Review article
The Anemonefish Symbiosis: What is Known and What is Not

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Abstract

The 26 species of anemonefishes (or clownfishes: *Amphiprion* and *Premnas*)
are obligate symbionts of 10 species of sea anemones. The fish are unaffected
by actinian nematocysts because of their mucus coating; whether the mucus
originates with fish, anemone, or some combination has yet to be resolved. The
source of their protection may bear on what happens when a post-larval fish
first encounters an actinian. There is conflicting evidence about whether the
fish displays acclimation behavior — then or ever. This may differ with species
of both fish and anemone. Indeed, not all combinations of species interact
identically, so data from one species pair may not be generalizable. An obvious
manifestation of such differences is that only some combinations of species exist
in nature. This specificity has at least four components: conditioned or innate
preferences by the fish (the more motile and shorter-lived partner, and therefore
responsible for the pattern), environmental requirements, competition by fish for
hosts, and chance. One benefit of the symbiosis to the fish is obvious: its major

source of protection is its anemone, which forms the core of its territory. The symbiosis has commonly been regarded as facultative for actinians. However, in at least some species, anemonefish provide protection against predatory fishes (especially chaetodontids) in the short term. Ultimately, their presence may have permitted evolution of the widely flared oral disc incapable of retraction that is characteristic of many host actinians. This unusual anatomy produces an enormous surface area to intercept light, upon which zooxanthellae depend. The intimacy of this three-way symbiosis invites investigation of the degree to which the actinians depend on their algae for fixed carbon and their fish for nitrogen and possibly other nutrients.

1. Introduction

"The most remarkable circumstance which I met with when wading upon a submerged reef in the China Sea was the discovery of some Actiniae of enormous size, and of habits no less novel than striking. . . .

While I was standing breast-high in the water, admiring this splendid specimen, I noticed a very beautiful little fish which hovered in the water close by, and nearly over, the Anemone. The little fish was 6 inches long, the head bright orange, and the body vertically banded with broad rings of opaque white and orange alternately, three bands of each. . . I made ineffectual attempts to catch him; he always eluded my efforts, not darting away, however, as I expected he would, but always returning to the same spot. Wandering about in search of shells and animals, I returned from time to time to the great Anemone, and each time I found the fish there, in spite of all my disturbance of it. This singular persistence of the fish in keeping to the same spot, and to the close vicinity of the great Anemone, aroused in me strong suspicions of the existence of some connexion between them.

These suspicions were subsequently verified. . . through what is the nature and object of that connexion remains to be proved."

Dr. C. Collingwood, 1868: Note on the existence of gigantic sea-anemones in the China Sea, containing within them quasi-parasitic fish, pp. 31–32

Thus the first person to record the living arrangement of certain members of family Pomacentridae (damselfishes) and some sea anemones described his discovery on Fiery Cross Reef, off the shore of Borneo. People have continued to be intrigued by that mysterious "connexion" ever since.

The fish of concern are the 25 species of genus *Amphiprion* and the one of genus *Premnas* (Allen, 1980) (Table 1), to which I refer as anemonefishes or clownfishes. Facultatively symbiotic pomacentride of the genus *Dascyllus*, which may occupy hosts instead of or along with "true" anemonefishes, primarily when small, are virtually unstudied (Mariscal, 1972). The 10 species of

Table 1. Distribution of fishes among actinians (from Dunn, 1981; Fautin, 1985, 1986, 1988). Species complexes of fishes (Allen, 1972) separated by horizontal lines. "?" indicates questionable record; field records lacking for *A. chagosensis* and *A. latifasciatus*.

| | Actinian species | | |
	Cryptodendrum adhaesivum	*Entacmaea quadricolor*	*Macrodactyla doreensis*
Fish species			
Premnas biaculeatus		x	
Amphiprion ocellaris			
Amphiprion percula			?
Amphiprion polymnus			
Amphiprion sebae			
Amphiprion latezonatus			
Amphiprion akallopisos			
Amphiprion nigripes			
Amphiprion perideraion			x
Amphiprion sandaracinos			
Amphiprion leucokranos			
Amphiprion ephippium		x	
Amphiprion frenatus		x	
Amphiprion mccullochi		x	
Amphiprion melanopus		x	
Amphiprion rubrocinctus		x	
Amphiprion clarkii	x	x	x
Amphiprion akindynos		x	
Amphiprion allardi		x	
Amphiprion bicinctus		x	
Amphiprion chagosensis			
Amphiprion chrysogaster			
Amphiprion chrysopterus		x	
Amphiprion fuscocaudatus			
Amphiprion latifasciatus			
Amphiprion tricinctus		x	
Number of fish	1	12	3?

Table 1. Cont.

| | Actinian species | | | |
	Heteractis magnifica	Heteractis crispa	Heteractis aurora	Heteractis malu
Fish species				
P. biaculeatus				
A. ocellaris	x			
A. percula	x	x		
A. polymnus		x		
A. sebae				
A. latezonatus		x		
A. akallopisos	x			
A. nigripes	x			
A. perideraion	x	x		
A. sandaracinos		x		
A. leucokranos	x	x		
A. ephippium		x		
A. frenatus				
A. mccullochi				
A. melanopus	?	x		
A. rubrocinctus				
A. clarkii	x	x	x	x
A. akindynos	?	x	x	
A. allardi			x	
A. bicinctus	x	x	x	
A. chagosensis				
A. chrysogaster			x	
A. chrysopterus	x	x	x	
A. fuscocaudatus				
A. latifasciatus				
A. tricinctus			x	
Number of fish	11?	12	7	1

Table 1. Cont.

	Actinian species			Total actinian associates
	Stichodactyla haddoni	*Stichodactyla gigantea*	*Stichodactyla mertensii*	
Fish species				
P. biaculeatus				1
A. ocellaris		x	x	3
A. percula		x		4?
A. polymnus	x			2
A. sebae	x			1
A. latezonatus				1
A. akallopisos			x	2
A. nigripes				1
A. perideraion		x		4
A. sandaracinos			x	2
A. leucokranos			x	3
A. ephippium			?	3?
A. frenatus				1
A. mccullochi				1
A. melanopus				3?
A. rubrocinctus		x		2
A. clarkii	x	x	x	10
A. akindynos	x	x	x	7?
A. allardi			x	3
A. bicinctus		x		5
A. chagosensis				–
A. chrysogaster	x		x	3
A. chrysopterus	x		x	6
A. fuscocaudatus			x	1
A. latifasciatus				–
A. tricinctus			x	3
Number of fish	6	7	12?	

actinians with which clownfishes associate (Table 1) are taxonomically much more diverse than their hosts, belonging to five genera and three families (Dunn, 1981). [There is some disagreement among actinian systematists in details of nomenclature and/or taxonomy (e.g. Cutress and Arneson, 1987; England, 1987, 1988.)] The most familiar host anemones belong to the two genera of family Stichodactylidae, *Stichodactyla* (previously referred to as *Stoichactis*) and *Heteractis* (previously referred to as *Radianthus*). Although often referred to as "giant anemones, " not all species are characterized by great size. However, individuals of *S. mertensii* attain the largest diameter of any sea anemone, 1.24 m having been documented (Mariscal, 1970a). Usually, fish of only one species occur with an individual actinian, but occasionally those of two species share a host (usually a large one, which they divide into exclusive territories, so that they are not actually sharing the space). In rare instances, fish of three species may coexist.

These actinians live in the tropical and suitable subtropical parts of the Indo-West Pacific region. Being zooxanthellate, they are confined to the photic zone, about as many species living in sediments surrounding or distant from coral reefs as on reefs themselves. Because clownfishes are obligate associates of sea anemones, their range cannot extend beyond that of their hosts. In fact, it is somewhat more restricted both geographically and ecologically — although some anemones tolerate moderately turbid conditions, individuals in murky environments seldom contain fish (personal observation). The greatest diversity of these animals is around New Guinea: all 10 host anemones and 9 fishes occur near Madang (Fautin, 1988). Numbers of both diminish outward from there; a typical central Indo-Pacific locality has up to five species of fish and about an equal number of anemones.

Two concerns originally dominated research on the anemonefish symbiosis: what prevents the fish being stung by actinian nematocysts; and what advantages and disadvantages has this living arrangement for the partners? Neither has yet been answered definitively. Aside from the symbiosis itself, the fishes have proven ideal for research on some aspects of reproductive biology and tropical marine ecology. Each sea anemone (or cluster of them, in some cases) is virtually immovably fixed; it and the surrounding water constitute the territory of its fish. With rare exceptions, an individual seldom ventures more than a few meters from its host for more than about a minute at a time, usually retreating into its tentacles when threatened (Allen, 1972). This sedentariness and site-attachment, which so intrigued Dr. Collingwood, permit long-term studies on identifiable animals, which have produced fascinating data on social organization and sex change. It also allows manipulative research on coral

reef fish community organization, a subject of recent controversy and vigorous research (summarized by Mapstone and Fowler, 1988).

My objectives in this paper are to (1) summarize critically what is known about this symbiosis (a word that I employ in its literal sense of "living together," without implication of benefit or detriment), concentrating on developments since Mariscal's (1966, 1970b, 1972) reviews, and (2) identify disputed issues and strategies for their resolution. Much of the supposedly conflicting information can be reconciled by viewing the anemonefish symbiosis not as a unitary phenomenon, but as a relationship with various manifestations, depending on the species of fish and actinian involved. Treating it as a three-way symbiosis, which includes the zooxanthellae of the actinians, also casts new light on the evolutionary background and significance of some phenomena.

2. Mechanism(s) of Protection

The existence, function, and toxicity of nematocysts (cnidarian stinging capsules) were known when the anemonefish symbiosis was described. Thus, Collingwood's (1868) prime concern was how the fish manage to survive in an environment deadly to fishes even larger than clownfishes. A number of hypotheses to account for this invulnerability have been advanced, and may be refuted, as follows. (1) Host tentacles do not contain nematocysts. Not only are they present (primary evidence summarized by Gudger [1946]) and "capable of exerting a strong adhesive force" (Lubbock, 1980, p. 44), but nematocysts of all 10 species of host actinians are typical in kind and quantity to those of most sea anemones (Dunn, 1981). (2) Fish do not actually touch the tentacles. While this is true of many of the more than 30 species of Caribbean fishes that associate with actinians (e.g. Albrecht, 1977; Hanlon and Hixon, 1986), genuine anemonefishes swim among tentacles and nestle into them at night (Verwey, 1930; Allen, 1972; Mariscal, 1972; Moyer and Sawyers, 1973). (3) The skin of these fishes is impenetrable to nematocysts. It is, if anything, thinner than that of other damselfishes (Caspers, 1939), and an unacclimated clownfish (see below) can be killed by its host's sting (Mariscal, 1966). (4) While a fish is present, the actinian will not discharge its nematocysts. Although cnidarians can exert some control over firing (e.g. Thorington and Hessinger, 1988), this does not explain the symbiosis because an actinian can sting both prey (Gohar, 1948; Mariscal, 1969b) and unacclimated anemonefish (Mariscal, 1969a) while harboring acclimated fish. This implies that the fish, rather than its host, is responsible for its invulnerability to being stung.

Anemonefish may nibble their host's tentacles (e.g. Verwey, 1930; Davenport

and Norris, 1958; Mariscal, 1972), which, it had been speculated, might immunize them against being stung (Gudger, 1946). [Fricke (1974), observing nibbling just prior to fish spawning, speculated that the resultant contraction may serve to protect newly-laid eggs from being nettled.] The term "immunity" is wisely, but erroneously, used to describe a fish's invulnerability to nematocysts; it has been convincingly demonstrated (Davenport and Norris, 1958; Mariscal, 1969a,b, 1970a) that the source of protection is not systemic, but resides in the surficial mucus coating of the fish.

Schlichter (1967, 1968b, 1976) proposed that this mucus originates with the host actinian and is transferred to a fish through acclimation behavior, first reported by Gohar (1948). Davenport and Norris (1958) detailed what happens when a clownfish that has been kept separate from an actinian is returned to one. Initially apparently stung, through a series of stereotyped motions the fish brings more and more of its body in contact with tentacles until finally they no longer cling. This process, which has since been described repeatedly (e.g. Schlichter, 1968b; Mariscal, 1969a; Allen, 1972; Trivedi, 1977; Miyagawa, 1989), may take minutes or hours. Protection of the fish can disappear, through time (Schlichter, 1968b; Mariscal, 1969a) and by disturbing the fish's mucus coat (mechanically: Davenport and Norris, 1958; Mariscal, 1969a,b; or chemically: Schlichter, 1975). A fish's normal behavior of returning frequently to its anemone can be interpreted as serving to maintain its protection (Schlichter, 1968b; Foster in Losey, 1978). Mucus proteins of acclimated and unacclimated fish differ; moreover, so do mucus proteins of a fish acclimated to different species of hosts (Schlichter, 1976). Having found radiolabeled amino acids that had been incorporated into an anemone's mucus on the surface of fish living with it, Schlichter (1970) hypothesized that "protecting substances" inhibit nematocyst discharge. Produced to prevent an actinian stinging itself, this material rubs onto clownfish and other objects in the environment with which the anemone comes in frequent contact (Schlichter, 1972). This results in the symbiont being chemically camouflaged (Schlichter 1972, 1976) — a fish in anemone's clothing. Thus, according to this theory, it is their behavior that allows clownfish to live in this peculiar habitat (Schlichter, 1968b).

Lubbock (1980b, 1981) inferred from his experiments that the protective mucus originates with the fish itself. In general, mucus from anemonefish did not stimulate nematocyst discharge as did mucus from other fishes, whether or not the source clownfish was living in an actinian. A glass rod coated with mucus from another pomacentrid elicited nematocyst discharge whether or not it had subsequently been coated in anemone mucus. Clownfish mucus, although 3–4 times as thick as and differing chemically somewhat from that of related

fishes, was no thicker on fish living in actinians than on isolated ones. Also, in contrast to Schlichter (1972), Lubbock did not find radiolabeled anemone mucus in appreciable amounts on resident clownfish; so anemone mucus on fish may be a *result* of the protection rather than its *cause*. Denaturation did not make anemonefish mucus more stimulatory to nematocysts, leading Lubbock to conclude that fish mucus does not inhibit nematocyst discharge but lacks "excitatory substances" that stimulate firing. According to this interpretation, the secret to a clownfish's peculiar habitat is biochemistry.

Experiments of Miyagawa and Hidaka (1980) and Miyagawa (1989) dealt mostly with naive post-larvae and juveniles, rather than adult fish artificially separated from actinians. Post-larvae were killed outright when forcibly brought into contact with anemones. However, juveniles of most species were killed only by non-symbiotic actinians, from which the investigators concluded that protection is innate. Nonetheless, they, like Lubbock (cited above), documented acclimation behavior.

There are several possible, not mutually exclusive, explanations for apparently contradictory evidence concerning how the fish are protected. As Mariscal (1970a) found for earlier research on this symbiosis, there may be flawed logic in experiment interpretation and lack of rigorous controls. Misapprehension about which partner acclimates appears to account for Fishelson's (1965) denial of its existence: it is not clear from his writing whether the fish had been isolated or were moved directly from one actinian into an inhabited one. This, therefore, may have been identical to Trivedi's (1977) experiment supporting the passive role of the anemone: when a fish from one host is transferred to another of the same species lacking symbiotic fish, reaction is absent in both. Nor does a fish necessarily acclimate when transferred between hosts of different species (Schlichter, 1968a). Miyagawa and Hidaka (1980) experimented on how an anemone is initially located, as well as how the fish is protected. Either experiment could have confounded the other, if the same individuals were used for experimental attraction to an anemone in a gauze bag and for forced contact. Schlichter (1975) found actual contact with an actinian unnecessary for acquisition of protection by a fish. Thus, a fish first used in the attraction experiment might have acquired protection sufficient to permit its survival at forced contact. Reciprocally, the period of forcible contact with an actinian might have sufficed to sensitize it to anemone chemicals, resulting in the observed attraction. Forcible contact also carries the risk of injury, particularly to tiny fish, or at least disturbance of the mucus coat, the key to fish protection. Repetition of critical experiments is necessary to resolve these questions.

Definition of "acclimation" is an issue, as Miyagawa (1989) recognized.

Despite providing a classic description of acclimation behavior, she asserted that acclimation was not involved because the fish "are never actually stung" (p. 41), based on the absence of discharged nematocysts on their scales. Indeed, she claimed that a fish might "behave as if stung" (p. 39) even when it had not been. Fukui (1973) attributed tentativeness of a fish's initial contacts with an actinian to "cautious testing" — a trial and error process to determine if it is of an appropriate symbiotic species. At issue seems to be whether behavior that has been associated with acclimation serves that end. Miyagawa's (1989; Miyagawa and Hidaka, 1980) report of the behavior in juveniles belies her explanation of it as an artifact of separating animals that normally are never parted. If an alternative or additional criterion, such as discharged nematocysts on fish scales (Fukui, 1973; Miyagawa, 1989), is invoked, the observed behavior must be explained in other than a *post hoc* manner. On the other hand, applying a single criterion might be inappropriate in a system as variable as this one (see below).

Both actinian and fish may contribute to the protective mucus. Using the nematocyst discharge assay, Fukui (1973) found that scales of unacclimated clownfish provoked slightly greater discharge than did those of acclimated fish, but scales of another pomacentrid elicited discharge several times greater. Lubbock (1980, p. 59), having established that the acclimation period of *A. clarkii* differs with species of actinian, posited that fish may be "able to reduce the levels of certain excitatory substances in their mucus, perhaps as a result of being stung by the anemone." Likewise, Miyagawa (1989, p. 41), while speculating that the "similar behaviour to that described in the acclimation process" may benefit clownfish "by increasing the thickness of their own protective mucus layer and decreasing their foreignness to the anemone," asserted that this "is not essential for acquiring protection against a host anemone." In an intriguing experiment, Brooks and Mariscal (1984) found that average acclimation time following prolonged separation of *A. clarkii* from its anemone *Macrodactyla doreensis* is reduced significantly if the fish had been kept with a surrogate sea anemone made of rubber bands glued to a Petri dish. Perhaps a substance synthesized by the fish in the presence of an "anemone" is altered or augmented by a real actinian.

Adaptation may differ among species or combinations of species. This symbiosis is far from the unitary phenomenon that Moser (1931) supposed it to be and as it is often implicitly treated in contemporary studies. Variability in interaction is well documented, as, for example, in advantages of the relationship (below), and in attachment of fish to host (Verwey, 1930; Allen, 1972). Lubbock (1980a) recognized that his data might be true only for those species on which he worked (although he made that point less explicitly in his more

technical publications [1980b, 1981]). Despite recognizing (1980a) that inconsistencies in the literature might be accounted for by different species having been studied, he concluded, from research with two actinians and one fish, that there are two classes of hosts: those to which fish have innate protection, and those to which fish must acclimate (during which process "the anemone's sting response to the fish dies down" [p. 154] for reasons described above).

Had Lubbock worked on more fishes he might have recognized, as Miyagawa (1989) did, that fish also vary. Moreover, the behavior of a single species may differ with alternative partners: Lubbock (1980a,b) found that *A. clarkii* required almost no time to acclimate to *S. haddoni* but nearly four days for "*Gyrostoma hertwigi*" (*Entacmaea quadricolor* [see Dunn, 1981]), and Miyagawa (1989) reported considerable differences in the way young *A. clarkii* approach two species of host actinians; conversely, actinians of one species, "*S. kenti*" (*S. gigantea* [see Dunn, 1981]), kill young of *A. clarkii* and *A. sandaracinos* but not of *A. ocellaris, A. frenatus*, or *A. perideraion* (see Miyagawa, 1989). While acknowledging that differences in specificity might bear on her experiments, Miyagawa minimized the variability she had found, such as some juveniles being slightly harmed by forced contact with an actinian and the death of the supposedly innately protected *A. perideraion* in "*S. kenti*" after it had lived with "*R. kuekenthali*" (*H. crispa* [see Dunn, 1981]). She overgeneralized from her results to conclude that "*Amphiprion* juveniles, at least from the coastal region of Japan, do not need to acclimate themselves with a symbiotic sea anemone as they already have an innate protection" (p. 41). Her extensive experiments clearly demonstrate that not all species combinations interact identically.

It may also be that the mechanism of adaptation changes through ontogeny. Thus, differing results from experiments with settling post-larvae and with adults separated from their hosts may be equally valid. To test this, experiments should be done on initial adaptation of naive fish, and then — months or years later — on the same fish artificially separated from the actinian host in which they had matured.

3. Specificity and Other Species Interactions

That the relationship between fishes and actinians is not monolithic is most obvious in host specificity (Table 1). Of the 26 fishes, only *A. clarkii* naturally occurs with all 10 anemones; about a quarter of the fishes live with a single species of actinian, and the rest for which hosts are known occur with several; conversely, nearly a third of the anemones harbor 12 fishes each, while two play host only to *A. clarkii*.

What governs which species occur together? Clearly, the fishes, being the shorter-lived and motile partner, are responsible for this pattern. But how do they choose? As Verwey (1930) recognized, only species that occur in the same geographical area and have similar habitat tolerances — sand or reef, deep or shallow — can potentially live together. But not all do. I have identified four additional factors, in diminishing order of importance, that control specificity (Fautin, 1986). (1) Fish have an innate or learned preference for only some of the anemones potentially available for colonization. I expand on this below. (2) There is division according to microhabitat of the host. Particular growth forms of an anemone species are favored by different fishes (Fautin, 1986). (3) Fish compete for anemones that belong to the subset of acceptable hosts. Once a fish settles into an anemone, it prevents occupation by members of other species (with rare exceptions) but not its own (Mariscal, 1972; Fautin, 1985, 1986). Fish of different species that simultaneously occupy an empty actinian compete with each other (personal observation). (4) Chance. A fish of a species that competes poorly is occasionally found in a highly preferred anemone (Fautin, 1988) that presumably missed being colonized by a member of a superior species. Once in possession of the anemone, it prevents occupation by individuals of other species, even competitively superior ones (Fautin, 1986).

The mechanism by which fish adapt to anemones may be reflected in their host specificity. If protection resides in a fish's own mucus, specificity might simply be due to the deaths of those that happen to settle into inappropriate hosts. Indeed, some anemonefish are killed by host actinians with which fish of that species do not normally occur (Miyagawa, 1989; personal observation). However, that mechanism does not explain how some can live with almost any host actinian in captivity (e.g. Allen, 1972), much less with anemones from temperate seas (Moser, 1931; Mariscal, 1969a, 1972) and the Caribbean (a popular host for home aquaria in the US is *Condylactis gigantea*). Nor can it account for Miyagawa's (1989) finding "*S. kenti*" and *A. clarkii* to be a lethal combination although it occurs in nature (Table 1). Further, any mechanism(s) must account for a range in host specificities among the 26 clownfishes.

Specificity is affected not only by how fish adapt, but also by how they locate hosts. Miyagawa and Hidaka (1980) and Miyagawa (1989) found that juvenile anemonefish are attracted chemically, but not visually, to host actinians. (Visual attraction was reported in adults by Davenport and Norris [1958], Mariscal [1972], and Fukui [1973]; Fricke [1974] documented chemical recognition of hosts by juveniles of *A. bicinctus* and visual recognition by adults, an example of ontogenetic difference, as proposed above.) Murata et al. (1986) characterized two compounds, one from each of two host actinians. Each substance attracts juvenile clownfish of a species known to occur normally with

that anemone but not fish that are not its natural symbionts. These data, while suggestive, do not entirely explain anemonefish specificity, for fish of other species that inhabit the two actinians were not attracted by the substances; in particular, *A. clarkii*, which lives with both subject anemones (not merely one, as stated), was drawn to neither.

At least for *A. perideraion*, which exhibited the strongest and most consistent reaction, field-collected animals (not naive ones), which had been living with hosts of the subject species, were used. There may be a similar flaw in Miyagawa's (1989) experiment. She apparently used post-larvae and juveniles raised from "eggs [laid] close beside the host anemone" (p. 20). If, as she speculated and I have long believed, embryos may imprint on dissolved anemone compounds, even hatchlings are not truly naive (Davenport and Norris [1958] reported that clownfish eggs do not provoke nematocyst discharge; according to Fricke [personal communication], once attached to the substratum, eggs of *A. bicinctus* are unaffected by contact with the anemone, but prior to that they may be eaten by it). Nor is it clear that she used appropriate controls in her experiments with *A. frenatus*, which "had been kept in complete isolation from sea anemones until immediately before hatching" (Miyagawa and Hidaka read 1980, p. 356). More germane to the experiment is how the fish were treated between hatching and experimentation.

Although it makes no operational difference to the patterns manifested in nature, distinguishing between innate preference (a closed developmental program) and imprinting (an open program) is of theoretical interest, and could be accomplished by rigorously controlled experiments. Assessing attraction to a variety of anemones by young fish raised isolated from anemones (as is possible for some species [Allen, 1980]) and water that has been in contact with them would permit distinction between open and closed programs (imprinting and general affinities, versus innate preference and specific affinity, respectively). Experiments with a species of fish that inhabits two species of hosts (four are known [Table 1]) would be especially interesting. Fish from eggs that developed beside each host and in isolation (if possible) would be given a choice between an individual of each anemone. Selection of the species beside which they were raised would imply the operation of imprinting, and thereby that the developmental course of an individual is less genetically canalized and more responsive to circumstance. Such behavior would promote assortative mating, and therefore could be an important mechanism of sympatric speciation. Selection of the species in which their parents lived, regardless of where the eggs were raised, would imply determinism in development and little individual flexibility. In addition to attraction to hosts, chemical attraction of

juveniles to conspecific adults should be investigated. Larvae of two species of *Dascyllus* locate settlement sites in this manner (Sweatman, 1988).

Having apparently found a chemical attractant for one species of fish, Murata et al. (1986) generalized to all, presuming that there must be another, as yet unidentified, to account for the symbiosis of *A. clarkii*. I have concluded from published data and my own observations that there is a spectrum of mechanisms by which fish locate and adapt to hosts. *Amphiprion clarkii* represents the extreme in generalists. It is no coincidence that the two actinians associated with only a single species of fish both harbor this, the least host-specific anemonefish (Table 1). Its broad host range is intimately related to its being the geographically most widespread species. These facts, plus its ability to adapt to exotic anemones (with which it has had no previous contact, as an individual or a species), make innate protection highly unlikely for *A. clarkii*. Schlichter's (1976) finding that the mucus of *A. clarkii* differed with the host to which it was adapted is strong evidence that its protection derives at least partly from the anemone. Miyagawa (1989, p. 41) termed the combination of *A. clarkii* and its kin with "*S. kenti*" "protection-ineffective," and conceded that in such cases acclimation behavior might occur, although she hesitated to term it such. Such behavior would allow generalists to be opportunistic, settling into whatever anemone might be available. I infer also that these fishes probably locate their symbionts at least partly by sight. Generalists find and adapt to hosts by virtue of behavior, as Schlichter (cited above) proposed.

At the end of the spectrum are specialist species — those specific to one or two hosts, of which *P. biaculeatus* is the extreme. I infer that the reason for this is their ability to locate their host(s) by chemical cues. It does not necessarily follow from chemical attraction that protection is innate, but these animals cannot readily adapt to other than their normal hosts, so the two are likely to have evolved together, as part of a closed developmental program. Indeed, *Premnas* does not respond to actinians other than *E. quadricolor* as potential hosts (personal observation). If acclimation behavior is truly absent (e.g. Verwey, 1930) in any anemonefish, I would predict it would be in (a) host-specific species. Chemically based location and adaptation, as proposed by Lubbock (cited above), confines these fishes to a limited array of hosts. Fishes with greater host specificity are competitively superior for their anemones to those with less specificity (Fautin, 1985, 1986). This is adaptive since they, unlike generalists, lack alternatives. I infer that the generalist-specialist spectrum in host specificity is paralleled by a behavioral-biochemical spectrum in how fish locate and adapt to hosts.

Specificity — and perhaps the individual's history (Davenport and Norris, 1958) — must be considered in the design of experiments. The most widely

used fish in the laboratory has been *A. clarkii* (e.g. Mariscal, 1969, as *A. xanthurus*; Lubbock, 1980; Miyagawa and Hidaka, 1980). This is related to its abundance and the ease with which it is kept in captivity (Lubbock, 1981), concomitants of its lack of host specificity. Companion experiments to crucial ones done with *A. clarkii* should be carried out with host-specific species (and vice-versa).

Sea anemones may be affected by their fish associates. Fukui (1973) found behavioral differences in actinians with and without fish, and Lubbock (1980) documented increased movement on the part of an anemone in the presence of fish. A host can affect its fish as well. Juveniles, but rarely sexually mature fish, occur with *H. aurora* and *H. malu* (e.g. Graefe, 1963, 1964; Fishelson, 1965; Fricke, 1974; Moyer, 1976; Dunn, 1981). These hosts, which Moyer (1976) and I (Dunn, 1981) consequently termed "nursery anemones, " are sufficiently hospitable that fish survival and some growth are possible in them. Given that host abundance limits anemonefish numbers (Allen, 1972), these actinians may allow residents the potential to move into hosts of more appropriate species by "jumping the queue" (see below) when larger. Although it is rare, some clownfish wander from their hosts (see below). Such fish are highly vulnerable, but if one occasionally survives the transition and reproduces, opportunistic settlement into "nursery anemones" could be successful, evolutionarily.

Some effects are characteristic of only particular combinations of species. Normally orange-colored portions of certain fishes darken when they occupy particular actinians (Allen, 1972, 1980) (this differs from melanism associated with size and some geographical populations [Allen, 1972, 1980; Bell et al., 1982].) Examples of combinations exhibiting this phenomenon are *A. chrysopterus* in *S. mertensii*, and *A. polymnus* in *H. crispa*. An orange fish of an appropriate species transferred to or from an anemone that affects it in this way will change color within a matter of days (or possibly less) (Allen, 1972). The adaptive value to either partner of this reaction is unknown.

Whether anemonefish ever enter a host's mouth is disputed (summarized by Mariscal, 1966, 1970b). I, like Verwey (1930) and Gohar (1948), had doubted its reality, attributing reports to fish being hidden in folds of the oral disc (Dunn, 1981). However, I have since seen a large female *A. polymnus* dive inside a large specimen of *S. haddoni* under field conditions in Papua New Guinea. I do not know what caused the behavior and could not elicit it again by pursuing the fish. Reports that are at variance may reflect variability in occurrence — only some fish may enter their hosts, and/or perhaps only certain hosts are entered. Certainly in other aspects of the symbiosis, as information

accumulates and more attention is paid to accurate identifications, it is becoming clear that one cannot speak of *the* anemone/fish symbiosis: there are nearly as many variants of its as there are combinations of species.

4. Advantages of the Relationship

With rare exceptions, post-larval clownfishes occur in nature only associated with an anemone (e.g. Gohar, 1948; Mariscal, 1970a; Allen, 1972; personal observation). When threatened, most dive among the host's tentacles, from which other fishes remain distant. Taking clownfish far from their anemones or removing anemones from beneath their fish usually results in the fish sooner (in the former instance) or later (in the latter) becoming prey of larger fish (Verwey, 1930; Eibl-Eibesfeldt, 1960; Mariscal, 1970b; personal observation). The obligate nature of the symbiosis to the fish is *prima facie* evidence of its being advantageous to them (Verwey, 1930); the exceptions only strengthen this conclusion. Moyer (1980) found that adults of *A. clarkii* in warm temperate southern Japan may range widely, away from actinians, but only after water temperature drops in autumn, when breeding activity has ceased. He attributed this increased mobility partly to reduced predation (on both fish and anemones), relative to tropical seas. Another apparent exception to anemonefishes being tied to their hosts is that juvenile, but not adult, fish may wander among clusters of actinians (Ross, 1978b; Fricke, 1979; but see Mariscal, 1970b). Without exception, residence in an anemone is essential to reproduction of the fish: their eggs, tended primarily by the male, are laid beneath the oral disc overhang of the host (Allen, 1972; Moyer and Bell, 1976; Fricke, 1979; Moyer and Steene, 1979).

Dependence of fish on actinians is behavioral, not physiological, as evidenced by their ability to survive alone in captivity (which is not to deny that fish might benefit by association with an anemone). In the absence of an actinian, captive fish will bathe among air bubbles or frondose vegetation, so appear to obtain tactile stimulation from anemone tentacles (Mariscal, 1970b, 1972; Fricke, 1974; Trivedi, 1977). The claim (Fishelson, 1965; Lubbock, 1980a) that fish are healthier when kept with anemones suggests that they profit in other ways, too.

The nutritive benefit fish derive from feeding on anemone waste/egestate or even tentacles (Verwey, 1930; Davenport and Norris, 1958; Mariscal, 1966, 1970b, 1972) does not appear to harm their hosts (i.e. the fishes are not parasites on their hosts). But neither are benefits to the actinians obvious, particularly since individuals of symbiotic species may lack fish in nature (Fishelson,

1965; Dunn, 1981). Like the fish, actinians survive in aquaria without symbiotic partners, although it has been claimed (e.g. Verwey, 1930, and other references cited by Mariscal, 1966) that anemones do better in captivity with fish. Among postulated benefits (Mariscal, 1966) that are unlikely to be real or, at least of much significance, are circulating water around the sea anemone (they live in areas of considerable water movement, and generally are much larger than the fish), and removing parasites from it.

Saville-Kent (1893) suggested that a fish benefits its host by luring other fishes into the anemone as food for it. In fact, the reverse is true. Apparently Moser (1931) was the first to suggest that the fish protects its host, but he thought that only the actinian derives benefit from the relationship. At least some species of butterfly fishes (Chaetodontidae) eat actinians (Fishelson, 1965; Sano, 1989). Presumably they are protected from nematocysts of anemones by the same (unknown) mechanism that protects them from nematocysts of corals, on which they also prey. In nature, chaetodontids will feed on actinians from which symbiotic fish have been removed (Allen, 1972 — Enewetak; Fautin, 1986 — Australia; Moyer, personal communication — Japan; personal observation — Papua New Guinea). Fricke (1974, 1975a) found that individuals of *A. bicinctus* selectively recognize and chase off those of *Chaetodon fasciatus* in the Red Sea. All documented cases of such predation involve the anemone *E. quadricolor*. Typically smaller than other clownfish hosts, it always contains fish in nature (Verwey, 1930, as Anemone 5; Fautin, 1986), except for some tiny individuals and in subtropical Japan, as discussed above. Its association with so many fishes (Table 1) assures it a symbiont wherever it is (Fautin, 1985, 1986); in aquaria, it tolerates the absence of fish least well of the actinians Verwey (1930) studied. Thus, for *E. quadricolor*, the relationship with fishes is mutualistic. Fish attractants are most likely to have evolved in actinians, such as this one, that obviously benefit from the relationship (at least 4 of the 12 fishes associated with *E. quadricolor* are specific to one or two hosts; by contrast, *C. adhaesivum* is rarely occupied by fish, and then it is only *A. clarkii* (Table 1). Although fish are not so obviously vital for all hosts, since at least some of the larger anemones can survive alone in nature, similar advantages may accrue to them (Fautin, 1985). It is possible that some derive no benefit from their relationship with clownfishes, as Schlichter (1967, 1968b) concluded was true for the relationship as a whole.

One frequently cited benefit to the anemone is being fed by its fish. This behavior, which varies with the species of fish (Verwey, 1930), has been described repeatedly (Mariscal, 1966, 1970b, 1972), mainly from aquaria. The natural diet of clownfishes is plankton from the water above the anemone and algae that grow around it (Mariscal, 1970a; Allen, 1972), so the fish eat their

food where they find it. The feeding of large morsels in an aquarium produces an artifact: unable to devour the piece immediately, a fish takes it to the security of its territory, which may consume the food (e.g. Moser, 1931; Allen, 1972)! During "many hours" of observation in nature, Allen (1972) twice observed a fish feeding its host, an Fricke (1974) saw it once in 1500 hours. Is this frequency sufficient for it to have been significant in the evolution of the relationship? However, a much more significant nutritive contribution of the fish to their hosts may be their wastes, which are rich in nitrogen and possibly other nutrients such as sulfur and phosphorus.

5. Evolutionary Implications of the Symbiosis

The vulnerability of fish outside an actinian, and of their actinian without them (because it will be either occupied by other fish or preyed upon), has led to extreme sedentariness in anemonefishes. Their unusual social organization and reproductive biology represent accommodations to the potential disadvantages of life in a small and relatively rare, but rather permanent, habitat. An anemone is typically occupied by an adult pair of fish (the larger being the female) and from none to many juveniles (the number being roughly species specific), each slightly smaller than the next (Verwey, 1930). Post-larvae settle from the plankton, at the bottom of the queue, as space becomes available by the disappearance of larger residents, thereby providing continual protection of the actinian, and securing it in perpetuity for occupation by fish of that species (personal observation). Monogamy, unusual in damselfishes, is an adaptation to the limited size of the social group that can be accommodated (Fricke, 1974, 1975b). Their protandry (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a; Fricke, 1979; Wood, 1986) guarantees clownfish a mate of the appropriate sex without its being sought (Fricke and Fricke, 1977; Fricke, 1979; Wood, 1986). Social control of sex and growth (Fricke, 1974, 1975b, 1983) assure a resident reservoir of potential mates and prevent over-exploitation of the limited resource. Thus the anemone partner may have been integral to structuring the social/sexual system of its fish symbiont.

Reciprocally, I speculate that fish — in concert with zooxanthellae — have had a key role in shaping the morphology of many host species. All host actinians have zooxanthellae within the endodermal cells of their oral discs and tentacles (Dunn, 1981). Presumably, as in other zooxanthellate cnidarians, the algae are capable of supplying a host's full needs for fixed carbon (Muscatine, 1974). The widely flared disc of a host anemone and its dense tentacles represent an immense area for the interception of light. I believe it is adapted to harvest photons as the gut epithelium of a vertebrate is to

absorb small molecules (Fautin, 1987). In response to perturbations such as threat by predators, a typical actinian retracts its oral disc, closing its upper column over its tentacles. A concomitant of a host actinian's oral disc breadth is weak musculature (Dunn, 1981), so most such anemones are unable to retract, but what would otherwise be a liability is not because of the protection provided by the fish. These anemones are likewise poorly adapted to capture prey. I suggest that the sea anemone's diminished predatory ability has been compensated for by fixed carbon from algae, and possibly nitrogen (and other nutrients) from fish waste. Indeed, host anemones feed only rarely and opportunistically, as when an echinoid blunders into the tentacles of one (personal observation). (Mariscal [1966] speculated that they may not need to do so at all, but captive anemones do better when fed occasionally [Verwey, 1930]).

Clownfish benefit by the virtual inability of actinians of most host species to close: while many anthozoans undergo diel cycles of contraction (Sebens and DeRiemer, 1977), symbiotic fish are continually protected. Indeed, when their fish are removed, anemones may contract (Fricke, personal communication; personal observation) or retract their tentacles (personal observation). Anemone breadth is roughly proportional to the number of fish it accommodates (Allen, 1972; Ross, 1978b; Fricke, 1979; personal observation). Clownfish may have functioned evolutionarily, with the contribution of zooxanthellae, to increase their territory size and thereby population, through positive feedback contributions to hypertrophy of anemone oral discs. This may be, for a macrosymbiont and on an evolutionary time scale, analogous to the control symbiotic coelenterates have over density of their zooxanthellae (Muscatine et al., 1985).

Analogously, clones of small individuals of *E. quadricolor* allow occupation by large numbers of demonstrably protective fish. In addition to the effects of fish upon hosts described above, the tentacles of this anemone develop a distal bulge within minutes of a fish's entering the anemone, as first noted by de Crespigny (1869); without fish, the tentacles generally lack bulbs (Dunn, 1981). This response may serve to expose more surface area to sunlight (as occurs with zooxanthellae-packed pseudotentacles of certain actinians (e.g. Lewis, 1974) and corals (e.g. Fricke and Vareschi, 1982). A functional hypothesis for this reaction and for the greater expansion of anemones in the presence of fish than in their absence (see above) that can be tested is that zooxanthellae are better able to make use of energy (C) in the presence of a source of nutrients (N, S, P, etc.) than they are in its absence.

Therefore, not only the anatomy of these anemones, but their extraordinary size and behavior as well, might have evolved through positive feed-back with both their algal and fish associates. Murata et al. (1986, p. 586), finding

that some compounds from "*R. kuekenthali*" were actually produced by their zooxanthellae, concluded "*Therefore* [emphasis added], these compounds probably do not play substantial roles in attracting fish." That result is among the strongest evidence for this being not merely two two-way relationships, but an intimate three-way symbiosis.

6. Conclusion

Collingwood's mysterious "connexion" would more accurately be rendered "connexions": there are nearly as many anemonefish symbioses as there are species combinations, and zooxanthellae may be an important component of this system. Many of the apparently contradictory data are probably accurate for the species and developmental stage on which they were gathered. Despite an appearance of uniformity, specific details on nature of interactions, degree of specificity, and mechanism of adaptation of fish to anemone appear to vary significantly. Disagreements in interpretation are likely to be resolved as it is appreciated that not all species pairs interact identically and that interactions or their mechanisms may differ with age of the fish. Future investigators need be especially careful to identify both partners accurately and consistently, to be explicit about which species and developmental stages were observed, and not to over-generalize from data. As these caveats are followed, the spectrum of variability and uniformity will become clear. Quantitative studies on the role of the actinian's algae are needed to complete the picture.

Acknowledgements

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