

High mobility of the protandrous anemonefish *Amphiprion frenatus*: nonrandom pair formation in limited shelter space

Akihisa Hattori[✉]

Faculty of Liberal Arts and Education, Shiga University, 2-5-1 Hiratsu, Otsu, Shiga 520-0862, Japan
(e-mail: hattori@sue.shiga-u.ac.jp)

Received: February 16, 2004 / Revised: October 20, 2004 / Accepted: October 26, 2004

Ichthyological Research

©The Ichthyological Society of Japan 2005

Ichthyol Res (2005) 52: 57–63
DOI 10.1007/s10228-004-0253-3

Abstract Protandry in anemonefishes has been attributed to random pair formation, which results from their limited mobility after random recruitment to isolated host anemones. The recruitment and movement of the anemonefish *Amphiprion frenatus* were investigated in relation to its group structure and the spatial distribution of its host anemone on a coral reef, where it inhabits isolated single hosts and interhost movement is rare. A juvenile tended to be recruited to a host from which a former resident(s) had disappeared, indicating that larval recruitment is not random. After mass bleaching of corals during which many hosts died, a quarter of adults moved between hosts on average 42 m in 3 weeks, indicating that their mobility is potentially high. The few migrations under normal conditions were probably due to the low benefit of movements. Even after the movements, a female was much larger than her mate in a host, and a large female tended to pair with a large male. Although body size of females was positively correlated with their host size, that of males was not. It is suggested that the size of a single host does not allow the coexistence of two or more large fish, and the size composition of each pair is affected by the host size. Protandry in the monogamous fish may be attributed to the nonrandom pair formation in the limited space of a host.

Key words Coral reef fish · Microhabitat structure · Movement · Recruitment · Sex change

Sequential hermaphroditism (sex change) is widely known in teleost fishes (e.g., Charnov, 1982; Warner, 1984). If the expected reproductive success (the number of viable offspring produced) differs between the sexes with body size, an individual that can change sex at the proper size will have more offspring than one that remains exclusively male or female (Ghiselin, 1969; Warner, 1975, 1988a,b; Charnov, 1982). This size-advantage model predicts that the direction of sex change in a species depends on its mating system. Sex change from female to male (protogyny) has been found in species with polygynous mating systems, in which larger males can monopolize mating opportunities and the expected reproductive success of males will increase rapidly with increasing body size much more than that of females (Charnov, 1982; Warner, 1984, 1988a,b; Kuwamura and Nakashima, 1998). Another type of sex change, from male to female (protandry), is expected to be found in species with mating systems in which the expected reproductive success of females increases with increasing body size, whereas that of males is less sensitive to their body size (Ghiselin, 1969; Warner, 1975, 1988a,b; Charnov, 1982). For example, in mating systems where random mating occurs, the expected reproductive success of males would be less sensitive to their body size than that of females, partly because large males cannot monopolize mating opportunities (Warner, 1984). However, little information is available on the mating systems of protandrous fishes except anemonefishes (genus *Amphiprion*) (Charnov, 1982;

Warner, 1988a,b; Shapiro, 1992; but see Shinomiya et al., 2003).

Anemonefishes are known for socially controlled protandry with a monogamous mating system and symbiotic association with sea anemones (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a,b; Fricke, 1979). They inhabit a single host anemone or colonial hosts, which are essential resources for their shelter and spawning sites (Allen, 1972). In a place where individuals inhabit an isolated single host, they usually form an isolated social group that consists of a breeding pair and a varying number of nonbreeders (Allen, 1972; Fautin and Allen, 1992; Hattori, 2000, 2002; Buston, 2003a,b). When a female disappears from a pair, protandrous sex change allows an easy pair formation and the sex change guarantees female to the largest member, which provides both members of the pair with higher fecundity (Fricke and Fricke, 1977; Warner, 1984, 1988a,b). The pair formation has often been regarded as a random event, because larval recruitment to an isolate single host is considered to be random and interhost movement after recruitment is highly limited (Fricke and Fricke, 1977; Kuwamura, 1988; Kuwamura and Nakashima, 1998). Accordingly, protandry in anemonefishes has often been attributed to the resultant random pair formation (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Warner, 1984, 1988a,b; Kuwamura, 1988; Kuwamura and Nakashima, 1998). However, the exact process of pair formation as well as juvenile recruitment process has not been studied in

anemonefishes inhabiting isolated single hosts. If the mobility of such anemonefishes is higher than it was believed so far, their pair formation might not be random.

In several species of anemonefishes that inhabit colonial hosts or high-density hosts, the process of pair formation has been well studied (Ross, 1978a,b; Fricke, 1979; Moyer, 1980; Ochi, 1989a,b; Hattori and Yanagisawa, 1991a,b; Hattori, 1994; Hirose 1995; Hattori and Yamamura, 1995). For instance, *Amphiprion clarkii* in habitats of high host density often moves between hosts, and the adult pair is formed size-assortatively (Moyer, 1980; Ochi, 1989a,b; Hattori and Yanagisawa, 1991a,b). Hattori and Yamamura (1995) suggested that protandry in the mobile anemonefish is maintained as an adaptive strategy for acquisition of breeding post. Thus, protandry in anemonefishes that frequently move between hosts may be common.

Amphiprion frenatus is a common anemonefish on coral reefs, Okinawa Islands, Japan (Allen, 1972; Moyer and Nakazono, 1978). At Sesoko Island in the Okinawa Islands, the host anemones are sparsely distributed, and *A. frenatus* inhabits isolated single hosts (Hattori, 1991; Hirose, 1995). Hattori (1991) observed that only 1 of 103 marked individuals moved between hosts during a 5-month study period. After mate loss caused by a removal experiment (Hattori, 1991) or typhoon events (Hirose, 1995), however, several adults moved to pair with new mates, indicating that the anemonefish can move between isolated single hosts under some conditions. In August 1998, mass bleaching of corals occurred in many coral reefs throughout the world (Glynn et al., 2001). One year later, many adults of *A. frenatus* moved between hosts at Sesoko Island in response to disappearance and weakening of the hosts. I observed interhost movements of marked individuals and analyzed the process of pair formation. I also reanalyzed the data on the juvenile recruitment pattern and group composition of *A. frenatus* before the occurrence of coral bleaching (Hattori, 1991). The aim of the present study is to reexamine the pattern of pair formation including juvenile recruitment in the sedentary and protandrous anemonefish.

Materials and Methods

The field study was conducted in 1988, 1999, and 2000 on a fringing reef in front of Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus at Sesoko Island (26°37'48" N; 127°52'2" E), Okinawa, Japan, where Hirose (1985) studied the distribution and abundance of host sea anemones in 1981–1983. *Amphiprion frenatus* inhabited the host anemone, *Entacmaea quadricolor*. Although *E. quadricolor* often forms large colonies in coral lagoons (Allen, 1972; Moyer and Nakazono, 1978; Dunn, 1981), it never forms a colony in the coral reef of Sesoko Island (Moyer and Nakazono, 1978; Hirose, 1985; Hattori, 1991).

Field observations were carried out for 5 months from June to November 1988 (see Hattori, 1991), for 3 weeks from June to July 1999, and for 2 weeks from June to July 2000. A map of the study area (87 m × 373 m) was made

with the aid of enlarged aerial photographs and underwater observations. Locations of hosts were plotted on the map, and the long and short axial lengths of each host were measured twice in August 1988, July 1999, and July 2000. The area covered by the tentacles of each host was regarded as an oval and was estimated as (long axial length) × (short axial length) × $\pi/4$ (see Hirose, 1985; Hattori, 1991, 1995). The larger of the two calculates was used as an index of a host size. Three hosts that were closely distributed near each other with about 0.5-m distance were regarded as one host, where *A. frenatus* moved freely among them (Hattori, 1991). Because the anemones rarely changed their location in this study area (Hirose, 1985, Hattori, 1991), hosts were individually recognized by their locations on the map. Their ages in 1999 and 2000 and the number of recruits in 1988 were estimated comparing with the spatial distribution of *E. quadricolor* shown in Hirose (1985: fig. 2).

All individuals of *A. frenatus* were captured with hand nets, and their standard lengths (SL) were measured underwater in the beginning of each study period. Individuals in a group were called alpha-, beta-, and gamma-individuals, according to the body size rank order. All individuals larger than 20 mm SL in 1988 and those larger than 25 mm SL in 1999 and 2000 were marked by injecting acrylic paint under the skin. At the end of each study period, the number of anemonefish on each host was counted. Individuals less than 25 mm SL were regarded as recruits, because all recruits (not migrants) after the removal of one or two adults from a group had been less than 25 mm SL (Hattori, 1991). During each study period, I checked disappearance and migration of the marked fish every 4 days in 1988 and every day in both 1999 and 2000. When I found a swimming fish between hosts, I chased it, keeping some distance (>2 m) away until it settled on a host, and recorded the swimming route and the number of agonistic interactions with other individuals. The agonistic interactions include rush, dorsal-leaning, ventral-leaning, and appeasement behavior such as head-standing, head-shaking, and substrate-biting (Yanagisawa and Ochi, 1986). The sizes of encountered individuals were estimated by underwater observation.

Results

Spatial distribution and size of hosts in 1988, 1999, and 2000. In 1988, 36 hosts with a total of 100 residents of *Amphiprion frenatus* (36 alpha, 36 beta, and 23 gamma individuals, and 5 other small fish) were sparsely distributed (Fig. 1). Comparing to Hirose (1985), at least 10 hosts were recruited and 10 hosts disappeared between 1983 and 1988. In 1999, after the bleaching event, at least 10 hosts had disappeared and 2 hosts were recruited: there were 28 hosts with 59 fish (28 alpha-, 23 beta-, and 8 gamma-individuals). Consequently, the nearest distance between host neighbors significantly increased after the bleaching event (1988: median = 7 m, range = 3–35 m, $n = 36$; 1999: median = 16 m, range = 3–35 m, $n = 28$; Mann–Whitney U test, $z = 2.86$, $P = 0.004$). In 2000, only 12 hosts with 15 fish (11 alpha- and 4 beta-individuals) were found: 5 hosts were

Table 1. Body size (mm standard length, SL) of alpha- and beta-individuals in 1988, 1999, and 2000

Size order	1988					1999 ^a					2000				
	<i>n</i>	Median	Range	<i>z</i>	<i>P</i>	<i>n</i>	Median	Range	<i>z</i>	<i>P</i>	<i>n</i>	Median	Range	<i>U</i>	<i>P</i>
Alpha	36	97	47–112			28	93	20–113			11	48	20–112		
Beta	36	55	20–77			23	58	20–76			4	33	20–49		
Mann–Whitney <i>U</i> test				6.6	<0.000001				5.4	<0.000001				12	>0.05

^aCoral bleaching occurred in 1998

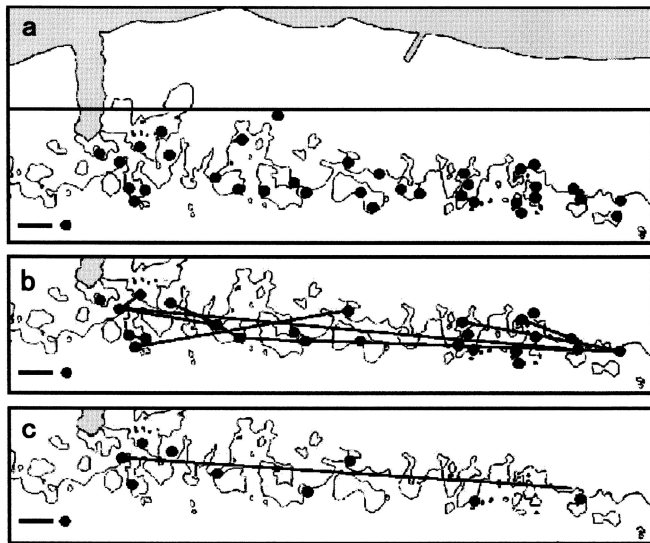


Fig. 1. Distribution of host anemone (*Entacmaea quadricolor*) of *Amphiprion frenatus* in 1988 **a**, 1999 **b**, and 2000 **c** at Sesoko Island, Okinawa, where coral bleaching occurred in 1998. *Square areas*, study area; *shaded area*, land. *Thin lines* indicate reef edges or patch reefs. *Solid circles*, location of host anemones; *straight lines*, fish movement between host anemones. *Bar* 10 m

estimated to be 12–17 years old and 6 were more than 17 years old. Host size in 1999 was significantly smaller than that in 1988 (Fig. 2; 1988: median = 577 cm², range = 30–1442 cm², *n* = 36; 1999: median = 308 cm², range = 13–180 cm², *n* = 28; Mann–Whitney *U* test, *z* = 3.4, *P* = 0.0005). There was no significant difference in host size between 1999 and 2000 (2000: median = 194 cm², range = 27–824 cm², *n* = 12; Mann–Whitney *U* test, *z* = 0.17, *P* > 0.05).

Anemonefish group composition and recruitment to host in 1988, 1999, and 2000. Alpha-individuals were much larger than beta-individuals in 1988 and 1999 but not in 2000 (Table 1). Their body sizes in a pair were positively and significantly correlated in 1988 and 1999 (Fig. 3). The sum of body sizes of pair members in a host was positively and significantly correlated with their host sizes in all study years (Fig. 4). The sum of body sizes of all group members in a host was also significantly correlated with their host sizes in all study years (Spearman's correlation analysis:

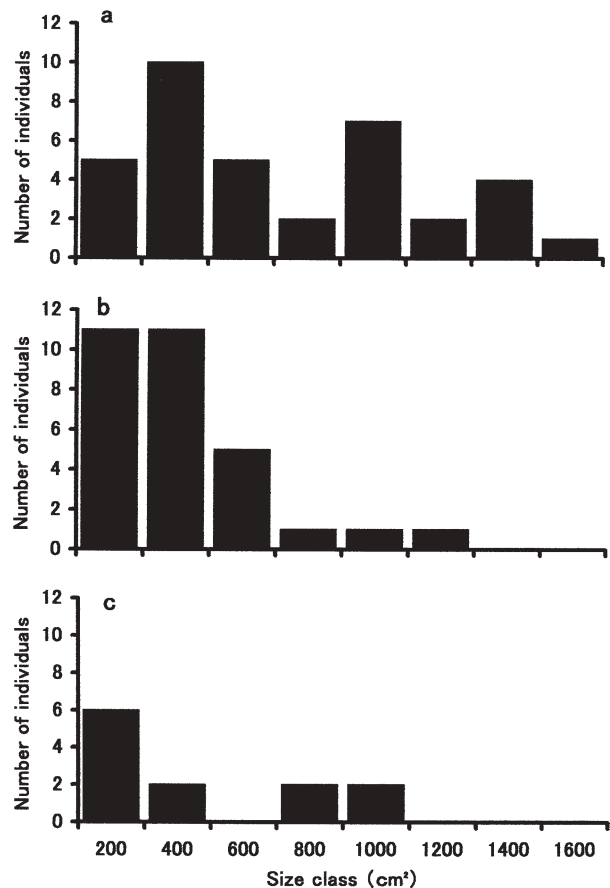


Fig. 2. Size-frequency distribution of host anemone (*Entacmaea quadricolor*) for *Amphiprion frenatus* in 1988 **a**, 1999 **b**, and 2000 **c**

1988: $r_s = 0.71$, *n* = 36, *P* = 0.00002; 1999: $r_s = 0.66$, *n* = 28, *P* = 0.0005; 2000: $r_s = 0.65$, *n* = 11, *P* = 0.029). Although the body sizes of alpha-individuals were significantly correlated with their host sizes in all study years (1988: $r_s = 0.71$, *n* = 36, *P* = 0.00002; 1999: $r_s = 0.67$, *n* = 28, *P* = 0.0004; 2000: $r_s = 0.75$, *n* = 11, *P* = 0.017), those of beta-individuals were not significantly correlated with their host sizes in 1999 and in 2000 (1988: $r_s = 0.65$, *n* = 36, *P* = 0.0001; 1999: $r_s = 0.28$, *n* = 22, *P* > 0.05; 2000: $r_s = 0.75$, *n* = 4, *P* > 0.05).

In 1988, 25 juveniles of *A. frenatus* were newly found on 36 hosts (per host, median = 1, range = 0–2). The number of recruits in a host was not correlated with the host

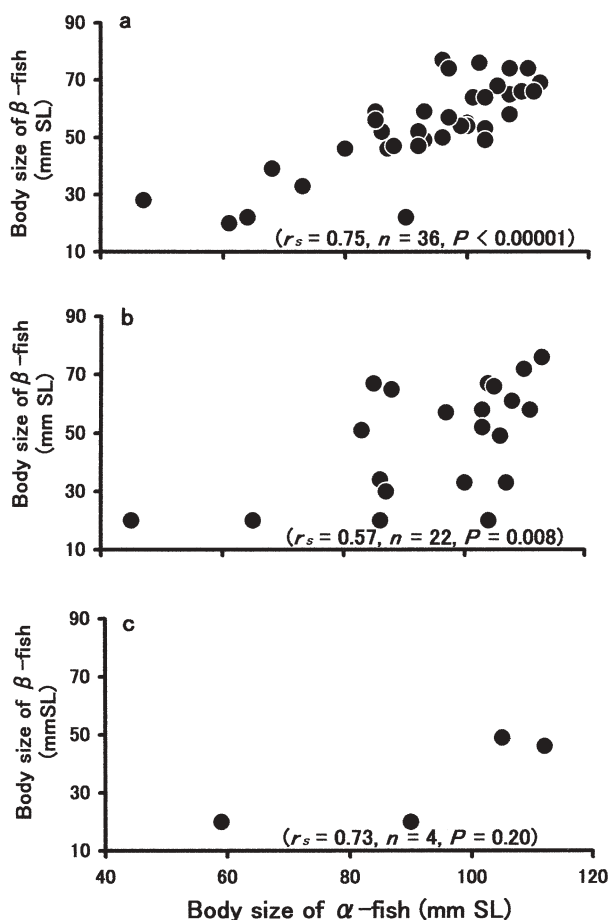


Fig. 3. Relationship between body size of alpha-individual and beta-individual in a group in 1988 **a**, 1999 **b**, and 2000 **c**. α , alpha; β , beta

size ($r_s = 0.16$, $n = 36$, $P > 0.05$) but was negatively correlated with the number of residents in the host ($r_s = -0.13$, $n = 36$, $P = 0.02$). The recruit number in a host was more significantly correlated with the number of group members that had disappeared from the host in the 5-month study period ($r_s = 0.66$, $n = 36$, $P = 0.001$). In 1999, 13 recruits were found on 28 hosts (per host, median = 0, range = 0–1), and the recruit number in a host was also negatively correlated with the number of residents in the host ($r_s = -0.51$, $n = 28$, $P = 0.024$). In 2000, however, the recruit number in a host was not correlated with that of residents in the host ($r_s = -0.206$, $n = 12$, $P > 0.05$): only 5 recruits were found on 12 hosts (per host, median = 0, range = 0–1, $n = 12$).

Anemonefish movement between hosts in 1988, 1999, and 2000. In 1988, only one alpha-individual (61 mm SL) moved between the nearest hosts (6 m apart) during 5 months (Hattori, 1991). In 1999, in contrast, 13 individuals moved 42 m on average during 3 weeks (median = 12 m, range = 3–195 m, $n = 13$); their movements were not limited to the nearest hosts (Fig. 1). In 2000, 1 alpha-individual (105 mm SL) moved between hosts with a distance of 239 m. In 1999, of the 13 migrants, 9 (69.2%) were alpha-

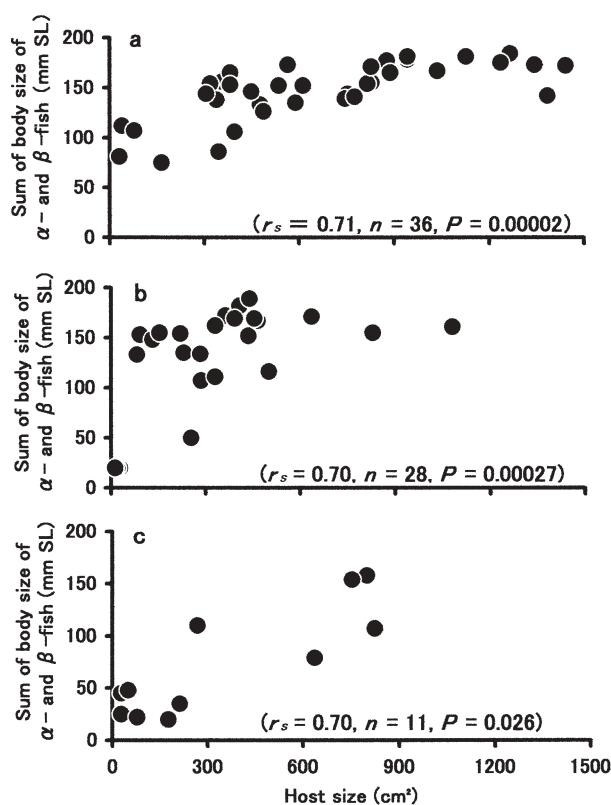


Fig. 4. Relationship between the sum of body sizes of alpha- and beta-individuals in a host and the host size in 1988 **a**, 1999 **b**, and 2000 **c**

individuals and 4 were beta-individuals; they were significantly larger than nonmigrants (migrants, median = 87 mm SL, range = 33–107 mm, $n = 13$; nonmigrants, median = 57 mm SL, range = 20–113 mm, $n = 49$; Mann–Whitney U test, $z = 2.6$, $P = 0.008$), and all migrants but 1 beta-individual (33 mm SL) were larger than the median of body size of beta-individuals (see Table 1). Excluding 1 case in which an alpha-migrant was replaced by a larger alpha-migrant, 8 alpha-migrants had smaller hosts before movements than nonmigrant alpha-individuals (hosts of migrants before movements: median = 259 cm², range = 82–566 cm², $n = 8$; hosts of nonmigrants: median = 408 cm², range = 154–1080 cm², $n = 13$, Mann–Whitney U test, $U = 22.5$, $P < 0.05$). There was no size difference between hosts used by alpha-migrants before (median = 286 cm², range = 82–501 cm², $n = 9$) and after (median = 330 cm², range = 92–829, $n = 9$) movements (Wilcoxon signed-ranks test, $z = 0.29$, $P > 0.05$). There was also no size difference in mates of alpha-migrants before (median = 20 mm SL, range = 20–65 mm, $n = 9$) and after (median = 49 mm SL, range = 20–65 mm, $n = 9$) movements (Wilcoxon signed-rank test, $z = 1.3$, $P > 0.05$). All four movements by beta-individuals occurred after the emigration of alpha-individuals.

In 1999, movements of three fish (70–90 mm SL) were directly observed. They were swimming at usual speed (Fig. 1). One of them moved a long distance (>150 m) in an hour,

Table 2. Number of aggressive behaviors of three migrants that were directly observed in 1999

Size of migrant	Observation time (min)	Number of encountered individuals		Number of aggressive interactions with encountered individual	
		Alpha (large)	Beta (small)	Alpha (large)	Beta (small)
Large	15	2	2	10	0
Large	60	8	9	23	0
Large	60	5	5	22	0

Size of fish is classified into large (≥ 70 mm SL) and small

visiting several hosts along the reef edges. They aggressively interacted with alpha-residents but never with beta-residents (Table 2).

Discussion

After the bleaching event, many anemones and most corals disappeared in the study site, and consequently potential refuges for *Amphiprion frenatus* decreased. Despite fewer refuges and lower host density, the anemonefish moved frequently between hosts, where their movements were not limited to neighbor hosts. Three migrants swam between isolated hosts, and one of them did so along the reef edges visiting several hosts. These results indicate that *A. frenatus* has enough motility to migrate between hosts.

Several authors suggest that a larger species of anemonefishes has higher mobility than smaller ones, and *A. frenatus* is one of the largest species (Allen, 1972; Fautin and Allen, 1992; Hirose, 1995). In this study, large individuals of *A. frenatus* tended to move between hosts. After mate loss by a female removal experiment (Hattori, 1991) or by typhoon attacks (Hirose, 1995), only large fish moved. In another large species of anemonefishes (*A. clarkii*), in contrast, small individuals move between hosts in spite of their putative lower mobility (Hattori, 1994, 1995, 2002). They often move to small hosts, because their growth and maturation are suppressed by cohabiting adults, which usually inhabit large hosts. In *A. frenatus*, adults also controlled the growth and maturation of subordinates (Hattori, 1991), but there were few newly settled small hosts to which the subordinates could escape. It is likely that the population dynamics of host anemones affect the interhost movement pattern of a large anemonefish. In the present study site, 23 hosts of *A. clarkii* were recruited in a year, and 2 of 71 hosts (2.8%) were more than 17 years old (Hattori, 2002). In contrast, no hosts of *A. frenatus* were recruited in a year (Hattori, 1991) and 6 of 26 hosts (23%) were more than 17 years old in 2000. Few migrants of *A. frenatus* before the occurrence of the coral bleaching may be related to few recruitments and high longevity of its hosts. Host size of *A. frenatus* in 1999–2000 was much smaller than that in 1988, and almost all alpha-migrants inhabited smaller hosts before movements than nonmigrant alpha-fish. The emigration of alpha-individuals after the bleaching event was probably due to the weakening or deterioration of the host.

In this study site, body sizes of males and females in pairs of *A. frenatus* were positively correlated before the bleaching event (Hattori, 1991; Hirose, 1995). Hirose (1995) implied that adults often move to replace or take over a member of a pair, and consequently they pair size-assortatively. In fact, however, *A. frenatus* rarely moved between hosts before the bleaching event, and replacement or taking over a member of a pair was rare (Hattori, 1991). Because a female *A. frenatus* strongly suppresses the growth of her mate, the male's body size cannot catch up the female's body size. This growth suppression is attributed to a long-term pair bonding (Hattori, 1991), and consequently body sizes of males and females were highly correlated.

Even after the movement of *A. frenatus* in 1999, alpha-individuals were much larger than beta-individuals, and their body sizes in pairs were positively correlated. Buston (2003b) suggests that in anemonefishes the growth modification of subordinates in a group is their strategy to coexist with the dominant fish. It is likely that the presence of two large fish with similar body sizes in an isolated single host exposes the smaller one to danger because of the limited host space. Actually, forcible pairing of females with similar body sizes always results in death or severe injury of the smaller one (Fricke and Fricke, 1977; Kuwamura and Nakashima, 1998). In this study site, large migrants of *A. frenatus* aggressively interacted with only large residents. After the movements, the sum of body sizes of pair members was still significantly correlated with their host size. Although the body sizes of alpha-individuals were correlated with their host size, those of beta-individuals were not correlated. These results suggest that the size of a host cannot allow the coexistence of two or more large fish, and the size composition of each pair is affected by the host size.

In anemonefishes, regardless of group size, the two largest individuals can reproduce and control the maturation and growth of subordinates: after the disappearance of a reproductive fish, a largest subordinate becomes a new adult (Allen, 1972; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978b; Fricke, 1979). If a juvenile is recruited to so small a host that harbors only one fish, it will have to wait for a long time to reproduce because a full-grown host is necessary for reproduction (Allen, 1972). If the juvenile is recruited to a full-grown host that harbors three or more fish, it will also have to wait for a long time to be an adult because its growth and maturation are suppressed by adults.

Accordingly, juvenile recruitment tactics may not be simply dependent on the host size. In fact, there was no significant relationship between recruit number and host size in *A. frenatus*. However, the recruit number was negatively correlated with the group size and positively correlated with the number of residents that had disappeared recently. Anemonefish settlers cannot discriminate between hosts with and without conspecific inhabitants (Elliott et al., 1995; Elliott and Mariscal, 2001), and randomly settled juveniles might have been chased out by the residents from a host that has no sufficient shelter space. It is suggested that randomly settled juveniles of *Amphiprion percula* are chased out by the residents from a host without sufficient space (Buston, 2003a). In the small damselfishes (genus *Dascyllus*) that inhabit branching corals and sea anemones, newly settled juveniles are chased out by the residents when their host has no sufficient shelter space (Schmitt and Holbrook, 1999), and the small juveniles tend to live in risky areas in a branching coral as a result of intraspecific competition for shelter space (Holbrook and Schmitt, 2002). Juvenile settlement in *A. frenatus* might be random but their recruitment was not random: it could be affected by the number and body size of residents and host size itself because of the competition for limited shelter space.

According to the size-advantage model (Ghiselin, 1969; Warner, 1975, 1988a,b; Charnov, 1982), protandry is expected to be found in species with mating systems in which the expected reproductive success via female function will increase more with body size than that via male function. In a social system where limited shelter space determines the total biomass of all group members, the expected reproductive success via male function will not increase with the increasing body size because the growth of a male retards the growth of females and the reproductive success of a male depends on the sum of the body size of females in the group. In *A. frenatus*, a host harbored a large fish and two small subordinates but never allowed the coexistence of two or more large fish. If *A. frenatus* were polygynous, the expected reproductive success of males could not increase with their body size. Its protandry may be attributed to a social system in which limited shelter space determines the total biomass of all group members. Further field study is needed to know whether the volume of a shelter space (host anemone) determines the total biomass of group members, and theoretical study is also necessary to clarify the relationship between the expected reproductive success of males in an imaginary polygynous mating system and their body sizes in various host sizes.

Acknowledgments I am grateful to Y. Yanagisawa, T. Kuwamura, G. Rosenqvist, M. Kobayashi, M. Migita, S. Sano, and Y. Mizukami for their valuable advice on the manuscript. Thanks go to K. Sakai, Y. Nakano, and other members of Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, for providing facilities during the investigation. This work was supported in part by a Grant-in-Aid for Science Research from the Japan Ministry of Education, Science, Culture, and Sports (No. 08780149). The author is a Guest Scientist at the Center for Ecological Research, Kyoto University. This study was conducted in compliance with the current laws of Japan, where the study was performed.

Literature Cited

- Allen GR (1972) Anemonefishes: their classification and biology. TFH, Neptune City
- Buston P (2003a) Forcible eviction and prevention of recruitment in the clown anemonefish. *Behav Ecol* 14:576–582
- Buston P (2003b) Size and growth modification in clownfish: sex change is not the only way these fish achieve dominance—they grow into the role. *Nature (Lond)* 424:145–146
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton
- Dunn DF (1981) The clownfish sea anemones: Stichodactylidae (Coelenterata: Actiniaria) and other sea anemones symbiotic with pomacentrid fishes. *Trans Am Philos Soc* 71:1–115
- Elliott JK, Mariscal RN (2001) Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Mar Biol* 138:23–36
- Elliott JK, Elliott JM, Mariscal RN (1995) Host selection, location, and association behaviors of anemonefishes in field settlement experiment. *Mar Biol* 122:377–389
- Fautin DG, Allen GR (1992) Anemonefishes and their host sea anemones. Western Australian Museum, Perth
- Fricke HW (1979) Mating system, resource defense and sex change in the anemonefish *Amphiprion akallopisos*. *Z Tierpsychol* 50:313–326
- Fricke HW, Fricke S (1977) Monogamy and sex change by aggressive dominance in coral reef fish. *Nature (Lond)* 266:830–832
- Ghiselin MT (1969) The evolution of hermaphroditism among animals. *Q Rev Biol* 44:189–208
- Glynn PW, Mate JL, Baker AC, Calderon MO (2001) Coral bleaching and mortality in Panama and Ecuador during the 1977–1998 El Niño-southern oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull Mar Sci* 69:79–109
- Hattori A (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Jpn J Ichthyol* 38:165–177
- Hattori A (1994) Inter-group movement and mate acquisition tactics of the protandrous anemonefish, *Amphiprion clarkii*, on a coral reef, Okinawa. *Jpn J Ichthyol* 41:159–165
- Hattori A (1995) Coexistence of two anemonefish, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone. *Environ Biol Fishes* 42:345–353
- Hattori A (2000) Social and mating systems of the protandrous anemonefish *Amphiprion perideraion* under the influence of a larger congener. *Aust Ecol* 25:187–192
- Hattori A (2002) Small and large anemonefishes can coexist using the same patchy resources on a coral reef, before habitat destruction. *J Anim Ecol* 71:824–831
- Hattori A, Yamamura N (1995) Co-existence of subadult males and females as alternative tactics of breeding post acquisition in a monogamous and protandrous anemonefish. *Evol Ecol* 9:292–303
- Hattori A, Yanagisawa Y (1991a) Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environ Biol Fishes* 31:139–155
- Hattori A, Yanagisawa Y (1991b) Sex change of the anemonefish, *Amphiprion clarkii*, in a habitat of high host density: a removal study (in Japanese with English summary). *Jpn J Ecol* 41:1–8
- Hirose Y (1985) Habitat, distribution and abundance of coral reef sea-anemones (Actiniidae and Stichodactylidae) in Sesoko Island, Okinawa, with notes of expansion and contraction behavior. *Galaxea* 4:113–127

- Hirose Y (1995) Pattern of pair formation in protandrous anemonefishes, *Amphiprion clarkii*, *A. frenatus* and *A. perideraion*, on coral reefs of Okinawa, Japan. *Environ Biol Fishes* 43:153–161
- Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868
- Kuwamura T (1988) Sakana no kosodate to shakai: darega kosodate subekika (in Japanese). Kaimeisha, Tokyo
- Kuwamura T, Nakashima Y (1998) New aspects of sex change among reef fishes: recent studies in Japan. *Environ Biol Fishes* 52:125–135
- Moyer JT (1980) Influence of temperate waters on behaviour of the tropical anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. *Bull Mar Sci* 30:261–272
- Moyer JT, Nakazono A (1978) Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. *Jpn J Ichthyol* 25:101–106
- Ochi H (1989a) Mating behavior and sex change of the anemonefish *Amphiprion clarkii* in the temperate waters of southern Japan. *Environ Biol Fishes* 26:257–275
- Ochi H (1989b) Acquisition of breeding space by nonbreeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. *Ethology* 83:279–294
- Ross RM (1978a) Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. *Copeia* 1978:103–107
- Ross RM (1978b) Territorial behavior and ecology of the anemonefish *Amphiprion melanopus* on Guam. *Z Tierpsychol* 46:71–83
- Schmitt RJ, Holbrook SJ (1999) Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. *Oecologia (Berl)* 118:76–86
- Shapiro DY (1992) Plasticity of gonadal development and protandry in fishes. *J Exp Zool* 261:194–203
- Shinomiya A, Yamada M, Sunobe T (2003) Mating system and protandrous sex change in the lizard flathead, *Inegocia japonica* (Platycephalidae). *Ichthyol Res* 50:383–386
- Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. *Am Nat* 109:61–82
- Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. *Am Sci* 72:128–136
- Warner RR (1988a) Sex change in fishes: hypotheses, evidence, and objections. *Environ Biol Fishes* 22:81–90
- Warner RR (1988b) Sex change and size-advantage model. *Trends Ecol Evol (TREE)* 3:133–136
- Yanagisawa Y, Ochi H (1986) Step-fathering in the anemonefish *Amphiprion clarkii*: a removal study. *Anim Behav* 35:1769–1780