COMPETITION BY ANEMONE FISHES FOR HOST ACTINIANS

COMPETITION ENTRE LES POISSONS CLOWNS POUR L'OCCUPATION DES ACTINIES-HOTES

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ABSTRACT

Ten species of sea anemones are symbiotic with 26 species of anemonefishes (Pomacentridae). Five of the former inhabit six of the latter at Lizard Island, Great Barrier Reef, Australia.

Direct challenge field experiments for actinians from among fish of all species normally inhabiting them support the hypothesis that competition is important in governing which species of symbionts occur together. The competitve hierarchy for Entacmaea quadricolor is ordered as is numerical abundance of fish individuals and proportion of anemones occupied by that species: Premnas biaculeatus, Amphiprion melanopus, A. akindynos. Congruence between competitive dominance of territories (= anemones) with number of individual fish and with proportion of the actinian population occupied by each holds as well for A. perideraion and A. percula (in that order) in Heteractis magnifica. Dominance is also a direct correlative of host specificity in both cases. Actinians of the other four species at Lizard Island (all members of family Stichodactylidae) host only the fish A. akindynos, which occupies the second greatest number of hosts.

Thus, in a particular locality, proportion of individuals of a host species occupied by its various symbionts, and number of specimens of each fish, are direct reflections of the dominance hierarchy among the fish. In addition, attractiveness of host actinians to anemonefishes is reflected in the number of species of fishes sharing that resource, either in one locality or over the range of the symbiosis as a whole. By this measure, Entacmaea quadricolor is the most attractive host. Probably not coincidentally, it is the only host actinian that has been demonstrated to benefit from its association with anemonefishes.

RESUME

Dix espèces d'anèmones vivent en symbiose avec 26 espèces de poissons clowns (Pomacentridae). Cinq anémones et six poisons clowns sont présents à Lizard Island, Grande Barrière, Australie.

Des expérimentations ont été réalisées sur le terrain au cours desquelles toutes les espèces de poissons ont été mise en présence des anémones qui les habitent habituellement. Ces expérimentations permettent de penser que les phenomènes de compétition sont importants pour déterminer les symbiontes qui s'associent. Pour Entacmaea quadricolor la hiérarchie compétitive est ordonnée de la même façon que l'abondance des individus de poisson et que la proportion d'anémones occupée par ces espèces: Premnas biaculeatus, Amphiprion melanopus, A. akindynos. La congruence entre la dominance compétitive du territoire (= anémone) et le nombre d'individus de poissons, d'une part, ainsi que la proportion de la population d'actinies occupée par chacun, d'autre part, est également valable pour A. perideraion et A. percula (dans cet ordre) dans Heteractis magnifica. La dominance est également directement correlée avec la spécificité de l'hôte dans les deux cas. Les autres espèces d'actinies à Lizard Island (appartenant toutes à la famille des Stichodactylidae) sont seulement habitées par le poisson A. akindynos; ce dernier occupe un grand nombre d'hôtes (cet hôte occupe la deuxième position quand à l'importance de l'occupation).

Ainsi dans une localité determinée le nombre d'individus d'une espèce hôte habitée par ses différents symbiontes, et le nombre d'individus de chaque espèce de poisson, correspondent à la hiérarchie des dominances chez les poissons. De plus, l'attraction des actinies hôtes sur les poissons détermine le nombre de poissons se partageant cette ressource aussi bien dans une localité que sur l'ensemble du secteur concerné par la symbiose. Ainsi Entacmaea quadricolor est l'anèmone la plus attractive. Ce n'est propalement pas par hasard que seule cette anémone retire des avantages de son association avec des poissons clowns, comme çela a été demontré.

INTRODUCTION

A textbook example of marine symbioses is that between 10 species of "giant" sea anemones (most belonging to family Stichodactylidae) and clownfishes or anemonefishes (family Pomacentridae) in shallow waters of the tropical Indo-West Pacific (Dunn, 1981). All 25 species of Amphiprion and the sole member of Premnas are obligately associated with sea anemones in nature except for a short planktonic larval stage (Allen, 1972, 1980). Clownfishes can survive alone in aquaria so physiologically do not require host actinians, but are behaviorally dependent on them, the anemone serving as the fish's territory and primary means of defense.

In nature, each species of clownfish consistently occurs with only certain sea anemones (Verwey, 1930; Mariscal, 1970, 1972; Dunn, 1981): Amphiprion clarkii has been recorded from nine of the 10 host actinians, most fishes associate with two to five, and eight occur with a single anemone (of five species) (Dunn, 1981). A species of host actinian harbors from one to 11 species of symbionts (Dunn, 1981). The fishes -- being the mobile and shorter-lived partner -- appear to govern these distributions.

Within the geographical limits of anemonefishes, individuals of most host species are inhabited, their number limiting fish population size (Allen, 1972; Fricke, 1979; Dunn, 1981). Having such an essential resource in short supply would be expected to promote competition. Fishes symbiotic with a particular actinian species may be considered a guild, within which competition for hosts might occur (Diamond and Gilpin, 1982). I conducted field studies with the two associates of Heteractis magnifica on the Great Barrier Reef to evaluate the importance of competition between fishes in partitioning the anemone resource.

MATERIALS AND METHODS

Investigations were done at and near Lizard Island Research Station, Great Barrier Reef, Queensland, Australia (14°38'S, 145°30'E), during October and November of 1981, and February of 1983. Field work by scuba diving included identifying each host actinian or cluster thereof on a 50 x 100 m patch reef extending from 2 to 10 m off Palfrey Island.

Fish were captured with hand-nets and, when absolutely necessary, small amounts of the anesthetic quinaldine (Allen, 1972, 1980), the effect of which was allowed to wear off before experiments were initiated. They were transported in water-filled plastic bags from which they were released directly into test anemones or an aquarium. Total length was measured to the nearest 5 mm with a plastic rule while the fish was held in the plastic bag.

Experiments discussed here involved a fish being transferred mainly to specimens -- occupied or not -- of Heteractis magnifica, either directly from another anemone or after up to three days in an aquarium. Except where specified, its original host was also H. magnifica. Replication of experiments to evaluate importance of size, sex, and prior residence to competitive dominance was limited by availablility of anemonefish.

RESULTS

Inventory

Five species of anemonefishes inhabit six actinian species around Lizard Island, each fish occurring with one to five species of partner (Table 1). These combinations were the same everywhere in the area, and were consistent in my two visits.

I located only three specimens of Heteractis magnifica in hours of exploration at Lizard Island, all on the study reef. One contained three specimens of Amphiprion percula, which had quite faint black lines separating the areas of orange and white on their bodies. The other two anemones, situated 3 m apart, harbored four and six individuals of A. perideraion. Through experimental manipulation, I eventually removed all fish from these actinians. Upon my return sixteen months later, the two specimens of H. magnifica near one another each had been reoccupied by three specimens of A. perideraion, while the other anemone harbored a single individual of A. percula having bold black lines. The only other specimens of either species that I found were two individuals of A. percula, both with bold black markings, in Lizard Lagoon, occupying a specimen of Stichodactyla gigantea.

Transfer Experiments

A 50 mm male Amphiprion percula, transferred to an anemone inhabited by a 50 mm male A. perideraion and two small juveniles, was gone when I returned 24 hours later, as was the smallest fish. Initially, however, the fish swam quietly in the anemone's tentacles, even brushing flanks, without interaction.

I introduced individuals of A. percula 40 and 70 mm long from a specimen of Stichodactyla gigantea to an anemone occupied by specimens of A. perideraion 30 and 40 mm. During the time that I observed them, the two 40 mm long fish dashed at one another, biting, while the other two fish did not interact. One day later only the pair of A. perideraion remained.

When an 80 mm female A. percula and a 70 mm female A. perideraion were released simultaneously into an unoccupied specimen of H. magnifica that had been home to neither, there was no initial overt aggression, but 24 hours later, the former was gone.

Reciprocal transfers of fish of the two species between individuals of Heteractis magnifica demonstrated that all are reacted to identically by both fishes. Specimens of Amphiprion percula acclimated to either H. magnifica or Stichodactyla gigantea did not engage in acclimation behavior when introduced to an individual of the other species, settling immediately into the tentacles. A specimen of A. percula from S. gigantea that I transferred to an individual H. crispa was stung. One from H. magnifica placed in S. gigantea engaged in no acclimation behavior, nor was it stung. Four specimens of A. perideraion placed in H. crispa did not seem to be stung, but swam off, whereas one introduced to S. gigantea was stung.

Several specimens of Amphiprion akindynos were introduced singly into an unoccupied specimen of Heteractis magnifica. Fish taken from individuals of Stichodactyla gigantea and

Entacmaea quadricolor were stung, and lay gasping on the anemone's oral disc as tentacles clung to them. Two fish from the host H. crispa showed less evidence of damage, eventually managing to break free and swim off. When specimens of A. melanopus were transferred from a clone of E. quadricolor to H. magnifica, a similar result was obtained, smaller individuals being killed and larger ones dashing off after a struggle.

Aquarium Observations

The Steinhart Aquarium of the California Academy of Sciences frequently displays individuals of Heteractis magnifica, Amphiprion percula, and A. perideraion. A pair of each species of fish were released simultaneously into a tank containing a specimen of the sea anemone. All animals had been acquired independently of one another. Within a short time, the pair of A. perideraion settled into the actinian, the other fish being restricted to the opposite side of the tank. They remained thus for as long as the display was retained -- well over a year. Currently two specimens of each of these fishes occupy a tank with an individual of Macrodactyla doreensis, which is monopolized by A. perideraion, the only species of fish besides A. clarkii known to inhabit it in nature (Dunn, 1981).

DISCUSSION

The data from experimental transfers pitting fish of one species against those of another, while admittedly limited, are consistent, and support the hypothesis that competition could be important in governing which species of symbionts occur together. Outnumbered fish were displaced. When numbers were equal, dominance determined outcome, Amphiprion perideraion being competitively superior to A. percula in Heteractis magnifica. Sex, prior residence, and size, insofar as they were manipulated, were immaterial to the results of direct challenges.

Thus there is a direct correlation between competitive dominance of territories (=anemones) and 1) numerical abundance of the two fishes at Lizard Island (in all hosts), 2) proportion of the actinian population occupied by each species, and 3) host specificity (at Lizard Island -- overall, the two have been recorded from the same three actinians, and A. perideraion occurs with Macrodactyla doreensis as well). I previously demonstrated such correlations for the three symbionts of Entacmaea quadricolor at Lizard Island (Fautin, 1985).

A dearth of animals precluded pitting fish of very different sizes against one another, but two resident Amphiprion perideraion only two-thirds the combined length of two intruders triumphed, and even with prior residence controlled, a specimen of A. percula was ousted by one of A. perideraion less than 90% its length. I suspect that a fish of the competitively inferior species would have to be considerably (more than 175%) larger than one of the superior species to triumph, as is true among associates of E. quadricolor, and in stomatopods (Caldwell and Dingle, 1979; Reaka, 1984). This is supported by the apparent displacement of the smaller juvenile A. perideraion by a 50 mm A. percula.

There was clear interspecific recognition among fishes. Precisely how/when specimens of Amphiprion percula abandoned or were driven from the anemone by those of A. perideraion are unknown, but initially they seemed quite evenly matched. By contrast, encounters between symbionts of Entacmaea quadricolor are almost invariably aggressive, with fish of one species quickly ousting those of the other (Fautin, 1985).

Individual anemones being repopulated by members of the species that had previously occupied them may have been due to chance, such small numbers were involved. The possibility of fish using the presence of conspecifics as indicators for appropriate settlement sites, as Sweatman (1983) found for Dascyllus, is not precluded by these observations, but they do indicate that fish are attracted to anemones themselves. Although actinians may influence anemonefish colors (Dunn, 1981), the repopulation experiment also suggests that host species is not responsible for the variability in intensity of Amphiprion percula's black markings.

Responses of specimens of Amphiprion akindynos and A. melanopus make me query records of these fishes' associations with Heteractis magnifica. A member of the clarkii complex (Allen, 1972), A. akindynos is similar to A. clarkii in morphology and lack of host specificity. I suggest that their similarity extends to not occurring in nature with H. magnifica, the sole record of the H. magnifica/S. akindynos association being a photo (Allen, 1972; Dunn, 1981). Individuals of A. akindynos at Lizard Island occur with two anemones (Stichodactyla gigantea and S. mertensii) not previously reported as hosting that fish (Dunn, 1981). If H. magnifica is removed from its list of hosts, A. akindynos inhabits anemones of six species, second in host diversity only to A. clarkii. No member of the ephippium complex other than A. melanopus is known from H. magnifica, the sole record of this association also a photo (Dunn, 1981). Until specimens of these species, taken together, are reliably identified, I will suspect these reports.

Based on data from experimental challenges among the three fishes occurring with Entacmaea quadricolor at Lizard Island, I invoked three factors to explain the distribution of fishes in anemones (Fautin, 1985), the first two of which apply as well to the symbionts of Heteractis magnifica dealt with here. 1) In nature, an intrinsic preference or one learned early in life restricts fish to certain of the hosts present. Individuals of most fish species seem able to inhabit specimens of most species of host anemones in captivity, and some are routinely kept with specimens of the Caribbean actinian Condylactis in commercial and home aquaria. However, even under artificial circumstances, some fish are incapable of inhabiting certain actinians, to judge by the experiments of Moser (1931) and Mariscal (1969, 1972), who were able to adapt clownfishes to some temperate anemones but not others. 2) Within the array of acceptable anemones, competition among fishes governs their distribution in hosts. 3) I explained the rare occurrence of the least competitive symbiont of E. quadricolor (i.e., Amphiprion akindynos) by a stochastic factor, but the very few specimens of H. magnifica at Lizard Island made observation of infrequent associations unlikely. The possibility of such partnerships should be investigated where asexually propagated clones of H. magnifica make it very abundant (Dunn, 1981).

I posited a direct correlation between number of symbiotic fishes and desirability of an actinian as host (Fautin, 1985). This is supported by the observation that the two anemones with one symbiont (and thus presumably only marginally suitable as hosts) both harbor Amphiprion clarkii, the least host specific clownfish (Dunn, 1981). I also hypothesized that the existence of Entacmaea quadricolor is largely dependent upon protection by anemonefishes, the actinian's vulnerability to predation having been a powerful factor in its evolving whatever attracts clownfishes (Fautin, 1985). Specimens of Heteractis magnifica are less vulnerable, being tough and massive, but generally occur fully exposed atop prominences (hence their popularity as photographic subjects) (Mariscal, 1972; pers. obs.). On the day following my removal of their fish, the column of one anemone had longitudinal scrapes, and a tuft of tentacles was missing from another. The most likely predators are fishes that feed on other coelenterates, hence are resistent to nematocysts, such as the butterfly fishes that opportunistically consume specimens of E. quadricolor when their protective anemonefish are removed (Fautin, 1985), and possibly parrot fishes. Thus, while demonstrably not essential to the survival of H. magnifica, clownfish probably protect their host, the survival of which is thereby enhanced. It is therefore not surprising that many species of fish associate with H. magnifica, assuring it at least one anywhere it occurs.

The distribution of fishes with Heteractis magnifica in the Indian Ocean provides an example of ecological release (Dunn, 1981) supporting the attractiveness of this actinian to symbionts. The only anemonefish in the Comoro Islands, Amphiprion akallopisos, occupies specimens of H. magnifica and the other host species present. In the Seychelles, A. akallopisos occurs only in H. magnifica, a second species of anemonefish inhabiting the other actinian. And in the Maldives, nearer the center of diversity of both groups, A. akallopisos and a third species of fish both associate with specimens of H. magnifica, sharing the resource as do A. perideraion and A. percula at Lizard Island.

If Amphiprion melanopus and A. akindynos are excepted, Heteractis magnifica hosts eight species, the fourth greatest number of the 10 actinians. I have asserted that Entacmaea quadricolor is the most desirable anemone, partly because it harbors the greatest number of fishes restricted to a single host (Fautin, 1985). Three fishes are exclusive to E. quadricolor, and its 11 fishes inhabit an average of 3.18 actinians. The eight associates of H. magnifica inhabit an average of 3.13 actinians, but only A. nigripes is restricted to it. Moreover, individuals of only this host species do not contain adult A. clarkii. That the two are not physiologically incompatible is attested by Mariscal's (1970, 1972) observation of juvenile A. clarkii in H. magnifica, and my keeping the two together in aquaria. My interpretation is that this fish cannot successfully retain possession of this highly desirable resource in nature. I speculate that everywhere these two species have been studied at least one fish outcompetes individuals of A. clarkii for it.

I believe that generalist actinians are such by virtue of their attractiveness to clownfishes, which serves to assure them symbionts wherever they are. A generalist fish is tolerant of many hosts and thus may be geographically widespread. However, its lack of host specialization puts it at a competitive disadvantage against specialist fishes. Evolutionarily, Amphiprion clarkii has survived by having refuge in less desirable anemones -- those remaining when the other clownfishes in the area have secured preferred hosts, i.e., those on which they are specialized and in which they are dominant. The generalist attribute of this species with respect to hosts has led to its being the most abundant and geographically widespread clownfish. Heteractis magnifica, second only to Entacmaea quadricolor in abundance and geographical extent [by my estimate; Mariscal (1972) believes it first], is arguably the most preferred host anemone, being the only one not occupied by the extreme generalist A. clarkii.

ACKNOWLEDGMENTS

A generous grant from the Cocos Foundation funded most of the field work at Lizard Island. Support from the California Academy of Sciences also contributed to this research. I am indebted to Anne Sparrow and John R. Ottaway for field and logistical assistance; to Barry Goldman, Director, and Lois Goldman, Administrative Assistant, for providing support at the Lizard Island Research Station; to Jerry Allen for fish identifications; and to many colleagues for comments on this manuscript and for stimulating discussions on the subjects of competition and evolutionary ecology.

LITERATURE CITED

ALLEN G.R., 1972. The Anemonefishes: Their Classification and Biology. T.F.H. Publ., Inc. Ltd., Neptune City, N.J. 288 pp.

ALLEN G.R., 1980. The Anemonefishes of the World: Species, Care and Breeding. Aquarium Systems, Mentor, Ohio. 104 pp.

CALDEWLL R.L. and J. DINGLE, 1979. The influence of size differential on agonistic encounters in the mantis shrimp, Gonodactylus viridis. Behaviour 69(3/4):255-264.

DIAMOND J.M. and M.E. GILPIN, 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia 52:64-74.

DUNN D.F., 1981. The clownfish sea anemones: Stichodactylidae (Coelenterata: Actiniaria) and other sea anemones symbiotic with pomacentrid fishes. Trans. Amer. Phil. Soc. 71(1):1-115.

FAUTIN D.G., 1985. Why do anemonefishes inhabit only some host actinians? Environ. Biol. Fish. in press.

FRICKE H.W., 1979. Mating system, resource defence and sex change in the anemonefish Amphiprion akallopisos. Z. Tierpsychol. 50:313-326.

MARISCAL R.N., 1969. An experimental analysis of the protection of Amphiprion xanthurus Cuvier & Valenciennes and some other anemone fishes from sea anemones. J. Exp. Mar. Biol. Ecol. 4(2):134-149.

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. 91:1-43.

MARISCAL R.N., 1972. Behavior of symbiotic fishes and sea anemones. Pp. 327-360 in H.E. Winn and B.L. Olla, eds., Behavior of Marine Animals, volume 2, Plenum Publ. Corp., New York.

MOSER J., 1931. Beobachtunger über die Symbiose von Amphiprion percula (Lacépède) mit Aktinien. Sitz. Gesell. Naturf. Freunde Berlin 2(4-7):160-167.

REAKA M.L., 1984. Size frequency distributions, aggressive behavior, and maintenance of species diversity (Abstr. 664). Amer. Zool. 24(3):127A.

SWEATMAN H.P.A., 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (Dascyllus aruanus and D. reticulatus) on coral reefs. Mar. Biol. 75(2/3): 225-229.

VERWEY J., 1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. Treubia 12(3-4):305-366.

Table 1. Species of fishes and anemones at Lizard Island. X = previously known combination present; N = new record; O = combination known elsewhere but absent at Lizard Island. (Based on records in Dunn, 1981.)

FISHES / ANEMONES	Premnas biaculeatus	Amphiprion percula	Amphiprion perideraion	Amphiprion melanopus	Amphiprion akindynos	Number fish associates
Entacmaea quadricolor	X			X	X	3
Heteractis magnifica		X	X	O	O	2
Heteractis crispa		O	O	O	X	1
Heteractis aurora					X	1
Stichodactyla gigantea		X	O		N	2
Stichodactyla mertensii					N	1
number anemone associates	1	2	1	1	5	