Coexistence of two anemonefishes, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone

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Synopsis

Social structure and interactions between the anemonefishes, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone *Radianthus kuekenthali*, were investigated on a coral reef of Okinawa Islands, Japan. In an 87×373 m^2 study area, 98 sea anemones were inhabited by both species (32.5%), by only *A. clarkii* (48.9%), or by only *A. perideraion* (18.6%). A group of *A. clarkii* often occupied two or more individual hosts, and group members often interchanged. However, a group of *A. perideraion* usually used only one host and migration between groups was rare. The larger *A. clarkii* suppressed reproduction of *A. perideraion* in cohabiting groups, while *A. perideraion* suppressed settlement of juvenile *A. clarkii* to its own hosts. Juvenile *A. clarkii* settled on small hosts as well as on large hosts, whereas juvenile *A. perideraion* settled only on large hosts. Coexistence appears to be possible in part by differences in settlement patterns between juveniles of the two anemonefishes.

Introduction

In freshwater or marine fishes, allied species requiring similar resources often coexist (reviewed by Sale 1980, Lowe-McConnell 1987, Wootton 1990). Mechanisms of coexistence have attracted attention because allied species requiring similar resources might be expected to compete severely to the local exclusion of one or the other (Begon et al. 1990). Since even congeneric species rarely require precisely the same resource, however, the coexistence of allied species is mostly due to fine partitioning of resources among species (Robertson & Lassig 1980; Lowe-McConnell 1987, Hert 1990, Wootton 1990).

In special cases, however, fishes do appear to require exactly the same resource. On a coral reef in the Red Sea, for example, two damselfishes (genus *Dascyllus*) inhabit the same corals, compete, and coexist with each other (Shpigel 1982, Shpigel & Fishelson 1986). Coexistence of these two species is attributed to random settling of juveniles from the planktonic life and predation pressure that strongly limits resettlement of the fishes (Shpigel 1982, Shpigel & Fishelson 1986). Information on the coexistence of species which require the same resources, however, is sparse.

Anemonefishes (genus *Amphiprion*) are known for symbiotic association with sea anemones (Allen 1972, Miyagawa 1989) and socially controlled pro-
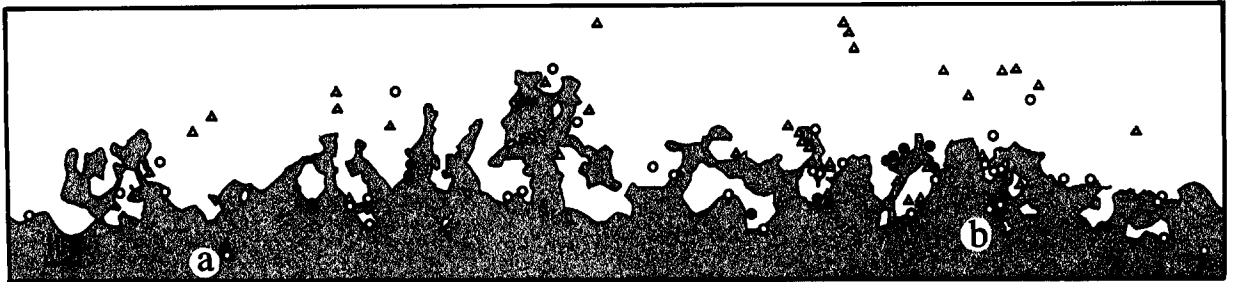
Fig. 1. Distribution of host sea anemones *Radianthus kuekenthali* in August 1989. Lines indicate the reef edge or patch reefs, and offshore sandy bottom is shaded. Specific patch reefs under study are denoted as 'a' and 'b'. Hosts inhabited by only *Amphiprion clarkii* (triangles), by only *A. perideraion* (solid circles), or by both species (open circles) are also indicated.

tandry with a monogamous mating system (Fricke & Fricke 1977, Moyer & Nakazono 1978, Ross 1978a, Fricke 1979). They usually live on or around the host sea anemones, which are an essential resource for their shelter and spawning site (Allen 1972). Social groups of the anemonefishes consist of a breeding pair and a varying number of nonbreeders. Distribution pattern and size of the host sea anemones are crucial determinants of the social and group structure of the anemonefishes (Ross 1978b, Fricke 1979, Moyer 1980, Ochi 1986, 1989a,b, Hattori 1991, Hattori & Yanagisawa 1991a,b).

Amphiprion clarkii and *Amphiprion perideraion* are common on coral reefs of Okinawa Islands, Japan, where they inhabit the same host species (Moyer 1976, Moyer & Nakazono 1978). To ascertain the mechanism of their coexistence, I investigated their host utilization and social structure as well as host distribution. Patterns of settlement and movement between hosts by juveniles were also determined.

Materials and methods

Study area and species

A field study was conducted in an 87 × 373 m² study area (Fig. 1) set on a fringing reef in front of Sesoko Marine Science Center, University of the Ryukyus at Sesoko Island (26°39′N and 127°57′E), Okinawa. *A. clarkii* and *A. perideraion* inhabited the sea anemone *Radianthus kuekenthali*. The three small individuals of *Radianthus simplex* inhabited by juveniles of *A. clarkii* were excluded from data analysis.

Collection of data on host distribution

A map of the study area was drawn based on an aerial photograph and underwater observations. Locations of the sea anemones were plotted on the map. The long and short axial lengths of the sea anemones were measured twice in August 1988 and twice in August 1989. The area covered by the tentacles of each sea anemone was estimated as (long axial length) × (short axial length) × π/4 and the larger value of the two measurements was used as an index of the anemone's size.

Collection of data on social structure and host utilization

Field observations on the two anemonefishes were conducted in three 6-month periods: June to November 1988 (period I), December 1988 to May 1989 (period II), and June to November 1989 (period III). Data for the three study periods were combined. All individuals of anemonefishes larger than about 20 mm in standard length (SL) were captured with hand nets and marked by injecting acrylic paint under the skin (Thresher & Gronell 1978). Their standard lengths were measured in June and November 1988 and 1989.

Swimming tracks of each individual larger than 50 mm SL (*A. clarkii*) and 20 mm SL (*A. perideraion*) were recorded for 15 min at least once in period I. The periphery of the track network was regarded as the boundary of the home range. At the same time I recorded agonistic behavior (rushing, dorsal leaning, and ventral leaning) and appease-

ment behavior (head standing, head shaking, and substrate biting) as in Yanagisawa & Ochi (1986).

Individuals with overlapping home ranges were defined as constituting a social group. Conspecific fish of a group were designated as alpha (α), beta (β), gamma (γ), and so on, according to its size order. Groups which included breeding pairs were called breeding groups. Alpha and β-individuals in breeding groups were always females and males, respectively (see Moyer & Nakazono 1978).

I surveyed all the host sea anemones in the study area every 4 days during June and September 1988, March and May 1989 (except April), and June and November (except 1 week in July, 2 weeks in August, and 2 weeks in October) 1989. The survey was also conducted once in November and December 1988 and 1989. The species and number of all anemonefishes in each host and the presence of egg masses were recorded. Eggs of *A. clarkii* and *A. perideraion* were distinguishable. Immigrants were defined as fish that had moved from another group and recruits as newly appearing small fish (< 20 mm SL).

Removal experiment

From six hosts inhabited only by *A. perideraion*, all fish were removed in November 1989. Numbers of recruits to the vacant hosts (experimental hosts) and the other 8 hosts inhabited only by the anemonefish (control hosts) were observed every four days until 12 days after the removal.

Table 1. Change in the number of resident fish species in host anemones, settlement of hosts, and disappearance of hosts. Each host was inhabited by *Amphiprion clarkii* (C), *A. perideraion* (P) or both species (B). D indicates disappearance of a host.

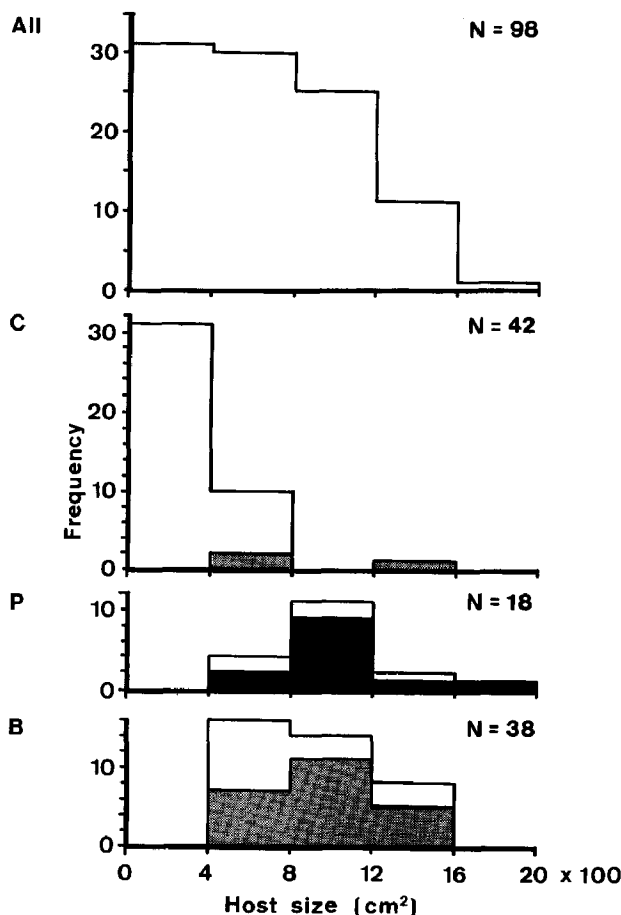| Beginning of period	End of period			
	C	P	B	D
No host	23	0	0	–
C	95	1	14	2
P	2	50	1	1
B	1	2	88	0

Fig. 2. Size-frequency distributions of host sea anemones inhabited by only *Amphiprion clarkii* (C), by only *A. perideraion* (P), and by both species (B) in August 1989. Shaded and solid bars indicate the hosts inhabited by breeding *A. clarkii* and *A. perideraion*, respectively.

Results

Distribution of host sea anemones and host utilization by the two anemonefishes

In 1988 and in 1989, 78 and 98 host sea anemones were found in the study area, respectively. During the study period, three sea anemones disappeared and 23 settled. The sea anemones were sparsely distributed except those on two patch reefs (a and b in Fig. 1). Average size of sea anemones did not differ significantly between two years (730 cm^2 ± 448 SD in 1988, 661 cm^2 ± 424 SD in 1989; Mann-Whitney U-test, Z = 0.73, p > 0.05).

Sea anemones (n = 98) were inhabited by *A. clarkii* only (48.9%), *A. perideraion* only (18.6%), or

both species (32.5%). There were no vacant host anemones. Inhabiting species changed during the study period in only a small number of hosts (16.8%, Table 1), mainly due to settlement of juveniles (< 20 mm SL) of *A. perideraion* to hosts which only *A. clarkii* inhabited (14 cases).

Hosts with only *A. clarkii* x̄ = 329 cm² ± 291 SD, n = 69) were smaller than those with only *A. perideraion* (x̄ = 1037 cm² ± 401 SD, n = 37; Mann-Whitney U-test, Z = 7.49, p = 0.0001) and those with both species (x̄ = 872 cm² ± 306 SD, n = 70; Mann-Whitney U-test, Z = 8.44, p = 0.0001), because all hosts smaller than 400 cm² were inhabited by only *A. clarkii* (Fig. 2). Hosts with only *A. perideraion* and those with both anemonefishes did not differ significantly in size (Mann-Whitney U-test, Z = 1.79, p = 0.73).

Hosts with only *A. clarkii* were distributed over the whole study area, while hosts with only *A. perideraion* and with both species were mainly along the reef edge (Fig. 1). Of 16 hosts with only *A. clarkii* in the inner reef flat (> 5 m from the reef edge), nine (56.3%) were smaller than 400 cm².

A. clarkii reproduced regardless of the presence of *A. perideraion*. In contrast, *A. perideraion* reproduced only in hosts without *A. clarkii*. *A. clarkii* inhabiting hosts smaller than 400 cm² never bred (Fig. 2).

Recruitment of juvenile *A. clarkii* was not random: they settled on hosts of any size but never did on hosts inhabited only by *A. perideraion* (Table 2). Settlement on hosts with only *A. clarkii* was more frequent than that on hosts with both anemonefishes (Mann-Whitney U-test, Z = 4.65, p = 0.0001).

Juveniles of *A. perideraion* also did not settle randomly: they settled on hosts irrespective of the presence of *A. clarkii* (Table 2) but never on hosts smaller than 400 cm². There was no significant difference in the number of *A. perideraion* recruits per host among the host types, if hosts smaller than 400 cm² were excluded (Mann-Whitney U-test of all pairwise combinations, Z < 1.28, p > 0.05).

On four out of six experimental hosts, one to four juvenile *A. clarkii* settled within a day after the removal of *A. perideraion*. At the end of the study, five experimental hosts were colonized by an average of 6.5 juveniles of *A. clarkii*, and another one remained vacant. By contrast, no juveniles of *A.*

clarkii settled on the control hosts (n = 8). No *A. perideraion* colonized the experimental and control hosts in the period.

Group structure and intergroup movement of A. clarkii

A social group occupied one to four host sea anemones (x̄ = 1.24 ± 0.55 SD, n = 173) and group size varied from one to 10 individuals (x̄ = 2.98 ± 2.04 SD, n = 173). Individuals larger than 80 mm SL often moved between hosts in a 15-min observation period, if they occupied two or more hosts. However, individuals smaller than 50 mm SL usually swam in the vicinity of a host. Group members often interchanged: 33 individuals moved between groups once or more (x̄ = 2.2 ± 1.8 SD, range = 1–7, n = 33). The average distance of the movements was 19.5 m ± 22.9 SD (range = 2–166 m, n = 71).

Reproduction, disappearance and growth of A. clarkii in the presence of A. perideraion

About half the groups of *A. clarkii* (n = 81, 46.8%) cohabited with *A. perideraion*. A cohabiting group sometimes (33.3%) occupied two or more hosts. Among the cohabiting groups which occupied two or more hosts (x̄ = 2.3 ± 0.55, n = 30), 60.0% included at least one host where only *A. clarkii* lived and

Table 2. Numbers of juvenile (< 20 mm SL) *Amphiprion clarkii* and *A. perideraion* settled on each host sea anemone.

Number of juveniles settled	Host inhabited by		
	A. clarkii N = 134	*A. perideraion* N = 51	Both N = 89
A. clarkii			
0	72	51	76
1	48	0	8
2	10	0	4
3–5	4	0	1
A. perideraion			
0	121	40	63
1	12	10	21
2–3	1	1	5

10.0% included one host where only *A. perideraion* usually lived but *A. clarkii* often intruded.

Alpha-individuals in groups cohabiting with *A. perideraion* were often (65.0%) breeders, while those of groups without *A. perideraion* were mostly (91.2%) nonbreeders (Table 3). Alpha-individuals in groups without *A. perideraion* were significantly smaller than β-individuals in groups with it (Analysis of Variance, F = 72.1, DF = 140, p = 0.0001). Disappearance rates of α- and β-individuals in groups without *A. perideraion* were significantly higher than those in groups with it, probably because of their small size. Alpha-individuals in groups without *A. perideraion* were as small as γ-individuals in groups with it ($\bar{x}$ = 51.4 mm ± 17.2 SD, n = 56; ANOVA, F = 1.86, DF = 123, p = 0.1751), and disappearance rates did not differ significantly between them (Chi-square test, χ^2 = 0.64, p > 0.05).

The range of body size of α-individuals in groups with *A. perideraion* overlapped widely with that of α-individuals in groups without it (Table 3). Growth increments of α-individuals were negatively correlated with their body size in both groups (in groups with *A. perideraion*, r = − 0.681, p = 0.0001, n = 74; in groups without *A. perideraion*, r = − 0.407, p = 0.0074, n = 42). Positions and slopes of the regression lines between body sizes of α-individuals and their growth increments did not differ significantly between the two groups (Analysis of Covariance, F = 1.107, DF = 112, p = 0.2949), indicating that *A. perideraion* does not influence growth of *A. clarkii*.

Group structure and intergroup movement of A. perideraion

Almost all social groups (97.9%) occupied one host sea anemone ($\bar{x}$ = 1.09 ± 0.35 SD, range = 1–3, n = 141) and group size varied from one to eight individuals ($\bar{x}$ = 2.20 ± 1.38 SD, n = 141). An individual usually lived within the vicinity of one host anemone, and migration between groups was rare: 16 individuals moved between groups once or more often ($\bar{x}$ = 2.6 ± 2.2 SD, range = 1–8, n = 16), but most of the movements (81%, n = 42) occurred in patch reefs a

Table 3. Body size (mm SL) and disappearance rate (D) of marked anemonefishes of different size order in a group with (+) and without (−) congeneric species. Data of breeders are given in parentheses.

Size order		A. clarkii		Test* result	A. perideraion		Test* result
		+	−		+	−	
α	SL x ± SD	95.4 ± 17.3 (102.0 ± 7.3)	56.3 ± 21.2 (97.0 ± 9.3)		34.6 ± 8.1	65.8 ± 8.1 (67.4 ± 7.0)	
	Range	26–118 (82–118)	23–112 (87–112)		22–53	44–82 (57–82)	
	N	80 (52)	68 (6)		78	47 (37)	
	D (%)	10.1	35.5	p < 0.001	13.2	14.0	p > 0.05
	N	79	62		53	50	
β	SL x ± SD	83.9 ± 16.5 (90.7 ± 7.6)	51.7 ± 23.0 (85.5 ± 6.1)		30.2 ± 7.5	50.4 ± 8.5 (51.7 ± 7.7)	
	Range	32–111 (68–111)	21–94 (78–94)		20–49	33–67 (39–67)	
	N	73 (52)	33 (6)		26	44 (37)	
	D (%)	10.5	33.3	p = 0.011	8.7	6.3	p > 0.05
	N	76	33		23	48	
≦ γ	SL x ± SD	43.4 ± 15.6	36.2 ± 13.1		39.3 ± 4.9	37.1 ± 9.3	
	Range	21–88	22–71		25–40	20–56	
	N	123	34		9	54	
	D (%)	22.9	41.9	p > 0.05	10.0	12.5	p > 0.05
	N	105	43		10	48	

* Fisher's exact probability test.

and b. All but three (11–14 m) movements were shorter than 2.7 m.

Reproduction, disappearance and growth of A. perideraion *in the presence of* A. clarkii

Many groups (n = 96, 68.1%) cohabited with *A. clarkii*. Alpha-individuals in groups cohabiting with *A. clarkii* were all nonbreeders, and breeders never cohabited with *A. clarkii* (Table 3). Individuals in groups with *A. clarkii* were all smaller than the smallest functional female (57 mm SL). Disappearance rates of individuals did not differ significantly between groups with and without *A. clarkii*.

Alpha-individuals in groups with *A. clarkii* were significantly smaller than γ-individuals in groups without it (ANOVA, F = 10.4, DF = 108, p = 0.0017), and the range of body size of the former individuals overlapped widely with that of the latter. Growth increments were negatively correlated with body sizes (α-individuals in groups with *A. clarkii*, r = – 0.594, p < 0.0001, n = 55; γ-individuals in groups without *A. clarkii*, r = – 0.695, p = 0.0002, n = 24). Positions and slopes of the regression lines between body sizes and growth increments did not differ significantly between α-individuals in groups with *A. clarkii* and γ-individuals in groups without it (Analysis of Covariance, F = 0.011, DF = 75, p = 0.9168), indicating that intra- and interspecific influence on growth of subordinate *A. perideraion* does not differ greatly.

Interactions between the two anemonefishes

A. clarkii in cohabiting groups attacked *A. perideraion* one to 20 times ($\bar{x}$ = 5.6 ± 6.0 SD) in 20 of 140 15-min observation periods, but the reverse rarely occurred (one to 3 times in 3 of 140 observation periods). *A. perideraion* in cohabiting groups were attacked by *A. clarkii* one to five times ($\bar{x}$ = 1.9 ± 1.3 SD) in 13 of 40 units of 15-min observation periods, but the former rarely attacked the latter (2 times in 2 of 40 observation periods). In other groups, aggressive behavior of *A. perideraion* against *A. clar*-

kii was observed on two occasions when *A. clarkii* (50–80 mm SL) happened to approach it.

Discussion

Suppression of reproduction in A. perideraion *by* A. clarkii

Interspecific suppression of reproduction has been reported in two competing damselfishes (genus *Dascyllus*) which inhabit the same corals (Shpigel & Fishelson 1986). The two species do not differ greatly in body size and behavior, and frequently interact with each other in the host corals. In each host with two species, only the largest individual of either species can reproduce with the mate. Unlike the two damselfishes, *Amphiprion clarkii* was always larger than *A. perideraion* in the same host. *A. clarkii* reproduced regardless of the presence of *A. perideraion*, while *A. perideraion* reproduced only in hosts without *A. clarkii*. This indicates that when occupying the same host, *A. clarkii* suppresses reproduction of *A. perideraion*, but the reverse does not occur. In a cohabiting group of *A. clarkii*, however, there often existed two or more hosts. This suggests that some *A. perideraion* in such cohabiting groups may have a chance to escape from the social suppression of *A. clarkii*. Actually, a few groups included a host where only *A. perideraion* usually lived. It may be possible for *A. perideraion* in such a host to form a group without *A. clarkii* at a future time.

Alpha-individuals of *A. perideraion* cohabiting with *A. clarkii* were all smaller than the smallest functional female in the *A. perideraion* population. Probably small body size is the primary cause for the reproductive inactivity of *A. perideraion* in cohabiting groups. This size difference was not due to growth suppression of *A. perideraion* by *A. clarkii*, because intra- and interspecific influence on growth of subordinate *A. perideraion* did not differ greatly. In cohabiting group, *A. perideraion* was often attacked by *A. clarkii* and the reverse rarely occurred. This suggests that *A. clarkii* may chase *A. perideraion* out of hosts when the latter grows large. However, disappearance rates of *A. perideraion* did not

differ significantly between groups with and without *A. clarkii* (Table 3), and the cause of small body size of *A. perideraion* cohabiting with *A. clarkii* is unknown at present.

Suppression of settlement of juvenile A. clarkii by A. perideraion

Juvenile *A. clarkii*, but not *A. perideraion*, settled on hosts even smaller than 400 cm^2. Although *A. clarkii* inhabiting small hosts never bred, they have the opportunity of moving to larger hosts at a future time because of their tendency to move between hosts. On the other hand, *A. perideraion* was less mobile than *A. clarkii*, and avoidance of settlement by *A. perideraion* on small hosts can be attributed to the lack of opportunity for subsequent interhost movements.

Juvenile *A. clarkii* never settled on hosts with only *A. perideraion*. However, after removal of *A. perideraion*, many juvenile *A. clarkii* settled on the vacant hosts. This indicates that *A. perideraion* defends the hosts against settlement of *A. clarkii* in the absence of large *A. clarkii*. In contrast, juvenile *A. perideraion* settled on hosts irrespective of the presence of *A. clarkii*. Probably it does not pay *A. clarkii* to defend the host against *A. perideraion*, because (1) juvenile *A. perideraion* has cryptic coloration and behavior and (2) reproduction and growth of *A. clarkii* were not influenced by *A. perideraion*.

Coexistence of the two anemonefishes

Hosts inhabited by *A. perideraion* were mostly distributed along the reef edge, whereas hosts inhabited by *A. clarkii* were widespread over both the inner reef flat and the reef edge. This distribution pattern does not result from habitat partitioning of the two anemonefishes but results from the different settlement pattern. Consequently, only juvenile *A. clarkii* settled on hosts smaller than 400 cm^2, which were distributed on the inner reef flat.

Some allied marine fishes requiring a similar resource often coexist without partitioning (Sale 1978, 1980, Robertson & Polunin 1981, Roughgar-

den 1986, Shpigel 1982, Shpigel & Fishelson 1986). Several authors suggest that random recruitment of juveniles is an important factor in coexistence of marine fishes which require a similar living space (Sale 1978, 1980, Roughgarden 1986, Shpigel 1982, Shpigel & Fishelson 1986). Furthermore, environmental variability may facilitate coexistence of fishes in the stochastic recruitment system (Chesson & Warner 1981, Chesson 1986). The anemonefishes *A. clarkii* and *A. perideraion* inhabited the same host species, and juveniles of both species did not settle randomly on host sea anemones.

In terrestrial animals, particularly insects, many congeneric species requiring the same resources often coexist, and they exploit resources which are divided into small, discrete patches, such as dung, carrion, fruit, fungi, and dead wood (Shorrocks et al. 1979, Atkinson & Shorrocks 1981, Kareiva 1986, Rosewell et al. 1990, Shorrocks et al. 1990). Several authors proposed factors that may promote coexistence of competing species in a patchy environment: e.g., clumped spatial distributions, fugitive species, and priority effects (Shorrocks et al. 1979, Atkinson & Shorrocks 1981, Kareiva 1986, Rosewell et al. 1990, Shorrocks et al. 1990). In patchy environments, the competitively inferior species can escape from competition by arriving at a patch first or by finding empty patches, which are the result of clumped distributions of the competitively superior species.

Host sea anemones of *A. clarkii* and *A. perideraion* can be regarded as homogeneous patches, although the size of each patch is different. The two species coexist utilizing different patches as spawning sites, but neither species is a fugitive species (*A. perideraion* rarely moved between hosts). The larger *A. clarkii* suppressed reproduction of *A. perideraion* in cohabiting groups, while *A. perideraion* suppressed the settlement of *A. clarkii* on its own host (Fig. 3). This life-interval dependent interspecific competition between the two anemonefishes may make their coexistence possible. Furthermore, the two species differed in recruitment pattern of juveniles: *A. perideraion* settled only on large hosts irrespective of the presence of *A. clarkii*, while *A. clarkii* settled on small hosts as well as large hosts without *A. perideraion*. This recruitment pattern
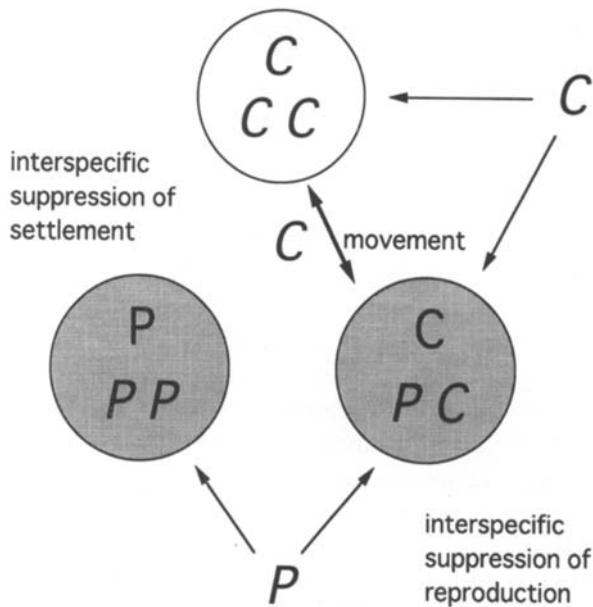
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Fig. 3. Model of coexistence of the two anemonefishes, *A. clarkii* (C) and *A. perideraion* (P), which utilize the same host sea anemones. Romans mark a breeding pair; in Italics are nonbreeders. Open and shaded circles indicate small and large hosts, respectively. Thin and bold arrows mean settlement and movement between hosts by juveniles, respectively.

prevents the exclusion of either species from the area.

Acknowledgements

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