

Small and large anemonefishes can coexist using the same patchy resources on a coral reef, before habitat destruction

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Summary

1. According to meta-population models, a superior competitor and a superior disperser can coexist in a patchy environment. The two anemonefishes, a large aggressive *Amphiprion clarkii* Bennett and a small less-aggressive *A. perideraion* Bleeker, use the same host anemone *Heteractis crista* Ehrenberg on a coral reef, Okinawa, Japan, where most of the hosts disappeared after the coral bleaching in 1998. Their microhabitat (host) use and coexistence, and the quality and quantity of microhabitats were investigated in 1988, 1989, 1999 and 2000 on the coral reef. Their interspecific interaction was also examined.

2. Before the habitat destruction, the two species coexisted. Although *A. clarkii* was behaviourally dominant over *A. perideraion* in a cohabiting group, *A. perideraion* was a superior competitor in terms of site displacement, because *A. perideraion* could displace a microhabitat. Adult *A. clarkii* emigrated from a cohabiting group probably due to the high cost of interactions with adult *A. perideraion*. Although it is easier to defend a small area for a larger species, sharing a host with adult *A. perideraion* may not pay for *A. clarkii* because *A. clarkii* needs a larger area.

3. *A. clarkii* was not only a superior disperser, which was able to find a vacated host, but also a pioneer species that was able to use newly settled small hosts. Larval *A. clarkii* settled on such a small host because they were able to move to larger hosts for future reproduction, while *A. perideraion* did not settle on a small host because of low mobility after settlement. Microhabitat (host) with various sizes might have promoted their coexistence.

4. After the habitat destruction, the superior competitor *A. perideraion* went extinct locally due probably to lack of small host utilization ability. The present study implies that the difference in body size between the two competitors plays an important role in their coexistence, because species with different body sizes can have different mobility and require different amounts of resources.

Key-words: body size, dispersal-competition trade-off, larval settlement tactics, microhabitat use, reproductive strategies.

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Introduction

According to meta-population models, two or more species that require a similar living space can coexist stably in a patchy environment, if they show an interspecific trade-off between dispersal (= colonization) ability and competitive ability (Tilman & Kareiva 1997). For instance, sessile organisms such as terrestrial plants compete severely for living space, and many species

coexist stably in a certain space: their coexistence is often attributed to the fact that less good competitors have better dispersal abilities so that their offspring can easily find unoccupied space that is caused by the death of individuals (Tilman 1994; Lehman & Tilman 1997). The dispersal-competition trade-off in terrestrial plants has sometimes been interpreted in terms of simple energy allocation such as seeds vs. roots: more energy to seeds means more seeds or longer-lived large seeds, that makes a better disperser, and more energy to roots means better nutrient acquisition, that makes a better competitor at a nutrient-limited site (Tilman 1994; Lehman & Tilman 1997). The coexistence mechanism of motile animals such as fish may be more complicated.

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The meta-population models also predict that competitively dominant species tend to go extinct locally after serious habitat destruction because they are less good dispersers (Tilman & Lehman 1997; Tilman, Lehman & Yin 1997). Although intermediate disturbance often makes possible multispecies coexistence by reducing the abundance of superior competitors and allowing inferior competitors to persist (Connell 1978; Syms & Jones 2000), a high level of disturbance or serious habitat loss that decreases species richness, would cause the local extinction of superior competitors first. This prediction from the meta-population models has not been well tested, possibly because it is difficult to conduct large-scale habitat destruction experimentally in the field.

A coral reef fish community is one of the richest animal communities in the world and many ecologically similar fishes coexist in a similar living space (Sale 1991). In addition, recent human activities and climate warming destroy various fish habitats on coral reefs in various levels (Roberts *et al.* 2002), which may provide us with opportunities to study changes of fish community structure after various levels of habitat destruction. Little is known about the processes of the local fish extinction after serious habitat destruction, although effects of intermediate disturbance on the local fish community were well-studied both empirically and experimentally (e.g. Jones & Syms 1998; Syms & Jones 2000).

All species of coral reef fishes have dispersal larval phases, and numerous studies have emphasized that random recruitment from drifting larvae is the crucial determinant for coexistence of competing fishes that live in a similar habitat (Sale 1978, 1980; Chesson & Warner 1981; Shpigel 1982; Chesson 1986). For example, many small territorial damselfishes coexist on a small patch reef in a coral reef lagoon. It is hypothesized that once a site on the reef becomes available after the loss of a territory holder, the species of a fish that settles there is determined by random recruitment (Sale 1978). However, recent studies have also revealed that a fish community is organized by a combination of the following factors: random recruitment, subsequent migration and interspecific competition within a habitat (Jones 1991; Williams 1991; Ault & Johnson 1998; Booth & Wellington 1998; Schmitt & Holbrook 2000; Syms & Jones 2000). Furthermore, larval settlement is not always random (Leis 1991; Victor 1991). Even in a stochastic recruitment system, species with large body size can be a superior disperser because larger body size usually means higher fecundity in fish. Large body size itself might involve being migratory. Because body size is often an important factor for interspecific behavioural dominance in a local fish assemblage consisting of ecologically similar species, a larger species is usually a superior competitor (Robertson 1996, 1998). Few studies have examined whether a dispersal-competition trade-off between coexisting species that require a similar living space applies to coral reef fishes.

Anemonefishes (genus *Amphiprion*, Pomacentridae) are small territorial damselfishes, mainly inhabiting coral reef regions, and always live on or around the host anemones that are an essential resource for their shelter and spawning sites (Allen 1972). Consequently, distribution patterns of host (microhabitat) are the crucial determinant of their social and mating systems (Fricke & Fricke 1977; Ross 1978a; Fricke 1979; Moyer 1980; Yanagisawa & Ochi 1986; Ochi 1989a) and also influence the pattern of their sexual maturation and reproductive tactics (Ochi 1989a,b; Hattori & Yanagisawa 1991a,b; Hattori 1991, 1994; Hattori & Yamamura 1995). Two or more anemonefishes often use the same anemone species as their hosts in a coral reef (Allen 1972), especially in a large barrier reef, where they usually have different distribution patterns among zones such as inner reef flat, mid-lagoon and outer reef slope (Fautin 1986; Elliott & Mariscal 2001). Within a zone, each species usually inhabits one species of host anemones (Fautin 1986; Elliott & Mariscal 2001). Planktonic larvae of each species usually show a clear host selection under natural and experimental conditions (Miyagawa 1989; Elliott, Elliott & Mariscal 1995; Elliott & Mariscal 2001).

In small fringing reefs of Okinawa Islands, Japan, however, *Amphiprion perideraion* Bleeker and *Amphiprion clarkii* Bennett inhabit the same anemone *Heteractis crispa* Ehrenberg within a zone (Moyer 1976; Moyer & Nakazono 1978), where adult *A. clarkii* are approximately twice as large as adult *A. perideraion* (Hattori 1995; Hirose 1995). In a cohabiting group, *A. clarkii* suppresses the growth and reproduction of *A. perideraion* (Hattori 1995). While *A. perideraion* inhabits only a large host but cannot reproduce under the presence of *A. clarkii*, *A. clarkii* inhabits a host of any size and can reproduce under the presence of *A. perideraion* but cannot reproduce at a small host. The two species have similar mortality rates and seem to coexist stably (Hattori 1995). Because *A. clarkii* does not prevent *A. perideraion* from settling, *A. perideraion* is allowed to settle on any large hosts. In contrast, *A. clarkii* settles on hosts of any size, but cannot do so on the large hosts that adult *A. perideraion* inhabits because adult *A. perideraion* prevents *A. clarkii* from settling (Hattori 1995). Hattori (1995) suggests that their different recruitment pattern prevent the exclusion of either species from the area. However, *A. clarkii* seems to be a superior competitor and also a superior disperser: adult *A. clarkii* is much larger and more behaviourally aggressive, and more motile than adult *A. perideraion* (Hattori 1995; Hirose 1995). In order to understand the coexistence mechanism of territorial reef fishes that require a similar living space, I examined the pattern of host use by the two anemonefishes and analysed their behavioural interactions, especially from the viewpoint of dispersal-competition trade-off.

In August 1998, mass bleaching occurred in many coral reefs throughout the world because of unusual high water temperature (Glynn *et al.* 2001), which

caused serious habitat destruction for many coral reef fishes including anemonefishes. Although it was not experimentally induced habitat destruction, the local extinction process is described of the two anemonefishes after the large scaled destruction of their natural habitat: data on their numbers and host utilization pattern as well as the quality and quantity of remaining hosts were taken in the large study site (87 m × 373 m). The aim of the present study is to understand the relative importance of larval settlement, subsequent migration and interspecific competition on a competing and coexisting coral reef fishes that require the same microhabitat.

Materials and methods

The field research was conducted in 1988, 1989, 1999 and 2000 on a fringing reef in front of Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus at Sesoko Island (26°39'N; 127°57'E), Okinawa, Japan, where Hirose (1985) studied the distribution and abundance of sea anemones from 1981 to 1983. Species of sea anemones were identified after Dunn (1981). A map was made of the study area (87 m × 373 m) based on an enlarged aerial photograph and underwater observations. Almost all the *A. clarkii* and *A. perideraion* inhabited the anemone *Heteractis crispa* (known previously as *Radianthus kuekenthali* Kwietniewski). The three small *Heteractis aurora* (Quoy and Gaimard, known previously as *Radianthus simplex* Haddon et Shackleton), which were inhabited by juvenile *A. clarkii*, were excluded from the data analysis (see Hattori 1995). Locations of the host anemone *H. crispa* were plotted on the map, and the long and short axial lengths of each host were measured twice within a month of each study period: August 1988 and 1989, and July 1999 and 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 1994, 1995, 2000). The larger of the two measurements was used as an index of the size of a host. Unlike my previous studies, neighbouring hosts within 0.6 m were regarded as one host because both anemonefishes used such hosts as if they were one host (Hattori 1994, 1995, 2000). One host was regarded as a microhabitat. Species and the number of anemonefish living around each host were recorded, and hosts were classified into three types based on their inhabitants: *A. clarkii*, *A. perideraion* and both species. Host anemones were individually recognized by their location and were compared with the spatial distribution of *H. crispa* shown in Fig. 2d of Hirose (1985): the longevity of some *H. crispa* and annual disappearance rates of *H. crispa* were estimated.

All individuals of the two anemonefishes larger than 25 mm in standard length (SL) were captured with hand nets and marked by injecting acrylic paint under the skin. Their standard lengths were measured in June of each study year. Other individuals were regarded

as newly settled juveniles (recruits). In 1988, agonistic behaviour was recorded (rushing, dorsal leaning and ventral leaning), as was appeasement behaviour (head standing, head shaking and substrate biting) (see Yanagisawa & Ochi 1986) of each fish larger than 50 mm SL (*A. clarkii*) and 20 mm SL (*A. perideraion*), for 15 min at least once from July to November (Hattori 1995). Social groups of each species were classified into four group types: (1) adult pair group consisting of one adult pair and a varying number of subadults and juveniles, (2) one-adult group consisting of one adult and a varying number of juveniles, (3) subadult group consisting of one or two subadults and juveniles and (4) juvenile group (Hattori 1994, 2000). The sexual state of each fish was estimated by its caudal fin coloration (Hattori 1994, 2000) and conspecific individuals in a social group were called alpha-, beta- and gamma-fish, according to the body size order. Alpha- and beta-fish in an adult pair group were always female and male, respectively, because of the protandrous sex change (Hattori 1994, 2000).

Results

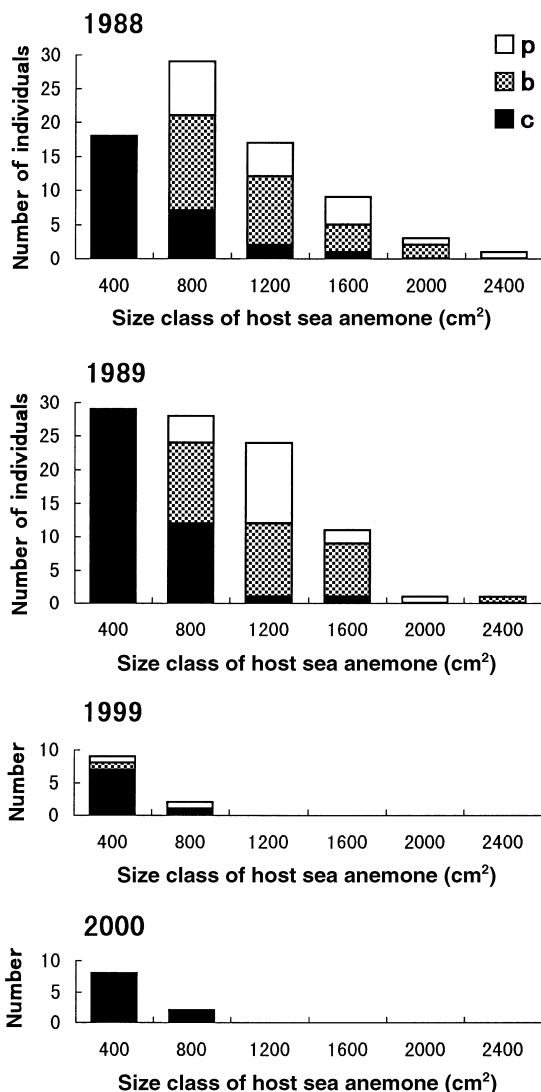
MICROHABITAT USE BEFORE CORAL BLEACHING

From 1988 to 1989, on average, there were 86 microhabitats (hosts) with 140 individuals of *A. clarkii* (50 adults, 20 subadults and 70 juveniles) and 80 individuals of *A. perideraion* (35 adults, 39 subadults and six juveniles) (see Hattori 1995). Comparing the data of Hirose (1985), at least 22 hosts had been newly settled and 17 hosts had disappeared from 1983 to 1988 (Table 1). In 1988 only *A. clarkii*, *A. perideraion* and both species used 35.5%, 25.0% and 39.5% of host anemones, respectively ($n = 76$), and in 1989, only *A. clarkii*, *A. perideraion* and both used 46.8%, 19.8% and 33.3%, respectively ($n = 96$) (Fig. 1). There was no significant difference in the ratio of the three host types between the two years ($\chi^2 = 2.26$, $P = 0.32$). All small hosts less than 400 cm² were inhabited by only *A. clarkii* (Hattori 1995). Out of 17 such small hosts in 1988, two disappeared within a year, and of the other 59 hosts, one disappeared. There was no significant difference in the annual rate of host disappearance between the two size categories (Fisher's exact probability test, $P = 0.123$).

From 1988 to 1989, 73 identical hosts were observed (Table 2). Of the 73 hosts, eight (11.1%) changed host type. There was no significant difference in size between hosts that only *A. perideraion* inhabited in the period and hosts that both species inhabited (Mann-Whitney *U*-test, $Z = 0.85$, $P > 0.05$). However, hosts that only *A. clarkii* inhabited in 1988 and juvenile *A. perideraion*, newly found in 1989, were significantly larger than those that only *A. clarkii* inhabited from 1988 to 1989 (Table 2, Mann-Whitney *U*-test, $Z = 2.0$, $P = 0.04$), indicating that juvenile *A. perideraion* had preferred large hosts at the time of settlement.

Table 1. Change of number of individually recognized host anemones and their disappearance rate per year. Disappearance rate of hosts that existed in 1983 is also shown. See text for details

	1983	1988	1989	1999	2000
Number of observed hosts	71	76	96	11	9
Newly found hosts	–	22	23	0	6
Survivors	–	54	73	11	3
Disappeared hosts	–	17	3	85	8
Disappearance rate per year (%)	–	4.8	3.9	8.9	72.7
Hosts that existed in 1983	71	54	52	6	2
Disappeared hosts	–	17	2	46	4
Disappearance rate of the hosts per year (%)	–	4.8	3.7	8.8	66.7

**Fig. 1.** Size–frequency distributions of host anemones *Heteractis crispa* before (1988 and 1989) and after (1999 and 2000) the coral bleaching in 1988, in relation to their inhabitants: only *A. clarkii* (c), only *A. perideraion* (p) and both species (b).**MICROHABITAT USE AFTER CORAL BLEACHING**

After the coral bleaching, the number of host anemones decreased greatly (Table 1): there were only 10

hosts, on average, from 1999 to 2000 (11.6% of the number of hosts in 1988–89). There was a significant difference in the annual rate of host disappearance between 1988–89 and 1999–2000 (Table 1, Fisher's exact probability test, $P < 0.00001$); the rate was much higher in 1999–2000 (72.7%) than in 1988–89 (3.9%). Of 96 hosts that existed in 1989, 11 were found in 1999; of 71 hosts that existed in 1983 (Hirose 1985), six were found in 1999 and two of them were also found in 2000: 11 lived more than 10 years, six of them lived more than 16 years and two of them lived more than 17 years (Table 1). There was a significant difference in the annual rate of disappearance of the hosts that existed in 1983 between 1988–89 and 1999–2000 (Table 1, Fisher's exact probability test, $P = 0.00043$); the rate was higher in 1999–2000 (66.7%) than in 1988–89 (3.7%).

After the bleaching event, the size of host anemones decreased greatly (Fig. 1): there was a significant difference in size between 1988–89 (median = 657 cm², range = 2262–12, $n = 172$) and 1999–2000 (median = 164 cm², range = 753–6, $n = 20$, Mann–Whitney U -test, $Z = 4.7$, $P < 0.0001$). Although seven individuals of *A. perideraion* and 17 individuals of *A. clarkii* were found in 1999, there were no *A. perideraion* and 14 individuals of *A. clarkii* in 2000. In 1999, most of the hosts (85.7%) were inhabited by only *A. clarkii*; but 9.5% and 4.8% of them were inhabited by only *A. perideraion* and by both species, respectively ($n = 11$, Fig. 1). There was a significant difference in the ratio of the three host types between 1988–89 and 1999–2000 ($\chi^2 = 14.7$, $P = 0.0006$). Of 11 hosts that were found in both 1989 and 1999, five hosts (more than 43.6%) changed the host type.

GROUP STRUCTURE AFTER CORAL BLEACHING

In 1999 there were two adult groups (an adult pair group and a one-adult group), two subadult groups and two juvenile groups of *A. clarkii*, while only one adult pair group and two juvenile groups of *A. perideraion* existed. In 1999, four newly settled juvenile *A. clarkii* (< 25 mm SL) were found on three hosts, while just one settler of *A. perideraion* (< 25 mm) was found on a small host. In 2000, 10 newly settled juveniles of *A. clarkii* were found on eight hosts, while *A. perideraion*

Table 2. Size of 73 host anemones that existed from 1988 to 1989 in relation to their inhabitants. Data of 2 years are combined

Inhabitant		N	Mean (cm ²)	Median (cm ²)	Min (cm ²)	Max (cm ²)
1988	1989					
<i>A. clarkii</i>	<i>A. clarkii</i>	40	425	349	28	1440
<i>A. clarkii</i> and <i>A. perideraion</i>	<i>A. clarkii</i>	4	540	577	179	829
<i>A. clarkii</i>	<i>A. clarkii</i> and <i>A. perideraion</i>	10	732	617	173	1335
<i>A. clarkii</i> and <i>A. perideraion</i>	<i>A. clarkii</i> and <i>A. perideraion</i>	54	933	877	424	2103
<i>A. perideraion</i>	<i>A. perideraion</i>	36	1027	917	484	2262
<i>A. clarkii</i> and <i>A. perideraion</i>	<i>A. perideraion</i>	2	1084	1084	1068	1100
Total		146	794	729	28	2262

was never recruited. There existed only one adult pair group and seven juvenile groups of *A. clarkii* in 2000. After the bleaching event, there was no significant difference in body size between the two species in 1999 (*A. clarkii*, median = 33 mm SL, range = 105–20, $n = 17$; *A. perideraion*, median = 33 mm SL, range = 68–20, $n = 7$; Mann–Whitney U -test, $U = 50.5$, $P > 0.05$).

INTERSPECIFIC INTERACTION IN COHABITING GROUP

In a cohabiting group, the alpha-fish of *A. clarkii* attacked *A. perideraion*, and the frequency of interspecific interactions was significantly larger than that of intraspecific ones (Fig. 2a, Mann–Whitney U -test, $Z = 1.71$, $P = 0.042$). Beta- and gamma-*A. clarkii* also attacked *A. perideraion* in the group: the frequency of interspecific interactions was not smaller than that of intraspecific ones (Fig. 2b,c, beta-fish, Mann–Whitney U -test, $Z = 1.38$, $P > 0.05$; gamma-fish, $Z = 0.10$, $P > 0.05$). Furthermore, there was a significant difference in the frequency of the interspecific interactions by alpha-*A. clarkii* between the two groups with and without large *A. perideraion* (> 50 mm SL) (with large *A. perideraion*, median = 9, range = 20–0, $n = 8$; without large *A. perideraion*, median = 0, range = 3–0, $n = 59$, Mann–Whitney U -test, $Z = 6.3$, $P < 0.000001$). Alpha-*A. perideraion* in a cohabiting group never attacked adult *A. clarkii* (Fig. 2d). They often attacked juvenile and subadult *A. clarkii* as well as beta-*A. perideraion*, and they were also attacked by juvenile and subadult *A. clarkii* as well as by adult *A. clarkii*: there was no significant difference in frequency of aggressive interactions per 15 min between the four categories (Fig. 2d, Kruskal–Wallis test, $H = 1.6$, $P > 0.05$).

Discussion

SMALL SPECIES IS A SUPERIOR COMPETITOR IN SITE DISPLACEMENT

In anemonefishes, large fish are aggressively dominant over smaller members in a group, where the largest two fish usually control the growth and maturation of subordinates (Allen 1972; Fricke & Fricke 1977; Moyer & Nakazono 1978; Ross 1978b; Fricke 1979; Hattori

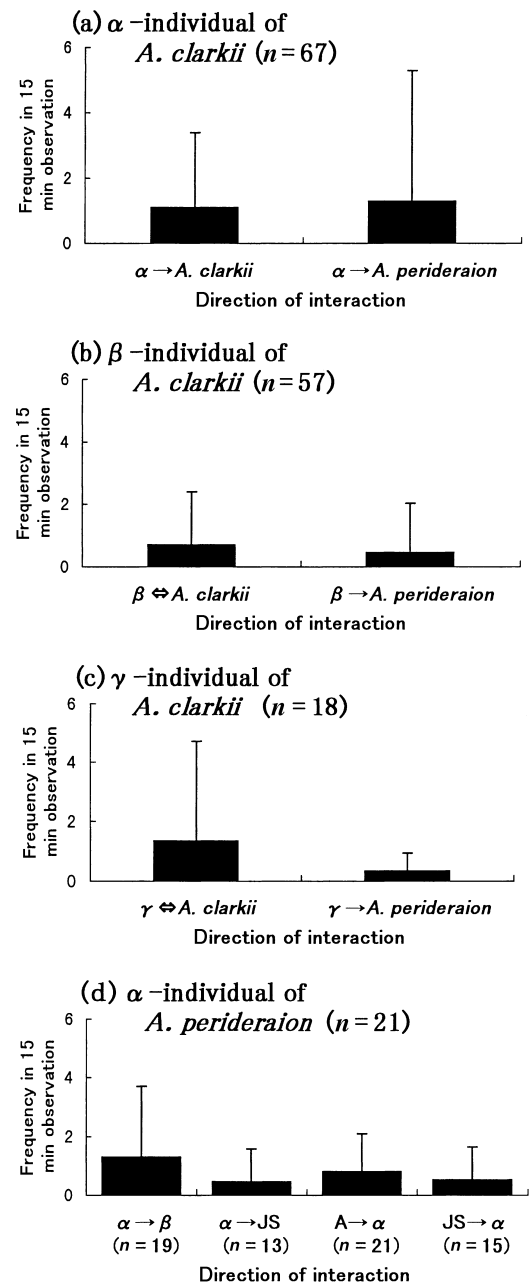


Fig. 2. Average frequency of intra- and interspecific aggressive interactions of the two anemonefishes in a cohabiting group per 15-min observation unit. Alpha, beta and gamma mean relative size order among conspecific individuals. JS means juvenile and subadult *A. clarkii*, and A means adult *A. clarkii*.

1991). In the present study site, *A. clarkii* was larger than and aggressively dominant over *A. perideraion* in a cohabiting group, where *A. clarkii* frequently attacked *A. perideraion*. The reverse rarely occurred, and *A. clarkii* suppresses the growth and reproduction of *A. perideraion* (Hattori 1995). The present study has revealed that in a cohabiting group, the alpha-fish of *A. clarkii* attacked *A. perideraion* more frequently than conspecific subordinates on average. Furthermore, the alpha fish of *A. clarkii* mainly attacked the large individuals of *A. perideraion* (> 50 mm SL). This result indicates that staying with small individuals of *A. perideraion* costs little to *A. clarkii*, but when *A. perideraion* is large, the cost of interspecific interaction is large.

While adult *A. clarkii* have a large home range, sometimes including two or more hosts, adult *A. perideraion* have a small home range, usually identical to the area of a host anemone (Hattori 1994, 1995, 2000). Since individual *A. clarkii* move easily between hosts (Allen 1972; Hattori 1995; Hirose 1995), the cost of interactions with *A. perideraion* may cause the emigration of *A. clarkii*. In fact, an adult pair of *A. clarkii* emigrates occasionally from a cohabiting group to a vacated larger host (Hattori 1995); after the emigration of *A. clarkii*, an adult pair of *A. perideraion* is observed to defend their host against intruders of *A. clarkii*, although they are greatly smaller than *A. clarkii*. It must be indispensable for adult *A. perideraion* to defend their host against *A. clarkii*, because they cannot reproduce in the presence of *A. clarkii* and cannot move to a better host. Since large individuals of *A. perideraion* can mature in the presence of *A. clarkii*, Hattori (2000) suggests that they wait for the emigration of *A. clarkii* from their group. The present study demonstrates that a host can live much longer than expected (> 17 years), which may allow *A. perideraion* to take the waiting strategy. In contrast, adult *A. clarkii* allow settling of juvenile *A. perideraion*, and they often move to another host (Hattori 1994, 1995). Although it would be easier to defend a small area for a larger species, sharing a host with adult *A. perideraion* may not pay for adult *A. clarkii* because *A. clarkii* needs a larger area. In terms of site displacement the small sedentary *A. perideraion* is a superior competitor, although it takes long time to take over a site. A small species, which usually requires a small amount of resources, can be a superior competitor in terms of a small site displacement.

LARGE SPECIES IS SUPERIOR MIGRANT AND DISPERSOR

Long-distance dispersal ability of coral reef fishes is usually dependent on the period of drifting larval phase (Sale 1978, 1980, 1991; Leis 1991; Victor 1991). However, their colonization success within a habitat would be dependent on appropriate microhabitat selection by settling larvae, and larval settlement tactics are often a crucial determinant of the spatial distribution

and abundance of small benthic coral reef fishes (Jones 1991; Williams 1991; Booth & Wellington 1998).

In a coexistence system of competing coral reef fishes, microhabitat selection by settling larvae can play an important role. For instance, two small damselfishes (genus *Dascyllus*) inhabiting the same isolated branching corals compete in a cohabiting group but coexist in a certain area due to a larval settlement tactic: settling larvae select corals actively in which conspecific members predominate, so that they can avoid interspecific competition after settlement (Sweatman 1983, 1985). In my study site, however, larval *A. perideraion* settles on *H. crista* irrespective of the presence of *A. clarkii* (Hattori 1995), indicating that the superior competitor *A. perideraion* does not avoid interspecific competition at the time of settlement. Larval *A. perideraion* never settles on a small host, probably because a large host is necessary for future reproduction, but the small body size of *A. perideraion* does not allow moving between hosts (Hattori 1995, 2000). In other words, *A. perideraion* uses only a good (large) microhabitat because of a poor migrant. In contrast, larval *A. clarkii* settles on a small host as well as a large host because *A. clarkii* can move to larger hosts for future reproduction (Hattori 1994, 1995; Hattori & Yamamura 1995). As a superior migrant, *A. clarkii* can use microhabitat with various sizes. Because the superior migrant *A. clarkii* never settles on a host with *A. perideraion* (Hattori 1995), it might have avoided interspecific competition at the time of settlement.

Microhabitat selection by settling larvae may be dependent largely on the possibility of subsequent migration within a habitat. In a place where the density of microhabitat is very high, for example, a settling larva would not need to select a good microhabitat because it could move subsequently to a better one. In a habitat of high host density (5.7 hosts per 100 m²), juvenile *A. clarkii* usually settle on small (= bad) hosts and subsequently move about to acquire better hosts (Ochi 1989b; Hattori & Yanagisawa 1991a,b). In the present study site (0.23 hosts per 100 m²), juveniles of motile *A. clarkii* settle on both small and large hosts (Hattori 1994), while juveniles of sedentary *A. perideraion* settles on only large hosts (Hattori 1995). If the density of hosts was much lower, larvae of the two species might select only large hosts. Elliott & Mariscal (2001) studied the host use of nine anemonefishes, including *A. clarkii* and *A. perideraion*, on a large barrier reef in Papua New Guinea, where host density is very low, and found that small *H. crista* (less than 400 cm²) is often unoccupied by any anemonefishes. Further work is required to clarify the relationship between microhabitat choice of drifting larvae of coral reef fishes and their movement after settlement.

COEXISTENCE OF TWO SPECIES IN DIFFERENT BODY SIZE

An interspecific trade-off between competitive ability and dispersal (= colonization) ability of competing

species living in a patchy environment often explains why so many ecologically similar species can coexist in a certain space (Tilman 1994; Lehman & Tilman 1997). The present study indicates that the inferior migrant *A. perideraion* was a superior competitor, while the inferior competitor *A. clarkii* was a superior migrant. In the meta-population models, the best competitor is defined as the most abundant species, as the best competitor usually occupies an abundance of sites (Tilman 1994; Lehman & Tilman 1997). In this study, however, the superior competitor was less abundant because it used only large hosts and took a long time to occupy them, while the superior migrant was abundant because of its use of hosts with various sizes. This suggests that a superior competitor is not always abundant. The species that can take over a site should be regarded as a superior competitor in a competitive coexistence system.

The meta-population models stress that the presence of empty sites is necessary to the coexistence of competitive species because unoccupied sites can be available for poor competitors if they are sufficiently good dispersers (Tilman 1994; Lehman & Tilman 1997; Tilman & Lehman 1997). In this study site, after *A. perideraion* takes over a host a group of *A. perideraion* seems to occupy the host for a long period, because the group of *A. perideraion* prevents *A. clarkii* from settling and migrating (Hattori 1995). Accordingly, an empty site is usually a newly settled small host because other hosts were basically occupied by one or two anemonefishes. The less good competitor *A. clarkii* was not only a superior migrant, which can find a vacated host easily, but also a pioneer species that can use a newly settled small (bad) host. Microhabitat (host) with various sizes might have promoted their coexistence. Probably, the characteristic of *A. clarkii* as pioneer is related closely to its wide range of host anemone species (Fautin 1986; Miyagawa 1989; Elliott *et al.* 1995). Consequently, the distribution of the pioneer species is widespread from tropical coral reefs to temperate rocky reefs (Allen 1972; Moyer 1980).

Tilman *et al.* (1997) predict that superior competitors among coexisting species tend to go extinct locally after serious habitat loss because they are not superior dispersers. In the present study site, after the bleaching event, serious habitat loss occurred: there were just 10 hosts (11.6% of the number of host in 1988–89). The number of both anemonefishes, especially *A. perideraion*, decreased greatly in 1999, and then no *A. perideraion* was found in 2000. Furthermore, only one settler of *A. perideraion* was found on a small host in 1999, while 14 settlers of *A. clarkii* were found in 1999 and 2000. Thus, the superior competitor *A. perideraion* went extinct locally, as predicted by Tilman *et al.* (1997). Although the bleaching event was caused by unusual high water temperature, the local extinction of *A. perideraion* is not due to its low tolerances of high water temperature because *A. perideraion* has higher tolerances than *A. clarkii* (Allen 1972; Moyer 1980)

and the extinction occurred 2 years after the event. Corals' death usually causes the growth of algae on the surface of dead corals, which may cause the increase of herbivores (Jones & Syms 1998). However, *A. perideraion* is more dependent upon such algae than *A. clarkii* (Allen 1972). Larger *A. clarkii* was aggressively dominant over *A. perideraion* before the bleaching event, but there was no size difference between them after the event, suggesting that no *A. clarkii* become to a superior competitor after the event. Because most hosts were smaller than 400 cm² in 1999 and 2000, the local extinction of *A. perideraion* is due probably to their lack of small host utilization ability. In contrast, the higher colonization success of *A. clarkii* after the habitat destruction seems to be caused by their small host utilization ability. As mentioned earlier, small host utilization ability is related closely to body size and mobility of fish. The body size difference between competitors seems to play an important role in their coexistence in a patchy environment.

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