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Mobility of *Stichodactyla gigantea* sea anemones and implications for resident false clown anemonefish, *Amphiprion ocellaris*

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Synopsis

For reef fishes that do not move between habitat patches following settlement, habitat selection is expected during settlement. Although false clown anemonefish, *Amphiprion ocellaris*, are sedentary following settlement, they are not especially discriminating during settlement, and are commonly found occupying anemones at which no apparent nest site exists. In this study I report on mobility of *Stichodactyla gigantea* sea anemones, including anemones with resident false clowns. I argue that anemone mobility can help explain why settling false clowns are not more discriminating: although the per annum probability of an anemone moving is low, the probability of that anemone moving over the course of a resident's life is considerably higher. Therefore, an anemone's current microhabitat may not be a good predictor of its microhabitat and suitability as a host in the future.

Introduction

Most coral reef fish species disperse widely as pelagic larvae but, after settling to a reef, adopt a much more sedentary habit within a small home range or territory (Sale 1980). Once settled, location of, migration to, and occupation of a new territory are difficult. Therefore, choice of an appropriate microhabitat during settlement should be critical. Fishes distinguish among sites based on habitat complexity and species composition, depth, and conspecific density, and we should expect such habitat preferences to match well with their effects on subsequent survival, growth, and reproduction (Booth & Wellington 1998). When the benefit of a habitat characteristic is not realized immediately on settlement, the fitness increment associated with a currently superior habitat, and therefore the degree of preference expected, depends on the stability of the habitat characteristic over time. Habitat features for which reef fishes' settlement preferences are observed are often those, like depth or coral cover, which can clearly be considered stable over the timeframe relevant to a settling fish (reviewed by Booth & Wellington 1998).

Anemonefishes, Amphiprion spp., Premnas biaculeatus, live in a close, obligate association with large sea anemones. The presence of an appropriate anemone species is one obvious necessary condition for a settling anemonefish to consider a habitat suitable. As expected, anemonefishes settle only on sea anemones and a given anemonefish species settles only on a subset of the available anemone species (Fautin & Allen 1992, Elliott et al. 1995, Arvedlund et al. 1999). Beyond settling on an appropriate anemone species, anemonefishes should make further distinctions based on other habitat variables with potential fitness consequences. The fishes generally lay their clutches on rock or coral beneath their host anemone's oral disc (Fautin & Allen 1992, Arvedlund et al. 2000). An individual without access to a nest site is, from an evolutionary perspective, dead. Therefore, anemonefishes should only settle on anemones at which a suitable nest site is present. And yet false clown anemonefish, Amphiprion ocellaris, are frequent occupants of Stichodactyla gigantea anemones found on shallow seagrass and sand flats, where suitable nest sites may be unavailable (this study). Why do false clowns settle

on anemones that, although suitable as protection from predators, do not appear to be suitable for reproduction?

Host mobility is one possible explanation for the apparent lack of habitat selectivity exhibited by settling false clown anemonefish. While generally treated as sessile, the species of anemone used as hosts by anemonefish are able to move (Fautin & Allen 1992, this study). Because anemonefish are relatively long-lived (Moyer 1986), that mobility may lessen the importance of discrimination among available anemone hosts during settlement. In this paper, I document mobility of *S. gigantea* anemones occupied by false clown anemonefish and consider the implications for the fish.

Methods

I collected data while monitoring groups of false clown anemonefish occupying S. gigantea anemones at two sites, 1.5 km apart and each spanning approximately 500 m of shoreline, at Bunaken Island, North Sulawesi, Indonesia (Site 1: 1.596N, 124.780E; Site 2: 1.608N, 124.770E). I used a tape measure to map anemone locations at both sites. I caught resident false clown anemonefish with a handnet, measured the total length $(\pm 1 \text{ mm})$ of each fish on a measuring board, and then tagged fish using subcutaneous acrylic paint injections (Thresher & Gronell 1978). I then visited each anemone at Site 1 at least weekly for 7 months, September 1997-March 1998, and at Site 2, less frequently for 6 months, beginning in October 1997. When an anemone disappeared, I searched an area of approximately 50 m diameter around its previous location and confirmed the identity of false clowns resident on anemones nearby. Site 1 was sufficiently familiar for me to record anemones found midway through the study season as new arrivals, rather than as anemones which had until then escaped notice. I could not assess anemone immigration to Site 2.

Anemone movement might be limited to small individuals or to individuals in shallow, marginal habitats, i.e., to anemones of less importance as hosts for false clowns. To assess this possibility, I estimated oral disc surface areas of anemones at both sites. On three occasions in February and March 1998, I measured the expanded long (L) and short (S) axes of each anemone's oral disc using a tailor's tape measure held above the oral disc at it widest point (long axis) and over centre of the anemone perpendicular to the long axis (short axis). I then induced each anemone to contract

by running a finger across its oral disc, after which I remeasured both axes. From these measures, I calculated two indices of anemone size under the assumption that oral discs were approximately elliptical (oral disc area = $LS\pi/4$). I used the largest of the three estimates of expanded disc area as my estimate of maximum oral disc size and the smallest of the three estimates of contracted disc area as my estimate of minimum oral disc size. Because measurements were made late in the field season. I could estimate oral disc area for anemones that appeared at Site 1 partway through the field season but could not estimate the size of anemones which disappeared from the two sites. I also measured the depth of each anemone at the time of the lowest low tide using a pole placed upright on the substrate adjacent to the anemone.

Results

At Site 1, 84 anemones were occupied by false clown anemonefish at some point during the field season. At 16 of these anemones, no permanent nesting substrate was apparent, i.e., there was no permanent, hard substrate under or abutting those hosts' oral discs. The fish occupying one of these anemones laid two clutches on debris that temporarily came to rest abutting their host (fabric in one instance and wood in the other) and I found 111 eggs on a 2 cm diameter pebble beneath a second anemone. (False clowns with access to larger and more permanent nest sites laid clutches of 60–1300 eggs as often as twice monthly throughout the field season.) False clowns larger than the smallest breeding female at the study site (55 mm) resided at 10 of the 16 anemones and fish larger than the site's smallest breeding male (41 mm) resided at 12 of the 16 anemones.

Of 84 anemones at Site 1, 6 appeared during the field season and 6, including 1 of those which appeared, disappeared from the site. Appearance of new anemones is unambiguous evidence of host immigration. When first observed, 3 of the immigrant anemones were occupied by single false clowns (37, 41, and 43 mm), and 1 by a group of 4 (69, 44, 35, and 22 mm). Two immigrant anemones were vacant. Fish resident on immigrant hosts were untagged and could not be accounted for as having migrated to their hosts from other anemones nearby, i.e., they appeared to have accompanied their hosts. On average, immigrant anemones' expanded and contracted oral disc areas were smaller than those of nonimmigrants, although neither difference was

Table 1. Oral disc areas and depths at the lowest low tide of anemones present at Site 1 throughout the study season (nonimmigrant) and that arrived at Site 1 part-way through the study season (immigrant). Data are the mean \pm standard error, with sample sizes in parentheses. Sample sizes for depth differ from those for anemone size because depth but not oral disc area was measured at 1 anemone which immigrated to Site 1 but subsequently disappeared and depths of 2 nonimmigrant anemones were not recorded. Anemone pairs and triplets (2 or 3 anemones occupied by a single group of false clown anemonefish) were excluded from analyses.

	Oral disc area (cm ²)		Low tide depth (cm)
	Expanded	Contracted	
Immigrant	$3152 \pm 506 (5)$	$1148 \pm 411 (5)$	8.2 ± 2.2 (6)
Nonimmigrant	4475 ± 193 (68)	1713 ± 98 (68)	8.3 ± 0.6 (66)
Two-tailed t test	t = 1.82, p = 0.07	t = 1.49, p = 0.14	t = 0.18, p = 0.86

statistically significant. Depths of immigrant and nonimmigrant anemones were not significantly different (Table 1).

At Site 2, 62 anemones were occupied by false clowns during at least part of the field season. Eight of these anemones disappeared. Anemonefish monitoring at Site 2 was less intensive and therefore not conducive to detection of immigrant anemones. However, two instances of anemone movement within Site 2 provided direct evidence that resident anemonefish will accompany moving hosts:

1. Anemone L41 hosted 2 tagged false clowns, 54 and 46 mm long. L41 was attached to exposed limestone raised slightly above the surrounding seagrass and 6 m from its nearest neighbour, L40. On 2 November, two days after my last visit, I found L41 (or an immigrant of similar size and colour) resting on, but unattached to, the substrate. Neither of L41's two residents was visible amongst the tentacles. Two days later, L41 had reattached its pedal disc in a limestone crevice 10 m from its previous location. The smaller of its two residents was still present but the larger was missing. On 11 November and again on 18 November, I observed L41's now lone resident attempting, unsuccessfully, to join the false clown group resident at L40, now 7 m away. Between and following those observations, the fish remained at L41.

2. Anemone L32 was also, initially, on limestone amidst seagrass, but in a marginally subtidal depression. L32 hosted 4 tagged false clowns (59, 38, 28, 16 mm). The anemone disappeared between 18 January and 3 February. On 7 February, I found L32 (or an immigrant of similar size and colour) on seagrass 20 m from its previous location. All four fish were present. On 7 March, L32 was lying loosely on the seagrass; the same four fish were still present. By my next visit, on 15 March, L32 had disappeared. I could

not relocate the anemone or any of its resident false clowns.

Discussion

For investigators whose primary interest is the fish living on an anemone, it is convenient to treat the host as sessile. This study demonstrates that S. gigantea anemones are not invariably sessile. Of 78 anemones remaining at Site 1 in March 1998, five (6.4%) had immigrated to the site over the preceding 7 months, a rate of 10% per annum. Immigrant anemones may be, on average, smaller than nonimmigrants, but they were not associated with shallower, marginal habitat and were suitable false clown hosts. Indeed, four of six anemones immigrating to Site 1 (one of which subsequently disappeared) were occupied by false clowns that were presumed to have accompanied their hosts. Both of the anemones observed moving shorter distances at Site 2 were accompanied by at least one of their resident false clowns. Thus, movement of S. gigantea anemones occurred at an appreciable frequency and resulted in post-settlement redistribution of false clown anemonefish.

Anemone mobility has been recognized implicitly or explicitly by other researchers. During Hattori's (1995) study of *A. clarkii* and *A. perideraion* anemonefishes occupying *Heteractis crispa* (as *Radianthus kuekenthali*) anemones, 23 of 101 anemones monitored appeared at the study site during the 18-month study period. Hattori did not state whether these anemones were immigrants or recruits. Schmitt & Holbrook (1996) took advantage of *H. magnifica* anemones' ability to re-attach to a substrate, and implicit mobility, to collect anemones and transplant them to their study site. Mariscal (1972) reported that both *S. haddoni* and *Entacmaea quadricolor* anemones (as *Stoichactis kenti* and *Physobranchia ramsayi*, respectively) moved 20 cm h^{-1} following release into aquaria, 'inching' along without detaching their pedal discs. Note that Mariscal (1972) described host locomotion, whereas use of the terms 'mobility' and 'movement' in this study is not intended to imply that those movements are self-directed. It seems more probable that anemones in this study detached their pedal discs from the substrate and were then carried by currents. I am not aware of any study in which the implications of anemone mobility for resident anemonefish have been considered.

Several consequences of host mobility are possible. If currents sweep detached anemones into areas that are unsuitable for fish then host mobility may be a source of fish mortality. Hosts carried past other anemones may also facilitate host-to-host migration of anemonefish. Finally, host mobility might lead settlers to be less selective when choosing a host, i.e., to discount differences in the habitat surrounding potential hosts because current habitat quality is not a reliable indicator of habitat quality in the future. In this respect, nest site availability is a particularly interesting component of habitat quality. Other habitat characteristics, like food availability and predation risk, make an anemone more or less desirable as a host, but no difference in other measures of habitat quality can compensate for the absence of a nesting site. Furthermore, whereas consequences of variation in food availability and habitat riskiness are felt immediately, several years may elapse between settlement and sexual maturation. The cumulative probability of host migration over those years may be appreciable. Selection should favour settling anemonefish that discount differences in nest site availability among potential hosts by the probability that those hosts will migrate before the settler matures.

The likelihood that an anemone will move before a newly settled anemonefish has matured can be approximated using estimates of the frequency with which anemones move and of the expected time to maturity for an anemonefish. Because a settling anemonefish's growth and maturation are inhibited by the presence of larger, more dominant, anemone residents, time to maturity depends on the mortality rate of earlierarriving group-mates (Fautin & Allen 1992): only the two largest fish in an anemonefish group breed; all others are sexually immature. If the female (the largest fish) is removed, the male changes sex to replace her and the now second-ranked group member matures as the new male. Therefore, assuming a settler survives, its expected rate of passage up a group's social hierarchy

is given by the rate equation $N_t = N_0 e^{-dt}$, where N_0 is the original group size excluding the settler, N_t is the number of individuals remaining ahead of the settler in the hierarchy after t years, and d is the annual mortality rate. (For simplicity, I assume that d is independent of size and rank.) The settler matures when all-butone earlier-arriving group members have died: when $N_t = 1$. The only published false clown mortality rate estimates are those of Nelson et al. (1996) for a population in Singapore. They report mortality rates of 24, 20, and 34% over 330 days for 1st, 2nd, and \geq 3rd ranked group members – an overall weighted mortality rate of 29% per annum. With d = 0.29, a false clown settling to an anemone already occupied by 3 fish expects to wait 3.8 years for 2 of the 3 earlier arrivals to die, allowing the settler to mature. Given that the annual likelihood of an anemone moving is 10%, there is a 0.32 probability that an anemone will move at least once before a settler to a group of 3 matures ($p = 1 - e^{-mt}$, where m = 0.1 is the annual probability of anemone movement and t = 3.8). Expected time to maturity will be longer and the likelihood of anemone movement, greater, for larger groups. False clown groups at Bunaken Island can have as many as 6 or 7 members (unpubl. data). For a settler to a group of 6 fish, the probability of anemone movement prior to maturation is 0.46. Settler choosiness should be further discouraged by the possibility of anemone movement during a settler's later tenure as a breeding male and/or female. Thus, host movement may help explain the presence of false clown groups on anemones whose pedal discs are buried beneath sand, such that no nesting substrate exists. These anemones may have been initially settled while living elsewhere. Alternatively, their occupants may have settled despite the absence of a nest site in because of the possibility that the anemones will later move.

False clowns might still settle to such hosts were they not mobile because, even in the absence of an obvious, permanent nest site, some level of reproduction is possible. At one of the anemones monitored, resident anemonefish took advantage of debris that came to rest against their host. That debris was gone again after the next windy day but a clutch had been laid in the interim and cared for until hatch. Likewise, the pebble used as a nest site at another anemone offered a limited surface area and was less stable than typical nest sites but did permit some level of reproduction. Thus, to categorize an anemone as unsuitable based on the apparent absence of a nest site is an oversimplification. Were anemones truly sessile, a limited reproductive expectation might still outweigh the cost of prolonging the search for an alternative. However, regardless of how one chooses to quantify variation in nest site quality, host mobility will tend to dampen that variation and, hence, lessen any benefit associated with discriminating among anemones based on the anemones' current habitat. That is, host mobility limits the circumstances under which settling anemonefish are expected to be discriminating.

Evidence that S. gigantea anemones can move, and the potential consequences of such movement for resident anemonefish, lead naturally to speculation that anemones in suboptimal habitats (from a fish's perspective) might be encouraged to move by those residents. I am not aware of any evidence to support such speculation. Reported changes in anemone behaviour when anemonefishes are present include a reduced frequency of spontaneous tentacle retraction (Fukui 1973), an increase in oral disc elevation above the substrate (Lubbock 1980), and more rapid expansion of contracted anemones (Mariscal 1972), but do not extend to pedal disc detachment. It seems more probable that anemones detach from the substrate to avoid wave-borne debris or to avoid predators (Fautin & Allen 1992).

Recent studies with a range of species have examined the relative contributions of various processes to determining distributions of coral reef fish (Caley et al. 1996). Predation and intraspecific competition are the two post-settlement processes most often considered. Post-settlement migration is generally discounted, particularly for weak-swimming species like anemonefishes. Moyer (1980) and Hattori (1995) discussed A. clarkii's inter-host migrations in temperate Japanese waters, where predation risk in-transit is low, and Fautin (1991) argued that the potential for subsequent migration may explain the willingness of some, relatively mobile, anemonefish species to settle on 'nursery anemones,' hosts either too small or of inappropriate species for later reproduction. False clowns are weak swimmers and face a high predation risk when not protected by an anemone (Fautin & Allen 1992). Migration between hosts is infrequent and is generally between anemones that are in close proximity (<10 m, Nelson et al. 1998), although longer distance migrations do occur (unpubl. data). Anemone mobility results in a novel mechanism of post-settlement redistribution for false clown anemonefish because fish accompany their hosts. Host mobility may also affect false clown distributions indirectly because the possibility that an anemone will move may result in false

clowns being less discriminating during settlement.

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