



Defense of Host Actinians by Anemonefishes

John Godwin; Daphne G. Fautin

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reduce competition for limited food resources, then individuals may be more likely to join (or less likely to leave) a heterospecific group than an equivalently sized group of conspecifics. Similarly, where mutualistic interactions among foragers are suspected, analyzing group dynamics may allow one to quantify the strength of attraction among conspecifics or heterospecifics in field situations where actual benefits to individuals are difficult to measure.

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- MARY C. FREEMAN AND GARY D. GROSSMAN, *School of Forest Resources and Institute of Ecology, University of Georgia, Athens, Georgia 30602.* Accepted 29 July 1991.

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DEFENSE OF HOST ACTINIANS BY ANEMONEFISHES.—The precise nature of the symbiosis between anemonefishes (*Premnas* and *Amphiprion*) and certain tropical actinians has been debated since its discovery more than a century ago (Collingwood, 1868). The relationship is obligate for the fishes: with few exceptions, postlarvae are found in nature only in sea anemones, and removal of a fish's host results in predation of the fish (e.g., Mariscal, 1970; Allen, 1972; but see Moyer, 1980). Residence in an anemone is essential to fish reproduction; eggs are laid beneath the oral disc of the host (Allen, 1972; Fricke, 1979; Moyer and Steene, 1979). The host actinian represents the territorial center and primary source of defense for anemonefish.

Although typically occupied by fish, individuals of some host anemone species may lack symbionts in nature (Dunn, 1981), so the symbiosis seems facultative for actinians. Despite this, protection of their hosts by resident anemonefishes has been inferred from the territorial nature of anemonefishes and their aggression toward other fishes (e.g., Mariscal, 1970). Studies by Allen (1972), Fricke (1975), and Moyer (1980) provided evidence that symbiotic anemonefishes protect anemones of the species *Entacmaea quadricolor*.

Entacmaea quadricolor is the most common and geographically widespread host anemone. In contrast with some other host actinians, in which oral disc diameter may exceed 1 m (e.g., *Stichodactyla mertensii* and *Heteractis magnifica*), an individual *E. quadricolor* is typically less than 100 mm wide (Dunn, 1981). Asexual reproduction by longitudinal fission in *E. quadricolor* produces clones of contiguous polyps that typically are anchored in depressions in the reef or attached to dead coral branches so that only their tentacles are visible. Anemonefish swim through the confluent tentacles of a cluster as through those of one large animal. The ability of *E. quadricolor* to harbor fish is presumably related to its cloning habit; the polyps are too small individually to accommodate an adult fish, and there is a linear relationship between area covered by tentacles of a cluster and the aggregate length of its resident *A. melanopus* symbionts (Ross, 1978).

In this paper, we present strong support for the hypothesis that the anemonefish symbionts of *E. quadricolor* provide aggressive protection against anemone predators and assert that this symbiosis is therefore mutualistic. Observations suggesting that certain of the symbioses between other anemonefishes and actinians are also mutualistic are presented.

Methods.—Field manipulations were performed originally for purposes other than for study of host defense by anemonefishes. Initial findings indicating defense of host actinians by resident anemonefishes were therefore serendipitous. These were followed by manipulations designed to determine whether the absence of anemonefishes influenced survival of their hosts. Details of these manipulations are summarized in Table 1. Some specific details of individual manipulations are described with the results for brevity. Removals of resident anemonefish were performed during daylight hours with handnets

TABLE 1. FIELD MANIPULATIONS: LOCATIONS, SAMPLE SIZES, HOSTS, AND RESIDENT ANEMONEFISH SPECIES.

Number	Date	Location	Number of clusters	Anemone species	Anemonefish species	N anemonefish resident/removed	Time period of removals
1	10/81	Lizard Island	1	<i>Entacmaea quadricolor</i>	<i>Amphiprion melanopus</i>	17/17	50 hours
2	10/81	Lizard Island	1	<i>Heteractis magnifica</i>	<i>A. percula</i>	3/3	<1 hour
3	10/81	Lizard Island	1	<i>H. magnifica</i>	<i>A. perideraion</i>	6/5	<1 hour
4	12/85	Madang, PNG	1	<i>E. quadricolor</i>	<i>A. melanopus</i>	23/23	3 days
5	10/87	Madang	1	<i>E. quadricolor</i>	<i>A. melanopus</i>	6/6	1 day
6	10/87	Madang	1	<i>E. quadricolor</i>	<i>Premnas biaculeatus</i>	2/2	1 day
7*	5/88	Guam	14	<i>E. quadricolor</i>	<i>A. melanopus</i>	3-8/2	<15 minutes
8	4/89	Lizard Island	1	<i>E. quadricolor</i>	<i>P. biaculeatus</i>	4/4	<15 minutes

* The adult pair was removed and the male was returned within 10 minutes (see text).

and quinaldine anesthetic over periods ranging from 15 min to three days.

Godwin investigated the possibility of aggressive protection of *E. quadricolor* by *A. melanopus* in Apra Harbor, Guam, in May 1988. A 30 × 30 cm plastic bag containing a single adult of the chaetodontid *Chaetodon ulietensis* ($n = 2$) or a similar sized individual (~10 cm TL) of the herbivorous acanthurid *Naso lituratus* ($n = 3$) was placed in the center of *A. melanopus* territories. Attacks by resident anemonefish on the models (defined as any rapid swimming movement directed toward and ending within 2 cm of the bag) were counted during the ensuing 5-min periods. Two pairs were presented first with *C. ulietensis* then *N. lituratus*, whereas a third pair was presented with only *N. lituratus*.

Results and discussion.—In Oct. 1981 on Lizard Island (GBR), Fautin removed 17 *A. melanopus* inhabiting an isolated cluster (1.0 × 1.6 m) of *E. quadricolor* to study recolonization of the hosts (manipulation 1, Table 1). As the removals progressed, the number of individual actinians diminished and the cluster was no longer continuous. The only remaining expanded anemones were occupied by symbiotic anemonefishes (two pairs of *A. akindynos* and a small *P. biaculeatus* at what had been the periphery of the cluster), and fishes of other species ventured nearer the actinians. Some small anemones were retracted in reef-top crevices, but well over 90% of the cluster members had disappeared by the time all *A. melanopus* had been removed. In the first days of the experiment, many chaetodontids, including *C. ulietensis*, and labrids picked at the substratum that had previously been covered by anemones and their tentacles. In 1989, Godwin removed four *P. biaculeatus* from a cluster of *E. quadricolor* at Lizard Island and also observed the disappearance of all but the smallest anemones in the cluster within two days (manipulation 8).

Thus, chaetodontids apparently preyed on actinians after removal of their symbiotic anemonefishes. The only surviving actinians were either within subterritories of remaining fish (Ross, 1978) or individuals small enough to retract completely into protective crevices. Other fishes subsequently fed in the area no longer defended by anemonefish on epibiota that had been exposed by the removal of the polyps. Sea anemones are known to be important in the diets of some chaetodontids (e.g., Birkeland and Neudecker, 1981; Sano, 1989).

Near Madang, Papua New Guinea, in 1985, Fautin removed *A. melanopus* from a cluster of *E. quadricolor*, this time to observe the fate of the anemones (manipulation 4). On the third and final day of removals, pairs of the chaetodontids *C. kleinii* and *C. oxycephalus* were observed preying on actinians, often fishes of both species simultaneously. The entire cluster was still defensible after a few anemonefish had been removed. However, once 50% of them had been captured, only anemones within the subterritories of the remaining anemonefish were defended; those outside subterritories were eaten. Even on the third day of the experiment, the single individual of *A. melanopus* that was left in the remnant of one of the clusters drove off a pair of *C. oxycephalus*. As at Lizard Island, other fishes also invaded the area, and damage was inflicted on a variety of the sessile biota, e.g., sponges were torn and overturned rocks were grazed clean. In 1987, Fautin removed anemonefishes from two clusters of *E. quadricolor* (manipulations 5, 6). Again, the larger anemones disappeared (presumably were preyed upon), and the smaller individuals retracted into crevices. She was unsuccessful in clearing an additional cluster of *A. melanopus*. This manipulation was in an area of deep crevices, where even rather large actinians could retract completely and anemonefish could hide, thereby avoiding capture. Moreover, it appeared that *A. melanopus* from neighboring clusters (of which there were several) replaced the captured fish; this species is known to swim between individual anemones or clusters that are not in direct contact (Mariscal, 1970; Ross, 1978; Dunn, 1981).

At Piti Bay, Guam, Marianas Islands, in 1988, Godwin removed pairs of adult *A. melanopus* from clusters of *E. quadricolor* as part of a study on fish sex change (manipulation 7). The female of each pair was kept, whereas the male was immediately returned to its anemone cluster after being measured and marked (fin-clipping). Each of the 14 clusters used contained only a single adult pair of *A. melanopus* and one to six juveniles and subadults. In two of 14 manipulations, anemones were preyed on during the approximately 10 min that the male was absent, despite the continued presence of juvenile and subadult anemonefish (four and six smaller fish in the two groups, respectively). Groups of three to seven individuals of the omnivorous chaetodontid *C. ulietensis* fed on anemone tentacles (Fig. 1). Individuals of the omnivorous chaetodontids *C. punctatofasciatus* and *C. bennetti*, and

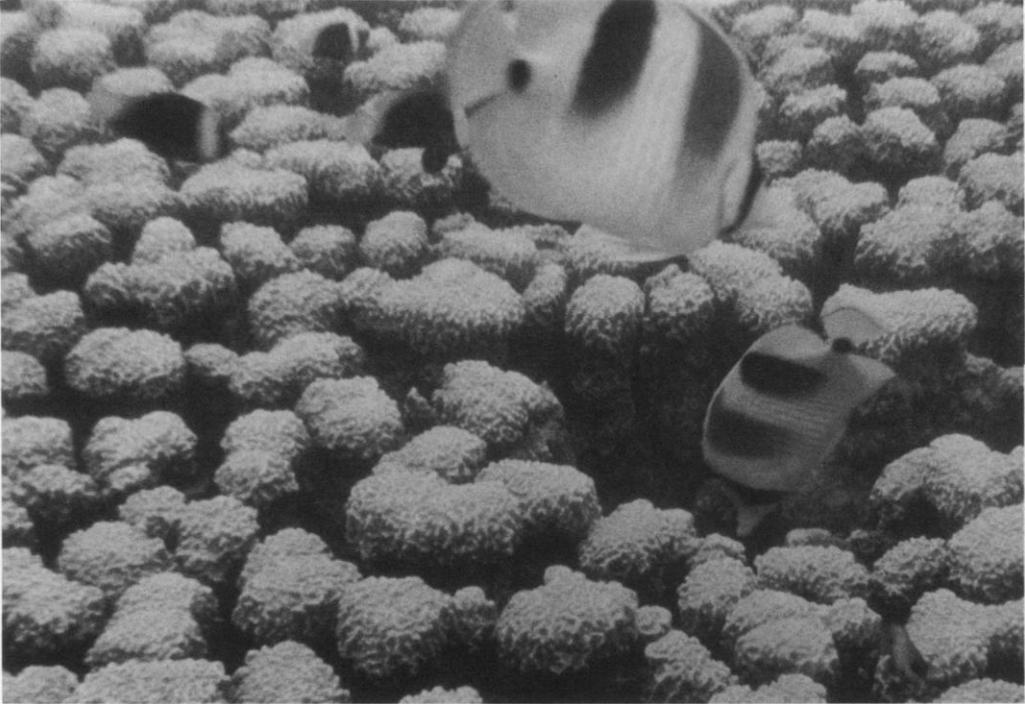


Fig. 1. *Chaetodon ulietensis* feeding on tentacles of *Entacmaea quadricolor*. (Photo by John Godwin)

the primarily herbivorous pomacanthid *Centropyge flavissimus*, did so as well. After detaching and consuming tentacles, many fishes shook their heads briefly. This behavior, also seen in coral-feeding chaetodontids (E. Reese, pers. comm.; Godwin, pers. obs.), may have indicated nematocyst discharge in the fishes' mouths. Although the remaining resident anemonefish did not interfere with feeding by the chaetodontids, they did not engage in normal activities (chasing, feeding, etc.) either, being continually oriented toward the intruders (Fig. 1). Once the males were returned to their clusters and recovered from quinaldine and handling for marking, they chased away the intruding chaetodontids. While at least one adult *A. melanopus* was present, chaetodontids never approached anemone clusters.

Individuals of the Red Sea anemonefish *A. bicinctus* display greater aggression toward chaetodontids than they do toward other fishes, keeping these potential actinian predators at great distance from their territories (Fricke, 1974, 1975). Godwin predicted that a known actinian predator, *C. ulietensis*, would elicit a higher number of attacks from *A. melanopus* than a species which was presumably not a threat to *E. quadricolor*, the herbivorous acanthurid *N.*

lituratus. *Chaetodon ulietensis* elicited 24 and 54 attacks in separate presentations to two pairs of anemonefish, whereas *Naso* provoked little reaction — 0, 0, and 4 attacks in presentations to three pairs, two of which were pairs to which the chaetodontid had previously been presented. Intensity of attack on the two model species also differed; many attacks on the chaetodontid included biting and tearing of the bag (indeed, the bagged individual was injured and bleeding after the second presentation, preventing its further use), but there was no contact with the bag during the *Naso* trials. Sample sizes are small, but the data suggest *A. melanopus* recognizes and shows greater aggression toward potential anemone predators than species which are not a threat to *E. quadricolor*.

Thus the relationship between *E. quadricolor* and at least several of its 12 anemonefish symbionts (see Fautin, 1991) is mutualistic, with each partner defending the other. This is consistent with the observation that *E. quadricolor* is the only one of the 10 host anemones invariably inhabited by fish in nature in the equatorial tropics. It does live without fish symbionts in warm-temperate Japan, which Moyer (1980) hypothesized was because predatory chaetodon-

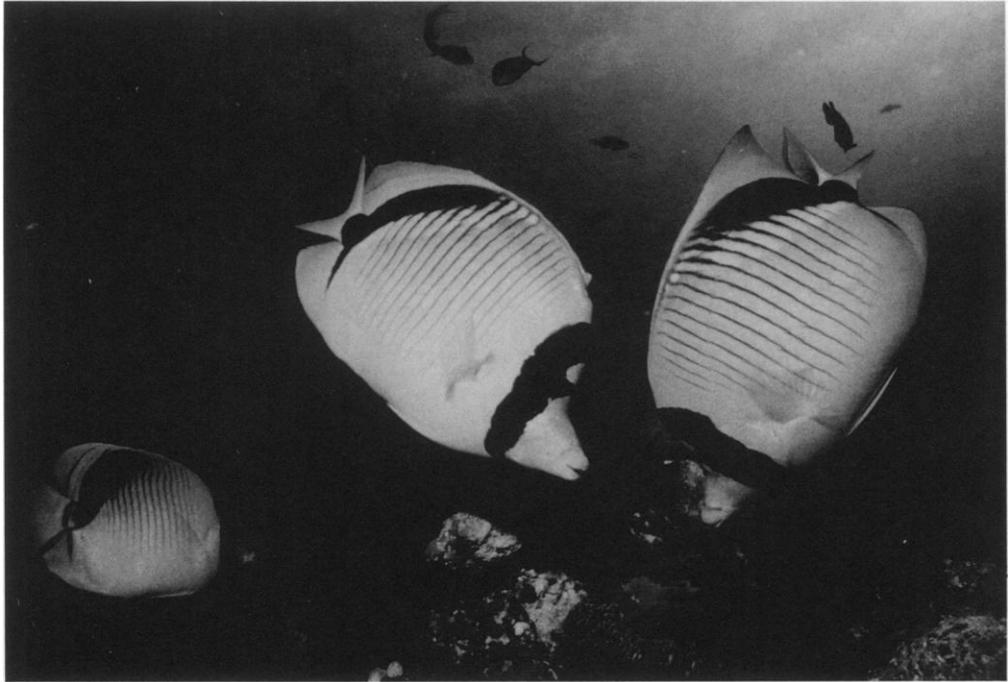


Fig. 2. *Chaetodon lineolatus* and *C. oxycephalus* feeding on *Heteractis magnifica*. (Photo by Claude Strobbe)

tids cannot persist in the relatively cold water. This explanation was given credence when unusually warm temperatures during the summer of 1977 allowed coral reef fishes to invade, survive, and grow more than usual at Miyake-Jima, and many uninhabited anemones were eaten (J. T. Moyer, pers. comm.).

Such interdependence does not hold true for all combinations of actinians and anemonefishes. Being the smallest and most delicate of the symbiotic actinians, *E. quadricolor* may be the most vulnerable to predation. Even in aquaria, it tolerated the absence of anemonefish least well of the actinians that Verwey (1930) studied. Nonetheless, other anemones benefit by association with anemonefishes. On Lizard Island, the day after Fautin removed the three resident *A. percula* from a specimen of the robust *H. magnifica*, its oral disc had closed so that only a central tuft of tentacles was visible (manipulation 2). The next day she reintroduced one *A. percula* to the anemone for an experiment, removing it a day later. The following day a tuft of its tentacles was missing, and five days later there were vertical scrapes on its column. The day after she removed five *A. perideraion* (leaving only one individual of less than 1 cm TL)

from another *H. magnifica* at Lizard Island, a tuft of its tentacles was withered and some appeared to be missing (manipulation 3). Her assistant observed a scarid hovering in the vicinity, occasionally nipping at the anemone's tentacles.

Tentacles of this anemone are often bifurcate or have small side branches, a feature attributed "to *Chaetodon* browsing" by Cutress and Arneson (Department of Energy, unpubl.; who used the name *H. ritteri* for the anemone) in their key to the actinians of Enewetak. C. Strobbe observed *C. lineolatus* and *C. oxycephalus* preying on *H. magnifica* in the Maldiv Islands several times (pers. comm.). On the day he documented it photographically (Fig. 2), the fishes had already destroyed two actinians, the symbionts of which he believes had been captured by aquarium fish collectors, leaving their hosts vulnerable. The sea anemones are easily identifiable in the original slides by their distinctive bright magenta color; also visible is a small anemonefish attacking the chaetodontids. [In addition, Strobbe's photos document the sympatry of these two chaetodontid species, of which Allen (1979) was uncertain.]

Fish are not the only actinian predators against

which anemonefishes are aggressive. G. Ochocki (pers. comm. to Fautin) witnessed three anemonefish attacking a hawksbill turtle (*Eretmochelys imbricata*) that was preying on their anemone(s) in about 8 m of water off Semporna, in Malaysian Borneo. Aggressive behaviors included pecking at the turtle's eyes. From the description, the actinian was probably *E. quadricolor*.

Entacmaea quadricolor and *H. magnifica* are two of the three actinians with the greatest number of anemonefish associates (Fautin, 1991), assuring them a symbiont wherever they are (Fautin, 1985, 1986). We infer that actinians that have a variety of symbionts and are usually occupied by anemonefish derive greater benefit from the association than do those with few associates and that are often unoccupied in nature. The protection against predation afforded them by their anemonefish is an obvious benefit to the actinians. There are probably other benefits as well, to judge by the fact that anemones of all host species except *E. quadricolor* can survive in the equatorial tropics without anemonefish, but most harbor them. The situation may be analogous to corals with symbiotic crustaceans surviving better than those from which they have been removed (Glynn, 1983).

Much or most of the energy on which these anemones live is probably derived from photosynthesis by their endosymbiotic algae (Fautin, 1991). It is therefore essential that they expand their tentacles/oral discs to intercept light. Anemonefishes allow these otherwise vulnerable actinians to occupy appropriately exposed habitats (and are likely to have permitted the evolution of their unusually wide oral discs [Fautin, 1991]). Indeed, few other actinians are found on typical Indo-Pacific reefs. On sand flats, the only other widely distributed anemones are of the family Actinodendronidae, which are protected by both a potent sting and the ability to retract completely into the sand (Fautin, pers. obs.). Anemonefishes provide comparable protection to their hosts, with adults being the primary defenders.

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- JOHN GODWIN, *Hawaii Institute of Marine Biology, P.O. Box 1346, Coconut Island, Kaneohe, Hawaii 96744-1346*, and DAPHNE G. FAUTIN, *Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Present address (DGF): Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045. Accepted 23 June 1991.*

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VARIATION IN THE STRUCTURE OF *POECILIA GILLII* POPULATIONS.—Fishes of the family Poeciliidae are one of the dominant groups in Central America and the West Indies and inhabit a wide range of habitats from large lowland rivers to fast flowing forest streams to small, isolated, stagnant pools (Rosen and Bailey, 1963; Bussing, 1987). Flexibility in diet (Dussault and Kramer, 1981), life-history strategies (Borowsky, 1987; Snelson, 1989; Trexler, 1989), and their ability to survive and reproduce under hypoxic conditions (Chapman, 1990; Kramer and Mehegan, 1981) may have facilitated exploitation of diverse habitats. There has been an increasing appreciation for the degree of variation that can be observed among poeciliid populations and the role of plasticity in their evolution (Stearns, 1983; Reznick and Miles, 1989; Trexler, 1989).

Here we compare the structure of *Poecilia gillii* populations (Kner and Steindachner, 1863) living in isolated residual pools of three inter-

mittent streams, to populations from two everflowing rivers in northwest Costa Rica. The intermittent streams we examined are highly seasonal and experience extreme physical conditions; some pool populations can be periodically decimated by severe floods or dry season desiccation (Chapman et al., 1991; Chapman and Kramer, 1991). The residual pools can remain isolated for up to 90% of the year, although during flooding there is the potential for movement and the mixing of pool populations (Chapman, 1990). In the everflowing rivers we examined, environmental conditions are less dynamic than in nearby intermittent streams, and *P. gillii* can potentially move throughout large stretches of the rivers providing the opportunity for sampling and selection of alternative habitats. We proposed that the fundamental differences between these habitats would be reflected in variation in the structure of *P. gillii* populations.

The ecology and behavior of *P. gillii* has been studied for 20 months over three years in Santa Rosa National Park, Costa Rica, and in nearby lowland areas (Chapman, 1990). Here we report data collected between Dec. 1987 and Feb. 1988. Sampling was initiated approximately 3.5 months after the major flood period of the 1987 rainy season. The climate of the region is characterized by two distinct seasons: the dry season, from mid-Dec. to late May in which virtually no rain falls, and the wet season which encompasses the remainder of the year. During the dry season, all of the water courses within Santa Rosa National Park are dry, with the exception of a few springs and permanent waterholes. In contrast, during the rainy season, the streams and rivers flow in association with major rain events. Lowland areas near the park have similar rainfall regimes, but there are both everflowing and intermittent rivers and streams. The everflowing rivers originate on the forested sides of volcanos and move down into the lowlands.

Residual pools from three intermittent streams within Santa Rosa National Park (Quebrada Jicote, Quebrada Costa Rica, and the upper section of Rio Calera) and sites within two everflowing rivers in nearby areas (Rio Tempisquito and Rio Centeno) were selected for study. The three intermittent watercourses lead into the large intermittent river, Rio Poza Salada. Sampling sites within the streams were upstream areas of the river system, and represented the more extreme areas of Santa Rosa