

Anemonefish Recruitment: The Roles of Order and Chance¹

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Abstract

Near Madang, Papua New Guinea, nearly all actinians of the species *Heteractis magnifica* contain anemonefish – either *Amphiprion perideraion* or *A. percula*. There were 2–6 *A. percula* per anemone; number of fish, length of largest fish, and total length of all fish correlated with host diameter. In *A. perideraion*, with 1–5 fish/anemone, “quantity” of fish was not correlated with actinian size. For both species, size interval between fish diminished with increased number of fish in an anemone; average size of female, male, and largest juvenile tended to be larger in anemones with more fish. Variation in carrying capacity of this actinian with species of symbiont demonstrates that generalizations from one species of fish or anemone, or one host-symbiont pair, may be unjustified. Removing none, some, or all fish from an anemone allowed evaluation of factors affecting recruitment. No post-larvae settled into actinians from which fish had not been removed. Only fish of the resident species recruited to anemones occupied by fish. Fish of either species settled into an empty actinian, but the number of anemones colonized by fish of each species was proportional to the fish's abundance in the breeding population. Therefore, although settlement into an individual host was stochastic, for the population as a whole settlement was deterministic.

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1. Introduction

Resolution of the debate (summarized by Sale, 1988) about coral reef fish recruitment necessitates accurate knowledge of the ecology of the species involved. One of the two major hypotheses holds that reef fish communities are highly structured, so that a settlement opportunity occurs for fish of a particular species only when a conspecific individual is removed. By contrast, the lottery hypothesis asserts that reef fishes belong to guilds, members of which are ecologically equivalent: any member of a guild species may replace an individual of any species in that guild. Both assume habitat saturation, so that settlement can occur only to effect a replacement.

I investigated recruitment of fish symbionts to the host sea anemone *Heteractis magnifica* (nomenclature of fishes follows Allen [1972] and of actinians Dunn [1981]) at the Christensen Research Institute (CRI), Papua New Guinea, to determine whether either of these hypotheses explains what controls the species and number of fish living in an individual actinian, and whether understanding anemonefish dynamics can contribute to comprehension of the more complex problem in coral reef fishes. I also sought to understand why one species of fish does not come to monopolize the resource. This system is ideal for empirical studies of carrying capacity and experimental studies of recruitment. Anemonefishes (or clownfishes; Pomacentridae) are obligately associated with actinians except during a brief planktonic larval period (Allen, 1972, 1980; Fautin, 1991; Fautin and Allen, in press). The actinian - a necessary but not sufficient condition for an anemonefish's existence - can be identified, measured, and manipulated, so natural habitat saturation can be directly evaluated, avoiding issues of whether artificial habitats are appropriate and equivalent. Recruitment to an anemone in most fish species is only by settlement of newly metamorphosed fry from the plankton. A host individual generally contains fish of only one species (Verwey, 1930; Mariscal, 1970, 1972; Dunn, 1981). The specificity of nearly all species (which is governed by the fish, the shorter-lived and motile partner) is known (Fautin, 1991).

Sea anemones reportedly limit populations of their fishes. Virtually all individuals of host actinians possess fish in the equatorial tropics (Allen, 1972; Ross, 1978; Fricke, 1979; Fautin, 1986) (although not necessarily at higher latitudes [Moyer, 1980]). There appears to be a characteristic number (or range in number) of individuals per anemone for each species of fish. In *Premnas*

biaculeatus, which is host-specific for solitary individuals of *Entacmaea quadricolor*, this number is two, or occasionally three (Fautin, 1986; Wood, 1986). For fishes that occupy more than one host species, number may differ with host. For example, Allen (1972) found one, three, or four specimens of *Amphiprion chrysopterus* in the three actinian species it occupies at Enewetak. Number may also vary geographically: the characteristic number of *A. melanopus* per cluster of anemones appears to be four in Guam (Ross, 1978) and three at Enewetak (Allen, 1972).

Allen (1972) recognized that size of both partners might influence carrying capacity. Indeed, actinians from which he had removed fish *in situ* were colonized by larger numbers of much smaller juveniles. Using two measures of anemone "quantity" (size of actinian cluster and number of individuals per cluster, respectively), Ross (1978; using *A. melanopus*) and Fricke (1979; using *A. akallopisos*) found a strong correlation with number of resident fish; Ross also found a correlation between cluster size and combined length of fish. This issue is complicated by the fact that growth (as well as sex: anemonefishes are protandrous) is socially controlled in clownfishes in which it has been studied (Fricke, 1974, 1979, 1983; Fricke and Fricke, 1977; Ross, 1978).

In a preliminary investigation (Fautin, 1985) near Lizard Island Research Station (LIRS), Great Barrier Reef, I found that 16 months after removing all specimens of *A. perideraion* and *A. percula* from the three individuals of *H. magnifica* on a reef, each anemone had been recolonized by fish of the species that had previously occupied it. I considered three possible explanations for this result: (1) stochastic - the odds of this distribution occurring by chance are 15% ($0.33 \times 0.67 \times 0.67$); (2) a fish's presence alters an anemone so as to make it suitable for future occupation only by conspecific fish; and (3) the actinians did not belong to a single species. I replicated and extended this experiment at CRI where nine anemonefishes occur (Fautin, 1988), compared to five at LIRS (Fautin, 1985), and where there is less seasonality, so recruitment is more uniform. After assessing empirically "carrying capacity" of anemones (the ecological and evolutionary implications for saturated and unsaturated resources are quite different [e.g. Wellington and Victor, 1988]), I studied larval settlement into manipulated and unmanipulated actinians. The resulting data on fish growth and development helped me to understand the process(es) leading to observed patterns of specificity and fish population size/composition. I conclude that both order and chance operate in regulating fish and group size as well as recruitment.

2. Materials and Methods

This research was done from Christensen Research Institute (CRI) (5°09'S, 145°48'E) during October-December 1985, September-November 1987, and August 1988, on two patch reefs in the Madang-Sek Lagoon, 7 km north of Madang, Papua New Guinea. The reef Depilik Tabus is approximately equidistant among the islands of Sinub, Tabat, and Wongat; Masamoz is 1 km south of it, about 1 km inside the barrier reef and 1 km off the coastal island of Riwo (Fig. 1). These reefs are environmentally and faunistically similar to one an-

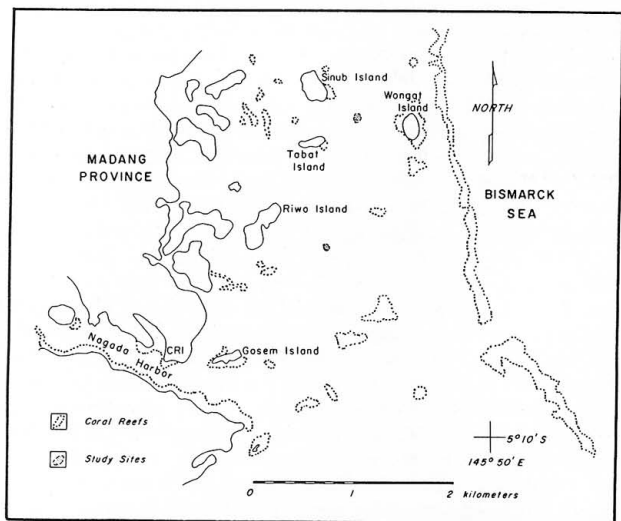


Figure 1. Vicinity of Christensen Research Institute. Patch reefs Depilik Tabus and Masamoz are indicated.

other and to the other patch reefs in the vicinity; I therefore considered them a single experimental unit.

In 1985, I mapped all sea anemones on Depilik Tabus, recording number and species of symbiotic fish inhabiting each. In December, I removed all fish from eight specimens of *Heteractis magnifica* at various depths; PVC pipes were erected beside them. Recolonization was evaluated in September 1987.

Also in September 1987, I mapped all specimens of *H. magnifica* on Masamoz and measured all species of *H. magnifica* and their fish symbionts on both study reefs. I defined anemone size as expanded oral disc diameter, averaged over several measurements made *in situ* during a month or more (Fricke [1979] discussed variability in anemone size). Fish were captured in a small hand net (with the aid of quinaldine only when extremely elusive), placed in a plastic bag where total length (TL) was measured to the nearest 5 mm (Fautin, 1986), then released into the anemone from which they had been taken. I assigned 24 individually identified specimens of *H. magnifica* containing *Amphiprion percula* on the two reefs to three experimental groups. I removed the two largest fish from all eight anemones containing four or five fish each. The others, harboring three fish each, were randomly assigned to two groups of eight. I removed the largest fish (the presumptive female) from anemones in one group, and the second largest (presumably the male) from the remainder. Approximately weekly thereafter, all fish were collected from one randomly selected actinian in each of the three treatment groups. They were measured *in situ*, then fixed and preserved for histological study. The extent of development of the three white body bars was also noted for each fish collected. On the day the collection was made, fish of the other 21 anemones in the experimental group were censused, and the specimens of *A. percula* in two control actinians on Masamoz Reef were counted and measured. (The number of controls was limited by the number of anemones on the reefs.) At the end of the two-month study, all fish in each of the 24 actinians were captured (a small amount of quinaldine was used to drive out hidden fish), identified to species, measured, then returned to their host.

Statistics used were correlation coefficient, Student's t-test, homogeneity of variances, Wilcoxon's two-sample test, and X^2 (Sokal and Rohlf, 1969). Means are expressed \pm standard deviation.

3. Results and Discussion

Empirical (census)

Figure 2 illustrates the distribution of symbiotic fish among 51 individuals of *Heteractis magnifica* on the two patch reefs prior to experimental manipulation: 43 specimens of *Amphiprion perideraion* occupied 14 anemones, and 128 specimens of *A. percula* lived in 37 anemones. Not included are one actinian with fish of both species (the only such natural occurrence in my experience), one with neither, and two touching one another that shared a group of *A. perideraion*. Fish of these two species occurred in no other host on the

patch reefs. With the following exceptions, I found no other species of clownfish in Madang Province inhabiting *H. magnifica*. In 1988, an anemone on Masamoz that had been the subject of experimentation in 1987 contained a specimen of *A. melanopus*; in 1987, one of the anemones on Depilik Tabus that I had studied in 1985 was shared by one immature *A. perideraion* and one immature *A. clarkii*; in 1985, I saw adults of *A. clarkii* in an individual of *H. magnifica* at Laing Island in northern Madang Province. (Previously, only juveniles of *A. clarkii* had been recorded *in situ* with this host [Mariscal, 1970, 1972]; this observation supports my belief [writing as Dunn, 1981] that competitive exclusion, not physiological incompatibility, explains the rarity of this host-symbiont combination.)

Data on number of fish, length of largest fish, and combined length of fish in each anemone, plus anemone size and depth, are given in Table 1, where comparisons between the two species of symbionts are also provided. Actinian diameter and depth do not differ statistically for hosts occupied by the two fishes. Color is also immaterial: fish of both species occupied chestnut, green, or blue anemones. The number of fish per anemone is similar for the two species in both mean and range: their distributions (Fig. 2) do not differ significantly (Wilcoxon's test). Nor are length of the largest fish and length of all fish in an actinian significantly different for the two fishes (Table 1).

Although individually neither these five parameters nor their variances differ significantly between the two symbionts, some pairwise correlation values between them do (Table 2). Two that differ in both species – length of the largest fish versus combined fish length, and number of fish versus their combined length – are correlated: as the largest fish grows, subordinate ones do so as well (Fricke, 1974, 1979; Fricke and Fricke, 1977; Ross, 1978), and combined length would generally be expected to track fish number. Because the length factors are related to fish number, rather than being independent, the other three significant correlations in *A. percula* – between anemone diameter and

Table 1. Mean and standard deviation of five parameters (three characteristics of the fish, two of the anemone), and value of Student's *t*-test comparing each parameter between symbiotic units differing in species of fish (d.f. = 49).

	<i>Amphiprion percula</i>	<i>t</i>	<i>Amphiprion perideraion</i>
Anemone diameter (mm)	478±122	-1.083	521±138
Number of fish	3.5±1.1	-1.098	3.1±1.1
Length of largest fish (mm)	66.2±11.9	-0.300	67.5±17.6
Length of all fish combined (mm)	169.4±57.4	-0.154	166.4±75.2
Depth (m)	8.9±1.7	-1.545	8.0±1.7

Distribution of Clownfishes in Anemones

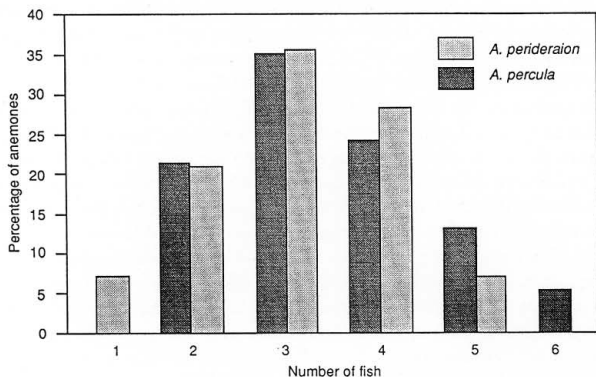


Figure 2. Number of fish (*Amphiprion perideraion* and *A. percula*) per host sea anemone (*Heteractis magnifica*) as a percentage of hosts. N = 37 anemones for *A. percula*; N = 14 anemones for *A. perideraion*.

Table 2. A - *Amphiprion percula*; B - *Amphiprion perideraion*: pairwise correlation coefficients for five parameters of Table 1. * = significant at 5%, ** = significant at 1%. Row attributes are numbered identically to those of the columns.

	1 Anemone diameter (mm)	2 Number of fish	3 Length of largest fish (mm)	4 Length of all fish (mm)	5 Depth (m)
A					
1	1	0.4502**	0.4256**	0.5867**	0.1298
2		1	0.1724	0.8520**	0.0439
3			1	0.6060**	-0.1619
4				1	-0.0247
5					1
B					
1	1	0.5079	0.3472	0.4575	0.4373
2		1	0.5804*	0.8866**	0.0617
3			1	0.8332**	-0.0160
4				1	0.0221
5					1

number and size of fish – probably represent a single underlying correlation of anemone diameter with fish number. The other correlation in Table 2 that may be biologically meaningful is between number of fish and length of largest fish in *A. perideraion*, there being no logical reason for these factors to be correlated, as, indeed, they are not in *A. percula*.

For both species, length of the third largest fish in each anemone (the largest juvenile) and second largest (presumably the male) increased with number of fish; the trend was the same but less regular for the largest fish (the presumed female) (Table 3). Moreover, length difference between male and female, and female and juvenile is 15 mm or less with four or five fish per host, but about 25 mm with two (where no comparison between male and juvenile is possible) or three. Thus aside from any constraints that host size may exert, for both species, fish in larger social groups are more closely "packed." From Table 3, it also appears that larger social groups tend to have larger females (greatest observed TL of *A. perideraion* was 95 mm and of *A. percula* 85 mm). The correlation between number of fish and largest fish is significant for *A. perideraion* but not for *A. percula* (Table 2) probably because in *A. percula* female length does not increase consistently with group size. I infer from these data,

Table 3. Average total length (mm; \pm s.d.) of anemonefish by number of fish in anemone and position of fish in social group for *Amphiprion percula* (upper entry) and *A. perideraion* (lower entry). The ♀ is the largest fish in an anemone, the ♂ the second largest, and the largest juvenile the third largest. Data are given only for categories in which $n > 2$. Within each species, all differences between adjacent categories are significant at 0.001 [e.g. for *A. percula*, length of females in anemones with two fish differs from length of females in actinians with three fish ($t = 9.305$); and for *A. perideraion*, length of females in anemones with three fish differs from length of males in hosts with three fish ($t = 15.330$)].

Fish/ anemone	n	Length ♀ (mm)	Length ♂ (mm)	Length of largest juvenile (mm)
2	8	55.6 \pm 10.2	30.6 \pm 16.3	—
	3	55.0 \pm 13.2	28.3 \pm 2.9	—
3	13	70.4 \pm 8.8	53.1 \pm 6.0	39.2 \pm 4.9
	5	77.0 \pm 14.4	60.0 \pm 16.2	45.0 \pm 23.7
4	9	69.4 \pm 7.3	56.1 \pm 6.0	43.9 \pm 4.2
	4	73.8 \pm 11.1	61.3 \pm 6.3	47.5 \pm 2.9
5	5	73.0 \pm 7.6	58.0 \pm 4.5	48.0 \pm 5.7
—				
Averages				
3.4 \pm 1.2		66.2 \pm 11.9	49.2 \pm 13.8	42.2 \pm 6.2
3.1 \pm 1.1		67.5 \pm 17.6	53.5 \pm 17.5	46.5 \pm 16.0

taken as a whole, that social group size of *A. percula* is responsive to territory (i.e. anemone) size – an external factor – whereas that of *A. perideraion* is affected by size of its largest member – an internal factor. Settlement into a larger anemone (growth of an anemone is negligible during the life of a clownfish) thus enhances the chance of an individual of *A. percula* growing larger and being part of a larger social group more than it does for one of *A. perideraion*. These relationships are not determinate: larger anemones do not always have more or larger *A. percula*, nor do anemones containing large females of either species always have more fish.

Size of male and female fish in a population may overlap considerably (e.g. Fricke, 1983; pers. obs.), and all the conspecific fish in an anemone grow slowly, in lockstep, retaining their relative sizes (Fricke, 1974, 1979; Fricke and Fricke, 1977; Ross, 1978). A female, therefore, attains great length by being female for a long time and/or having “grown up” in a group headed by a large female. Amount of “space” for fish in her anemone is directly proportional to her size (which eventually reaches a maximum), so she ultimately controls the size of those fish. I hypothesize that size interval between successive fish in a group, which is inversely correlated with fish number, reflects stability of the group. Disappearance of a fish simultaneously diminishes number of fish in an anemone and increases mean length difference among them. In stable situations, the interval between successive fish is gradually reduced to some minimum (apparently, on average, 15 mm for these species). In this way, even without the loss of a fish, “space” can be created for more settlers. Stability on the order of many months to a few years is probably necessary to build up large individuals and large numbers of fish, given (1) the longevity of these animals (Fricke, 1974; Fautin and Allen, in press) and (2) that I detected no growth in control fish during 2 months.

Therefore, even though unmanipulated actinians at CRI varied in number of symbionts, I infer that they were functionally “full,” supporting the impression that hosts, which are an essential resource for anemonefishes, limit fish population size (Allen, 1972; Fricke, 1979; Dunn, 1981). Thus, theoretically, the potential for competition exists.

Experimental (recruitment)

Partial defaunation

In the short term, at least one post-larva settled into 11 of the 24 experimental anemones after one or two fish had been removed from each (Table 4). The first was sighted 38.5 ± 10.5 d after defaunation; this probably overestimates recruitment time because as many as 9 d elapsed between censuses. There was

Table 4. Recolonization of partially defaunated anemones

No. recruits/ anemone	No. anemones from which 2 fish had been removed	No. anemones from which 1 fish had been removed	Days from removal to sighting first fish ($\bar{X} \pm$ s.d.; range)
0	5	8	[18.5±10.1; 6-33]*
1	2	4	42.0±11.7; 26-55
2	1	4	34.2±9.0; 19-40
Mean±s.d.	0.50±0.76	0.75±0.86	

* Days until end of partial defaunation experiment

no significant difference between the mean number that settled in those from which only one fish had been removed (0.75) and those from which two had been removed (0.50) ($t = -0.669$). No post-larvae settled into the two control actinians, nor into more than a dozen others examined sporadically, despite the demonstrable presence of fry in the plankton throughout this study. This observation further supports resource saturation.

All recruits, varying in total length from 7 to 12 mm when first seen, were *A. percula*. The two possible explanations for post-larvae being conspecific with the fish occupying the anemone into which they settled cannot be distinguished by this experiment. Resident fish may competitively exclude non-conspecifics: aside from being highly territorial, anemonefishes are able to distinguish among reef fishes, including species of clownfishes (Fricke, 1974; Fautin, 1986). Alternatively, potential recruits may be differentially attracted to anemones occupied by fish: larvae of other damselfishes may locate appropriate habitats by chemical attraction to resident conspecifics (Sweatman, 1988).

For the relatively short period of observation, growth was measurable but variation was high: average length of fish that were juveniles when one or both reproductive fish in an actinian were removed increased by $9.59 \pm 12.3\%$; fish that were presumably female at the beginning changed by $3.0 \pm 6.4\%$; and males changed by $4.4 \pm 9.1\%$. Negative changes in length were recorded mainly during the first week (4/7 animals measured the first week, 1/7 the second week, 1/6 the fourth week). The eight fish in two control anemones did not change length. There was no indication that magnitude of growth was related to an animal's position in the size/sexual hierarchy nor of enhanced growth of fish immediately smaller than a fish that had been removed. Development of body bars seems only loosely tied to length and not at all to social position/sex.

Total defaunation

Of the 21 actinians emptied 8–51 d prior to the experiment's end (i.e. excluding the three from which fish were collected on the last day of the experiment), 17 (81%) were recolonized (Table 5). Two contained individuals of *A. perideraion*, 12 had *A. percula*, and three had both. Elapsed time between defaunation and first sighting of a newly settled fish was 8–38 d (22.9 ± 11.1). In some actinians that were recolonized by more than one fish, all fish were seen simultaneously; in others they accumulated over time. Of the three hosts with mixed populations, one had a fish of each species when first seen, one with *A. percula* initially had two *A. percula* and one *A. perideraion* when next seen, and the third had *A. perideraion* 13 d after it was emptied, acquired *A. percula* by 2 weeks later, and was occupied by an additional *A. perideraion* within 2 weeks after that.

In August 1988, I found and examined 23 of the 24 actinians from which I had removed all fish 9–11 months previously (Table 6). No anemone was visibly harmed during the period it lacked fish (cf. Godwin and Fautin, 1992).

Table 5. Recolonization of totally defaunated anemones. Figures in parentheses are for *Amphiprion percula* only.

No. recruits/ anemone	No. defaunated anemones	Days from removal to sighting first fish ($X \pm$ s.d.; range)
0	4	[26.8±19.0; 8–51]*
1	7 (6)	20.7±12.3; 8–38
2	6 (4)	25.0±11.2; 13–38
3	4 (2)	23.5±11.4; 13–38

* Days until end of experiment

Table 6. Occupation of defaunated anemones 9–11 months after experiment

	Occupant at last examination in 1987		
	<i>A. perideraion</i>	<i>A. percula</i>	none
Occupant in August 1988			
<i>A. perideraion</i>	1	2	2
<i>A. percula</i>	1	7	5
<i>A. melanopus</i>		1	
Mixed species		1*	
Anemone not located		1	

* 1 individual of *A. perideraion*, 5 of *A. percula*

Unmanipulated anemones of all species (i.e. not only *H. magnifica*) contained fish of the same species on successive visits (1985/1987 and 1987/1988).

Recolonization of some anemones by members of a different species than had initially occupied them implies that all specimens of *H. magnifica* on the patch reefs constitute a unitary resource from the perspective of the fishes. This eliminates my second and third possible explanations for the pattern of settlement observed at LIRS. Thus, chance appears to explain occupation of an actinian: the "guild" of potential settlers is the subset of the nine anemonefishes at CRI (Fautin, 1988) and five at LIRS (Fautin, 1985) that is attracted to and/or can survive in *H. magnifica*. At LIRS, it consists of *A. perideraion* and *A. percula*, and at CRI, rarely *A. melanopus* and *A. clarkii* as well.

However, for the population of anemones, as opposed to any individual actinian, there appears to be strong determinism in pattern of settlement. At LIRS, number of anemones reoccupied by fish of each species was the same as had originally occupied them. At CRI, during a time interval (1985-1987) similar to that of the initial experiment at LIRS, three of eight emptied *H. magnifica* were recolonized by *A. perideraion*. This is close to the number (two) that had originally been occupied by that species and the number (2.4) that would be expected if the proportion of anemones hosting *A. perideraion* were to remain constant. In the shorter interval between late 1987 and late 1988, of 23 defaunated anemones that had been occupied by *A. percula*, six were recolonized by *A. perideraion*, a number not significantly different from the expected number, 6.9 ($.302 \times 23$) ($X^2 = 0.168$; $X^2_{[.05,1]} = 3.841$). Immediately following defaunation, 14 actinians were recolonized by fish of one species; *A. perideraion* settled into two, whereas 4.2 would have been expected based on 30% of the censused anemones harboring fish of that species. These numbers do not differ significantly ($X^2 = 1.646$; $X^2_{[.05,1]} = 3.841$). Although by the 1988 observation, about a third of the anemones had fish of different species than they had acquired immediately after defaunation, the ratio of anemones occupied by fish of the two species remained stable.

4. Interpretation

Dynamics of recruitment

Population

Post-larvae settled into 46% of partially defaunated anemones, compared to 81% of those same actinians once they had been vacated. The partially defaunated anemones into which no post-larvae settled were available in that condition, on average, a shorter time (18.5 d) than mean time for first settlement into actinians that acquired new recruits (38.5 d) ($t = 4.7098$; significant

at 0.5%). However, some anemones remained vacant longer (up to 33 d) than the shortest recruitment time (19 d). Of the four actinians that stayed empty, two had attracted no additional fish while partially vacated, one had added one, and one had added two. All seven animals that were empty in early November 1987 (the four mentioned above and the three from which all fish were removed on the final sampling day) were occupied in August 1988. I infer, therefore, that animals remain uncolonized not because they are unsuitable hosts but because of the random nature of the recruitment process.

Time from defaunation to first settlement was longer (38.5 d) into partially occupied than into empty actinians (22.9 d) $t = -3.6852$; significant at 0.5%). That is, partially defaunated anemones acquired post-larvae at the rate of one every 45 d, whereas recruitment to empty ones was at the rate of one per 19.9 d. A possible interpretation is that settlement is more difficult in the presence of larger conspecifics. These animals engage extensively in intraspecific aggression (e.g. Allen, 1972; Fricke and Fricke, 1977; Fricke, 1979; pers. obs.).

An alternative explanation concerns the pool from which recruits are drawn. Recruits to partially occupied anemones are limited to *A. percula* whereas post-larvae of *A. perideraion* may also recruit to empty actinians. If I assume (1) recruitment from the local vicinity, which is consistent with the small size of settlers (equal to that of *A. clarkii* [see Ochi, 1986], and less than that of *A. melanopus* [see Ross, 1978]), and (2) roughly equal fecundity in fish of the two species, then only 70% as many potential recruits are available to partially occupied anemones as to empty actinians (30% of the anemones being occupied by *A. perideraion*). Mean settlement time for the 17 empty anemones into which recruits settled divided by 70% (32.7 ± 15.9 d) does not differ significantly from mean settlement time into partially occupied hosts (38.5 d) ($t = 1.0539$), supporting the hypothesis that actinians are repopulated by fish of each species in proportion to their occupation of anemones in the entire population (which is also proportional to the number of breeding pairs).

Some anemonefish at both LIRS and CRI are more abundant and less host specific than either *A. perideraion* or *A. percula*. Yet only fish of those two species recolonized empty individuals of *H. magnifica*, with rare exceptions. Thus, it seems that "an intrinsic preference or one learned early in life restricts fish to certain of the hosts present" (Fautin, 1985: 375). Miyagawa and Hidaka (1980), Murata et al. (1986), and Miyagawa (1989) demonstrated in the laboratory that species-species "synomones" attract juveniles of some fishes to anemones with which they normally form symbioses but not to others. Aside from some problems with experimental protocols and interpretation (see Fautin, 1991; Shick, 1991), the results of Miyagawa and co-workers do not

entirely explain specificity because (1) some of their experimental fishes were not attracted to anemones with which they naturally occur, and (2) as with *A. perideraion* and *A. percula* in *H. magnifica* in this study, anemones of one species can host fish of more than one species.

Individual level

Several factors affect which species successfully appropriates an individual anemone. Prior to my experiments, one in 54 individuals of *H. magnifica* on the two reefs contained fish of more than a single species of *Amphiprion*. Three mixed populations developed following total defaunation. One factor determining which species ultimately takes possession of the host is apparently priority. For both instances in which sequence of settlement could be determined, fish of the species that arrived first increased in number, and a year later were in sole possession of the anemone. Another factor is dominance. The actinian occupied apparently simultaneously by one individual of each species contained only fish of *A. perideraion* a year later. These "natural experiments" had the same outcome as manipulations I did with these species: mixed populations rarely persisted more than a few hours; when I introduced a fish of each of these two species into an anemone that had been home to neither, *A. perideraion* drove off smaller, and often even larger, *A. percula* (see Fautin, 1985); commonly, an outnumbered fish of any species was ousted (Fautin, 1986). In 1988, one specimen of *A. perideraion* shared an anemone possessed by five individuals of *A. percula*; 9 months earlier it had contained a single *A. percula*. Thus, a heterospecific may rarely be recruited; it would be instructive to know whether this had occurred while the actinian was occupied by only one small, newly-settled fish.

By contrast with their active exclusion of heterospecifics, I infer from vacant anemones being settled by fish of the two species in proportion to the fish's relative abundance in the breeding population that resident fish neither inhibit nor promote settlement of conspecifics. However, once an anemone is "filled," additional settlement is apparently prevented. Such competitive exclusion presumably accounts for the absence of recruitment to unmanipulated actinians.

5. Conclusions

As a rule, once a host is pre-empted by fish of one species, it is suitable henceforth for settlement only by conspecific post-larvae. This apparently indefinite monopolization of an individual actinian by fish of one species is a

powerful deterministic force in the population. Stability is further served by decoupling short-term reproductive success from long-term population dynamics: these long-lived fishes that live in social groups composed of fish of a range of ages persist in their peculiar habitat regardless of whether reproduction is poor for a season or two. Average size interval between fish may be a good indicator of population stability during the immediate past.

Only in the rare event of total extirpation of fish from an actinian is there a lottery, and that of limited scope. Settlement of post-larvae into vacant anemones in proportion to the fish's relative abundance in the breeding population also tends to conserve the structure of the community. Competition, apparently mainly among small individuals, for possession of a host leads to some turn-over, in dynamic equilibrium.

In contrast to CRI, where post-larvae settled rapidly into some partially and completely vacated individuals, none did so at LIRS. Moreover, compared with pre-defaunation levels, after about a year and a half, there were fewer fish per anemone at LIRS compared to their original number, despite there having been two settlement periods in the interim, one of which was good for reef fish in general (J. Leis, pers. comm.). Thus, the anemone resource may not be saturated at higher latitudes or otherwise marginal habitats for the anemonefish symbiosis, or it may take longer to achieve saturation. At CRI, anemonefish population appears to be habitat-limited; at least in the short term, that at LIRS may be more recruitment-limited. However, in both places, the longer the interval since defaunation, the nearer the fish population approached its premanipulation level. A time course of several years is not unreasonable for fish that may live as much as a decade (Fautin and Allen, in press).

This study joins other recent analyses of coral reef fish communities that reveal them to be structured in subtle but profound ways. Factors such as priority, microhabitat, and species interactions are important in the anemonefish system, as in others recently investigated (e.g. Shulman et al., 1983; Sale and Steel, 1986; Clarke, 1988). Details may differ, however. For example, although Sweatman (1983) found, as I did, exclusion of heterospecifics, in his system presence of either of two species of damselfishes enhances recruitment of conspecifics, while in "full" hosts, clownfishes apparently interfere with recruitment of conspecifics as well as heterospecifics. In other studies (cited by Sweatman, 1983; Jones, 1987), residents do not affect recruitment.

Thus, both deterministic and stochastic forces operate on recruitment of anemonefishes. A major conclusion of my study is that these forces vary with scale: which species settles into any individual anemone is unpredictable, but, for the population as a whole, settlement is highly deterministic. Compared

with most reef fish communities, such forces may be easier to discriminate in the sedentary and monogamous anemonefishes, where survival depends on a reserve of potential mates in the form of resident immatures (Fricke, 1979). The small size of the "guild" of symbionts of any one host species, settlement of fish into vacant anemones in proportion to their representation in the breeding population, and the ability of resident fish to exclude heterospecifics (or, alternatively, to allow recruitment only of conspecifics) provide considerable structure that serves to perpetuate this system.

The number of fish that inhabit an anemone was previously found to vary with host species. My data demonstrate the reciprocal: carrying capacity of a particular species of anemone varies with fish species. The precise number within the range of anemonefish typically accommodated by an individual actinian is modified by circumstance. Because the two fishes in this study inhabit other host actinians elsewhere (Fautin, 1991), they would be appropriate subjects to evaluate whether all hosts affect their "quantity" similarly (cf. Allen, 1972), and if number of fish of these two species differs in *H. magnifica* in other parts of their mutual range or where only one fish species occurs. Such information would contribute to determining which parameters are invariant in particular species or species combinations, and which respond to local conditions. For, based on available data, it is obvious that "the anemonefish symbiosis" is not a unitary phenomenon – what is true of one species pair may not be generalizable to all, or any others.

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