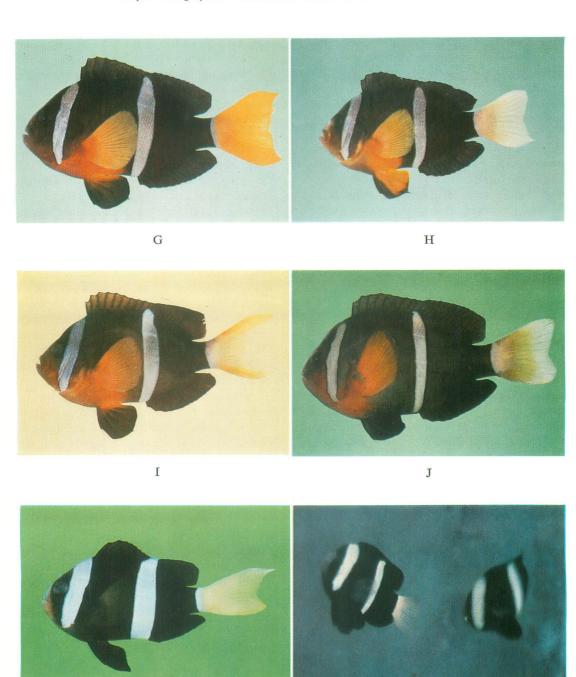


Fig. 2. A. Yaeyama-type male. TMBS 751225-01. B. Yaeyama-type male. TMBS 751223-01. C. Yaeyama-type female. TMBS 751225-01. D. Okinawa-type male. TMBS 760219-02. E. Okinawa-type male. TMBS 760219-01. F. Okinawa-type female. TMBS 760219-02.



G. Miyake nesting (dominant) male. TMBS 750623–01. H. Miyake nesting (dominant) female. TMBS 750714–01. I. Miyake subdominant female. TMBS 750714–01. J. Miyake. Old female, TMBS 751129–01. K. Melanistic phase female, Okinawa. TMBS 760220–01. L. Bonin Islands: nesting pair. TMBS 740629–01. Photos $A \sim K$ by John W. Shepard.

L

K

of the body color from black to grey, especially noticeable when the fish is under stress conditions. Fish showing the colors of old age generally die in the following winter.

Subdominant adult males and females appear identical to nesting adult males from Okinawa, both sexes of the northern form displaying orange borders on the caudal fin. This confusing phenomenon is related to dominance patterns in Japan-type fish, and will be discussed below. The dorsal fin is invariably black. As in Okinawan populations, fish inhabiting *Stoichactis haddoni* anemones are of the melanistic color phase, but continue to exhibit the sexually diagnostic solid orange or creamy-white caudal fins of the northern form (see discussion). From Kyushu to Miyake-jima, *Parasicyonis* anemones are preferred, but *S. haddoni* occasionally serves as the host species.

Color as a sign of dominance

As has been stated, an important characteristic that distinguishes Japan-type A. clarkii from the Okinawan form is the presence of color patterns which are related to social dominance. Subdominant fish of both sexes at Miyake have orange borders to the caudal fin, identical in appearance to the caudal fins of nesting males in Okinawan waters (Fig. 2 I). Sexually active, dominant fish of the Japan-type gradually develop solid caudal colors (orange in males, creamy-white in females). In Miyake populations, even when dominance is achieved, considerable time is required before sex-distinguishing caudal patterns fully develop. Because a given anemone colony typically shelters more subdominant adult fish than nesting, dominant fish, the presence of sexual dichromatism in A. clarkii in Japanese waters has either been overlooked or not clearly understood, and therefore omitted from important reference books on Japanese fishes (see Matsubara, 1955; Masuda et al., 1975).

Due to the size of most colonies of *Parasicyonis* anemones and the territorial requirements of nesting males and females, often only one pair of dominant fish is present at a given site, although as many as $4\sim5$ subdominant fish and $1\sim2$ juveniles may be present. In large anemone colonies more than a single pair of dominant fish may be present, each pair occupying clearly defined territories within the colony. (Four

dominant pairs and from 14~16 subdominant fish have occupied Toga Colony C since 1972).

After establishing dominance, usually due to the death or disappearance of the previously dominant fish, females begin to exhibit a gradual narrowing of caudal borders, which eventually almost entirely disappear. The orange borders on male caudal fins gradually thicken, either uniformly along the length of the upper and lower lobes or posteriorly from the base of the tail, until the fin is entirely or nearly entirely orange. At a nest in Igaya Bay two complete breeding seasons were required before the orange completely disappeared from the dominant female. The male still showed a thin pale band in the mid-caudal fin after two summers of dominance. The sex of both could easily be distinguished by the end of the second summer. However, although substrate biting had been observed the pair never nested. Unfortunately, the female was illegally collected by aquarium hobbyists at the end of the 1975 season.

This Igaya pair represents an unusual example, because both fish matured simultaneously. A more frequent occurrence is the disappearance of one member of a pair, after which the highest ranking remaining member of that sex becomes dominant. Again the color change is slow, the complete transition requiring more than one breeding season; however, the fish spawns while still displaying subdominant colors. For example, the male at a nest at Sabigahama exhibited subdominant colors in 1974 (Moyer and Bell, 1976: fig. 2), but had developed the orange caudal fin of a dominant male by the 1975 breeding season. He mated and tended clutches of eggs in both seasons. Considering the length of time required for caudal colors to change sufficiently to make sexual identification possible, it is interesting that sexual dichromatism can be clearly recognized in 96 (92%) of 104 nesting A. clarkii for which complete color data is available. However, only eight (13%) of 55 non-nesting adult fish show totally orange or yellow caudal fins (Table 2). Juveniles usually display solid pale yellow caudal fins. Details of transition from juvenile to subadult color patterns are not yet clearly understood, but the orange caudal borders begin to appear at about 45~50 mm S. L.

Usually darkening of the anal fin and, less

frequently, the pelvic fin from orange to black accompanies caudal fin color changes in both sexes, taking somewhat longer in time (Table 3). For example, anal fin colors of both male and female at a nest at Okubo changed from orange to black and their caudal fin colors changed from the subdominant orange borders to dominant solid colors during the 1975 spawning season. The anal fins of the males at two other nests also darkened during the 1975 summer.

The body also darkens with dominance, beginning on the sides anterior to the caudal peduncle and spreading gradually foreward. Darkening of the body precedes that of the fins, and is nearly complete prior to the first nesting, some orange remaining around the pectoral and pelvic fins and the head.

Discussion

1. Host anemones

Uchida et al. (1975) discuss the symbiotic relationship between A. clarkii and various sea anemones in Japan. Our records add four new members to the list of sea anemones known to shelter Japanese populations of this anemonefish: Radianthus malu, Radianthus simplex, Radianthus gelam?, and Radianthus papillosa? (Marcanthea cookei Verrill is recognized as a junior synonym of R. papillosa by Dunn, 1974). The association of three juvenile A. clarkii with R. papillosa? at Miyake-jima during the summer of 1974 seems to constitute the first example of this relationship yet recorded. Dunn (personal communication) found our photographs of this species somewhat unlike specimens from Hawaii, and therefore, our identification remains tentative. This anemone is not listed by Allen (1972) Mariscal (1970, 1972), or Uchida (1975). Stevenson (1963 a, b) observed juveniles of Dascyllus albisella Gill associated with it in Hawaiian waters. We have recorded only juveniles or small sub-adults in R. papillosa?. Similarly, we have never seen a nesting pair of anemonefish in Parasicyonis actinostoloides, although nests are frequently seen in mixed colonies of P. maxima and P. actinostoloides. I observed 10 juvenile A. clarkii in the anemone, Radianthus simplex, at Sesoko Island, Okinawa, and Okamoto (personal communication) lists only juveniles from that species in the Yaeyama Islands. Allen (1972: 177) found juveniles of

both A. chrysopterus Cuvier and A. tricinctus Schultz et Welander associated with R. simplex at Eniwetok.

Allen (1972) and Mariscal (1972) do not indicate the sizes of A. clarkii observed in various anemones. Our studies suggest that some anemone species, e.g. Radianthus simplex, R. papillosa?, and Parasicyonis actinostoloides, are not suitable habitats for reproductive purposes, and may serve only as nurseries or temporary shelters for juvenile and subadult fish, who may later move into a more suitable habitat. For example, the young male who took over the P. actinostoloides anemone in the fight described in Moyer and Bell (1976), moved more than 30 m from that anemone to a P. maxima colony, replacing the male at Toga Y, who had disappeared early in 1975. It appears that at Miyake, only Parasicyonis maxima, combinations of P. maxima and P. actinostoloides, and Stoichactis haddoni are suitable habitats for pair formation and spawning of A. clarkii. The concept of "nursery anemones" needs further investigation.

Allen (1972: 124) suggested that Stoichactis anemones might contribute to the development of melanism in various species of Amphiprion. He found that Amphiprion tricinctus changed from orange to black several days after being placed in Stoichactis giganteum Forsskål. Later, he found melanism in A. percula (Lacepède) inhabiting S. kenti (Allen, 1973). He lists A. clarkii and A. ocellaris Cuvier as having melanistic phases and suggests the possibility that such phases might result from association with S. giganteum. Our Miyake data add considerable weight to Allen's hypothesis. Both pairs of A. clarkii inhabiting S. haddoni in Toga Bay, Miyake-jima, are of the melanistic color phase. Furthermore, both sexes at Toga S. h. I had orange pectoral fins in June, 1975, but were totally black except for the white bars and sexually diagnostic caudal fins by September. Photographs in Masuda and Abe (1972), Tateishi (1974), and T. Uchida (1975) of A. clarkii in S. haddoni anemones from Okinawa show only melanistic forms. I collected a melanistic A. clarkii (TMBS 760220-01) from Stoichactis haddoni in Okinawa (Fig. 2 K). Masuda (personal communication) reports a similar situation from the Kerama Islands, near Okinawa.

The cause of increased melanism in *S. giganteum* and *S. haddoni*-inhabiting species of *Amphiprion* is yet to be investigated. The synonymy of these anemones has been suggested by both Allen (1972 appendix table, p. ii) and Mariscal (1972).

2. Geographic variation, sexual dichromatism, and social dominance

Allen (1972: 112) discusses geographic variation in A. clarkii populations, suggesting a relationship to geographic locality. According to him, the most consistent features in color patterns "... are the pale caudal fin and abrupt light-dark boundary on the caudal peduncle" (Allen, 1972: 112). Even this pattern is not totally consistent, as shown by photographs in Allen (1975: 48). Such variability provides genetic potential for natural selection to work in a number of ways. The peculiar requirements posed by environmental differences between the Yaeyama Islands, Okinawa, and Miyake-jima (and presumably from Kyushu northward) have apparently resulted in the evolution of the different forms described.

In the Yaeyama Islands, the species is apparently not common. Anemone hosts are rather widely scattered, and we have never observed two pairs of A. clarkii within visual range of each other. Instant visual recognition of sex and/or dominace is not required, due to strong site attachment and familiarity with the mate and the $1\sim2$ juveniles within the host anemone (Fricke, 1974). A wide variability in caudal fin patterns exists, both sexes showing orange, mixed, and pale yellow caudal fins. Although in some pairs, males have orange borders to caudal fins and females do not, sexual dichromatism is not distinct in this population. Judging from photographs in Allen (1972) and Burgess and Axelrod (1974), similar situations occur at Taiwan, Philippines, and Guam.

In Okinawan waters Radianthus kuekenthali is abundant and several may share the same patch of reef. Most R. kuekenthali anemones shelter a single pair of A. clarkii adults and 2~3 pairs may be in visual contact with each other and may forage over the same range. Under these conditions, sexual dichromatism would prove advantageous for intra-specific recognition. Males always have orange borders on the caudal fin (Fig. 2 E). Females have a pale yellow tail (Fig. 2 F). Our observations suggest that both

sexes are less agonistic toward conspecific intruders of the opposite sex. The occasional occurrence of polygamy bears this out. Sexual dichromatism may therefore facilitate quick recognition by territorial fish of intruders of the same sex.

In Japanese waters, north of the Amami Islands, a major change takes place in the habitat of A. clarkii. Radianthus kuekenthali is replaced by Parasicyonis maxima as the important host anemone for A. clarkii (Uchida et al., 1975). P. maxima lives in dense colonies and also occurs with P. actinostoloides. These colonies often form carpets of anemones covering several m². As many as 20 or more fish may inhabit the same anemone colony. In other cases, anemone patches may be in close proximity to each other. In these situations, suitable nesting space is at a premium and dominance becomes important for control of the most suitable spawning surface. Under these circumstances, natural selection appears to favor easy recognition of dominance status. Our collections at Yaeyama indicate that genetic material is available for orange borders to caudal fins in females as well as males. Orange bordered caudal fins, apparently selected against in Okinawan females, become advantageous to subdominant fish of both sexes in crowded northern populations (Fig. 2 I). Selective pressures toward sexual dichromatism still exist in these populations, and dominant males develop solid orange caudal fins, whereas females lose the orange borders to their caudal fins (Fig. 2 G~H). Recognition of dominance is further simplified by darkening of anal and pelvic fins in dominant fish.

Populations of A. clarkii in the Bonin Islands need further study. Reasons for melanism in this area are not understood. Interestingly, all of our observations of A. clarkii in the Bonin Islands are with Radianthus anemones rather than Stoichactis species.

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Literature cited

- 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.
- Allen, G. R. 1973. Amphiprion leucokranos, a new species of pomacentrid fish, with notes on other anemonefishes of New Guinea. Pac. Sci., 27 (4): 319~326, figs. 1~4, 1 tab.
- Allen, G. R. 1975. Damselfishes of the south seas. TFH Publications, Inc. Neptune City, N. J.: 1~240, many figs.
- Burgess, W. and H. R. Axelrod. 1974. Pacific marine fishes. vol. 4. TFH Publications, Inc., Neptune City, N. J.: 848~1110, many figs.

- Dunn, D. F. 1974. *Radianthus papillosa* (Coelenterata, Actiniaria) redescribed from Hawaii. Pacific Sci., 28 (2): 171 ~ 179, figs. 1 ~ 6.
- 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.
- Fricke, H. W. 1975 a. Evolution of social systems through site attachment in fish. Z. Tierpsychol., 39: 206~211.
- Fricke, H. W. 1975 b. Sozialstruktur und ökologische spezialisierung von verwandten fischen (Pomacentridae). Z. Tierpsychol., 39: $492 \sim 520$, figs. $1 \sim 11$, tabs. $1 \sim 8$.
- Imai, S. 1972. Kumanomi (anemonefishes). Animal Life, 50: 1379~1382. In Japanese.
- Ishikawa, C. 1904. Notes on some new or little known fishes of Japan. Proc. Nat. Hist. Tokyo Mus., 1: 1~17, figs. 1~7.
- Mariscal, R. N. 1970. A field and laboratory study of the symbiotic behavior of fishes and sea anemones from the tropical Indo-Pacific. Univ. Calif. 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, Pleunum Press, London-New York: 327~360, figs. 1~4.
- Masuda, H. and T. Abe. 1972. Sea fantasy. Mainichi Newspaper, Tokyo: $1 \sim 201$, figs. $1 \sim 172$.
- Masuda, H., C. Araga, and T. Yoshino. 1975. Coastal fishes of southern Japan. Tokai Univ. Press, Tokyo: 1~379, figs. 1~11, pls. 1~142.
- Matsubara, K. 1955. Fish morphology and hierarchy, II. Ishizaki Shoten, Tokyo: 791 ~ 1605, figs. 290 ~ 536. In Japanese.
- Moyer, J. T. and L. J. Bell. 1976. Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. Japan. J. Ichthyol., 23 (1): 23 ~ 32, figs. 1 ~ 2.
- Moyer, J. T. and C. E. Sawyers. 1973. Territorial behavior of the anemonefish, *Amphiprion xan-thurus*, with notes on the life history. Japan. J. Icthyol. 20 (2): 85~93, figs. 1~2.
- Stevenson, R. A. 1963 a. Life history and behavior of *Dascyllus albisella* Gill a pomacentrid reef fish. Ph. d. dissertation, Univ. of Hawaii: 1~221, figs. 1~36, tabs. 1~13.
- Stevenson, R. A. 1963 b. Behavior of the pomacentrid fish *Dascyllus albisella* Gill in relation to the anemone, *Marcanthea cookei*. Copeia, 1963, (4): 612~614.
- Tanase, H. and C. Araga. 1975. Observations of breeding and taxonomy of the anemonefish,

- Tateishi, A. 1974. Okinawa no umi to shizen. Shogaku-kan Co. Ltd. Tokyo: 1 ~ 281, many figs. In Japanese.
- Temminck, C. J. and H. Schlegel. 1842. Siebold's Fauna Japonica. Leiden, 323 pp., many figs.
- Uchida, H. 1975. Symbiosis between sea anemones and fishes. In T. Uchida, ed., "Marine flowers". Nat. Elec. Co., Tokyo: 55 ~ 60, figs 1 ~ 4.
- Uchida, H., K. Okamoto, and T. Fukuda. 1975. Some observations on the symbiosis between anemonefishes and sea-anemones in Japan. Bull. Mar. Park Res. Sta., 1 (1): 31~46, figs. 1~2, 1 tab., pls. 1~3.
- Uchida, T., ed. 1975. Marine flowers. Nat. Elec. Co., Tokyo: 1~111, many figs.

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クマノミの地理的変異と群内序列 Jack T. Moyer

小笠原諸島,八重山諸島,沖縄,三宅島のクマノミの地理的変異を記載し,三宅島における,色彩と群内序列との関係を論じた.八重山の個体は,最も色彩の変異が激しいが,性差は顕著でない.沖縄の場場では、成熟雄は常に尾鰭がオレンジ色に縁取ら三宅島の個様尾では、中河の低い個体は雌雄共に,沖縄の職能と形のでは、佐田の低い個体は雌雄共に,沖縄の職能と発生を腹壁は強した。 唯一也となる。 三半数 個質が高く,体側の縞模様が狭い.小笠原では黒化個体が高く,体側の縞模様が狭い.小笠原では黒化個ケが高く,体側の縞模様が、黒化個体は Radianthus 属のイソギンチャクに住む・沖縄と三宅島のハタゴイソギンチャクに住むクマノミも暗色である.

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