Inter-Habitat Migration of the Anemonefish *Amphiprion Ocellaris*

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Abstract

The rate and distance of inter-habitat migration of the anemonefish Amphiprion ocellaris was considered over 600 days at three sites on different reefs off Singapore's Southern Island group. Individual identification of the fish was based on the shape of the three vertical lateral white bars. The rate of emigration from host anemones was observed to increase with time and decrease with increasing distance to the next nearest habitat. The total migration distance of a fish also increased with time. Fish migration distance was found to increase with time. No migration was observed between anemones more than 1.65 m apart. Neither length of an individual nor an arbitrary social status were identified as significant factors in inter-habitat migration.

Introduction

The need for coastal marine management policies in Southeast Asia has been recognised and has achieved considerable attention (Chou, 1994; Hooten & Hatziolos, 1995; Hotta & Dutton, 1995). However, from a research perspective, data on most tropical coastal marine species are still limited to an extent where management of coastal resources must be considered at a habitat level, such as a coral reef. Whilst the need for habitat management policies certainly exists (Chua & Scura, 1991), they fail to identify management strategies for specific species which can be used as guidelines to maximize their exploitation on a sustainable basis. It is hoped that ongoing research regarding the anemonefish, *Amphiprion ocellaris,* will provide information which can eventually lead to exploitation management proposals for this species. For example, a study on the larval recruitment rates of *A. ocellaris* (one of the two factors which can increase the number of individuals in a anemone habitat) is currently being conducted. The work presented here aims to identify the extent of the other factor, inter-anemone migration of *A. ocellaris,* on two fringing and one patch reef off Singapore's Southern Island group. Identification of the maximum distance between anemones that *A. ocellaris* can traverse can, in turn, be used to estimate the maximum habitat size for the species, where aggregated or adjacent anemones can be

grouped as individual habitats, discrete from other anemones.

Except for a short pelagic larval life, *Amphiprion* spp. are confined as obligate symbionts to the immediate surroundings of their host anemone or aggregated group of anemones (Mariscal, 1970; Allen 1972). Protandrous hermaphroditism has been studied in several species of the genus (Fricke & Fricke, 1977; Moyer & Nakazono, 1978; Fricke 1979, 1983; Ochi, 1989a, b; Hattori, 1991; Hattori & Yanagisawa, 1991 a, b; Godwin, 1994), and there is a pronounced social structure within anemones (Moyer & Nakazono, 1978; Fricke, 1979; Nelson *et al.,* 1996). In Singapore, *A. ocellaris* has been identified with three species of anemones, *Heteractis magnifica, Stichodactyla gigantea* and *S. mertensii.* The largest individual in an anemone is usually a female, with a smaller dominant male and several other smaller individuals (Fautin & Allen,1992).

Amphiprion individuals recruit into an anemone following a pelagic larval phase (Bell, 1976) which, estimated at between 15 and 22 days, is relatively short compared to other coral reef fish species (Wellington & Victor, 1989). Attraction of larvae to a host anemone is thought to be chemo-sensory (Fricke, 1974; Miyagawa & Hidaka, 1980; Murata *et al.,* 1986; Miyagawa, 1989) although there is no evidence to suggest whether a larva can move between a number of habitats until a suitable one is found (i.e. a habitat containing conspecific anemonefish where intra-specific competition allows the survival of an additional individual). At least once settled, migration from a habitat appears restricted, as the host anemone remains its primary means of defence (Mariscal,1970).

As *Amphiprion spp.* are only observed in the immediate surroundings of a host anemone species, distribution of these fishes must be limited to an extent by the distribution of the host anemone species. Therefore, a suitable host anemone species can be considered as a potential and quantifiable habitat. From a fisheries management perspective, pelagic larval recruitment and inter-habitat migration will determine replenishment time, the density of fish in a habitat and the capability of reproduction within the habitat (i.e. the habitat possessing a sexually mature female and male fish).

Results are discussed with reference to the significance of migration in determining the density of *A. ocellaris* in a habitat and their reproductive potential. In addition, attention will be given to the relevance of this research to *A. ocellaris* in other localities.

Materials and Methods

The study was conducted between April 1993 and November 1994 off Singapore's Southern Islands, an area consisting of around 50 fringing and patch reefs. Two fringing reefs, Raffles Lighthouse (RL) and Kusu Island (Kl), and a patch reef Terumbu Pemalung Besar (TPB) were selected as study sites. Each of the three sites possessed considerable numbers of anemones, mainly *H. magnifca* inhabited by *A. ocellaris.*

The three sites differed considerably in their physical and biological attributes. The fringing reef Kl was closest to the mainland (4.2 km) and possessed a gently sloping reef slope with a low percentage of coral cover and a poorly defined reef crest. The site consisted solely of a large number of *H. magnifica* anemones, many aggregated to form large habitats. The RL site, also a fringing reef, was furthest from the mainland (13.6 km). It possessed a well defined reef crest, a steeper reef slope and a high percentage of coral cover. The dominant anemone species was also *H. magnifica,* individuals of which were also often aggregated. The site at TPB, a patch reef, possessed a lower density of anemones compared to the two other sites, consisting mainly of *H. magnifica* and *S. gigantea.* The TPB site was 8.85 km from the mainland, with low coral cover.

Initially areas below a 15 m length of crest down to a depth of 10 m below the

crest were surveyed at each site. All anemones within the sites were identified, marked with labelled stakes and assigned relative grid positions. Accuracy was ensured by laying guide tapes parallel to the crest, thereby breaking the quadrate into manageable strips. This method proved particularly effective for accurate sampling of relatively large areas of reef in waters of high turbidity. Anemones less than 10 cm from each other were marked as a group. When fully expanded, the oral discs of anemones within such close proximity will presumably be continuous, or near continuous, and can be considered as a potential habitat for *A. ocellaris*. In this way, it was initially assumed that anemones greater than 10 cm apart constituted discrete habitats. The distance between habitats was measured directly for adjacent habitats or estimated from the site maps for others.

A total of 107 *A. ocellaris* (RL=84; Kl=12; TPB=11) were initially photographed in April 1993 (t_0) in 33 habitats (RL=23; Kl=6; TPB=4) following Nelson *et al.* (1994), which yielded fish length data. Records were made of the identity of the host habitat of each fish. Photographs of individuals from 12 subsequent surveys (RL=7; Kl=2; TPB=3) were matched with the original set. Individual identification was based on the shape of the three vertical lateral white bars. No attempt was made to match individuals under 40 mm in total length which have been shown to display less band variation due to the development of the caudal bar and the lower photographic resolution (Nelson *et al.*, 1994), except where variation in the head and middle bar was especially obvious. Fish over 40 mm in total length that were not identified as present in the original survey (an additional 29 individuals) were included in subsequent surveys. A total of 137 individuals were therefore considered over the entire survey period (RL = 81; Kl = 23; TPB = 32).

As not all habitats at each site were visited during each survey, due mainly to time, weather and tidal current constraints, the number of different periods (t_{i+1}-t_i)

between individual identification (22), which varied between 3 and 600 days was greater than the total number of return surveys (12). For each survey the identity of the host habitat of each individual was compared with the identity of the host habitat from the last survey in which the individual had been identified.

Following each survey interval ($\Delta t=t_{i+1}$-t_i) several variables were recorded for each fish. These included whether or not the fish was identified in a different habitat (migration: S=1; no migration: S=0), the distance of the fish's host habitat at t_i to the nearest adjacent habitat (A), its total migration distance over the survey interval (D = the distance between its host habitats at t_i and t_{i+1}), and the longest necessary distance moved between two habitats during the survey interval to get to the recipient habitat (L). The method of calculation for each of these variables is shown diagramatically in Figure 1.

Statistical methods used include the independent t-test, one-way analysis of variance and multiple regression analysis. Means are presented ± S.D.

Results

A total of 136 individuals (RL = 81; Kl = 23; TPB = 32) were photographed up to a maximum of four times over the study period, making a total of 213 records (RL = 125; Kl = 33; TPB = 55). Of these records, 55 (%M = 25.82%) were identified as having migrated (Table 1). Migration between habitats was observed at two of the three sites, RL (39.20% of records) and Kl (18.18%). No migration was observed at TPB.

Mean oral disc areas of habitats ($\overline{H}_o$), the mean depth of habitats below the reef crest ($\overline{H}_d$), the mean density of fish per habitat (calculated as the mean number of fish per habitat ($\overline{H}_f$), the mean combined length of fish per habitat ($\overline{H}_c$) and the mean number of fish per cm2 of habitat oral disc ($\overline{H}_v$) did not differ significantly between the three sites (Table 2). Due to the similarity of these

Legend for Figure 1

(Nelson et al. "Inter-habitat migration of the anemonefish...")

Fig. 1. Diagrammatic representation of the method of calculation of the variables recorded for *A. ocellaris* migration between the host (a) and recipient (b) habitats. Each circle represents one habitat. Variables include: the nearest habitat to the host habitat in cm (A); the distance between the host and recipient habitats in cm (D); and the longest necessary distance moved by a migrating individual between habitats to get to the recipient habitat in cm (L).
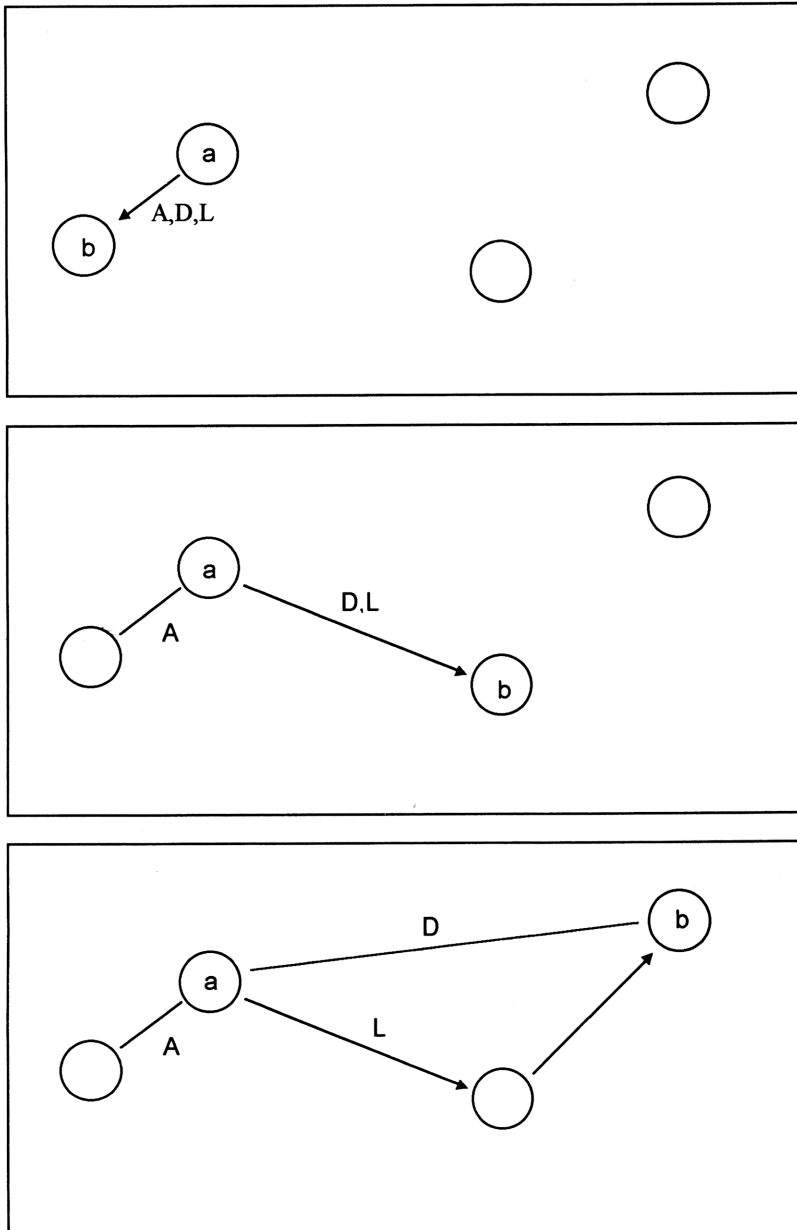
variables between sites, and the relatively small sample sizes at TPB and Kl, the data from the three sites were pooled for subsequent statistical analysis.

The maximum migration distance (D_{max}) was 10.30 m, the maximum distance to the nearest adjacent habitat of a migrating fish (A_{max}) was 1.30 m and the longest necessary distance moved by a migrating fish between habitats to get to the recipient habitat (L_{max}) was 1.65 m. The mean migration distance of fish which had migrated ($\overline{D}$) was 0.98 $\pm$1.105 m and the mean longest necessary distance moved between habitats ($\overline{L}$) was 0.62 $\pm$ 0.501 m. Mean results for discrete survey intervals are presented in Table 3.

TABLES (Nelson et al. "lnter-habitat migration of the anemonefish...")

Table 1a. Summary of the migration results of *A. ocellaris* at the three study sites and pooled data. Results refer to all surveyed individuals. Variables include: n = number of fish surveyed; b = number of records; $\overline{G_{ti}}$ = mean initial length of fish in mm; %M = percentage of records where fish were seen to have migrated; $\overline{\Delta SS}$ = mean change in arbitrary social status; $\overline{A}$ = mean distance to an adjacent habitat in cm; $\overline{D}$ = mean migration distance of a fish in cm; and $\overline{L}$ = mean maximum distance moved by a migrating fish between habitats to get to the recipient habitat in cm.

	RL	KI	TPB	Total
n	81	23	32	136
b	125	33	55	213
$\overline{G_{ti}}$	58.9 $\pm$ 17.7	56.0 $\pm$ 16.3	52.0 $\pm$ 20.0	56.6 $\pm$ 18.3
%M	39.20	18.18	0.00	25.82
$\overline{\Delta SS}$	0.00 $\pm$ 0.64	0.03 $\pm$ 0.64	–0.05 $\pm$ 0.40	–0.01 $\pm$ 0.58
$\overline{A}$	46 $\pm$ 35	42 $\pm$ 18	500 $\pm$ 0	162 $\pm$ 202
$\overline{D}$	40.7 $\pm$ 87.5	7.0 $\pm$ 17.4	0.0 $\pm$ 0.0	24.8 $\pm$ 69.6
$\overline{L}$	24.9 $\pm$ 44.9	6.5 $\pm$ 16.8	0.0 $\pm$ 0.0	15.5 $\pm$ 36.7

(Nelson et al. "Inter-habitat migration of the anemonefish...")

Table 1b. Summary of the migration results of *A. ocellaris* at the three study sites and pooled data. Results refer only to fish which were observed to have migrated (M=1). Variables include: b = number of records; $\overline{A}$ = mean distance to an adjacent habitat in cm; $\overline{D}$ = mean migration distance of a fish in cm; $\overline{L}$ = mean maximum distance moved by a migrating fish between habitats to get to the recipient habitat in cm; and $\overline{\Delta SS}$ = mean change in arbitrary social status.

	RL		Kl		TPB	Total	
b	6		49		0	55	
$\overline{A}$	39.71	30.04	30.00	20.74	-	38.65	29.17
$\overline{D}$	106.5	114.5	38.3	22.1	-	98.8	110.2
$\overline{L}$	65.04	51.82	35.83	23.33	-	61.74	50.15
$\overline{\Delta SS}$	- 0.02	0.78	- 0.17	0.75	-	- 0.04	0.77

(Nelson et al. "Inter-habitat migration of the anemonefish...")

Table 2. One-way analysis of variance (ANOVA) comparing the means of the habitat oral disc area ($\overline{H}_o$) in cm², depth of the habitat below the reef crest ($\overline{H}_d$) in m, number of fish per habitat ($\overline{H}_f$), combined length of fish per habitat ($\overline{H}_c$) in mm, and number of fish per cm² of habitat oral disc area ($\overline{H}_v$) at the three sites.

	TPB	KI	RL	F	Sig	Pooled
n	4	6	23	-	-	33
$\overline{H}_o$	1713 ± 553	4438 ± 2926	4319 ± 3109	1.43	n.s.	4025 ± 2962
$\overline{H}_d$	0.917 ± 0.183	0.927 ± 0.420	1.150 ± 0.212	2.74	n.s.	1.081 ± 0.270
$\overline{H}_f$	3.000 ± 0.817	2.000 ± 1.414	3.652 ± 3.171	0.86	n.s.	3.273 ± 2.776
$\overline{H}_c$	149.0 ± 49.99	106.8 ± 83.2	173.0 ± 157.0	0.54	n.s.	156.0 ± 134.5
$\overline{H}_v$	18.20 ± 4.94	9.19 ± 11.72	9.24 ± 5.08	3.20	n.s.	10.32 ± 7.09

(Nelson et al. "Inter-habitat migration of the anemonefish...")

Table 3. Results of *A. ocellaris* mean migration rates ($\overline{M}$, ranging from 0 - 1) from the host habitat, and for those fish which migrated, the migration distance in cm ($\overline{D}$ + S.D.) and the longest necessary distance moved between habitats to reach the recipient habitat in cm ($\overline{L} \pm$ S.D.) for the different survey intervals ($\overline{\Delta t}$ in days).

Survey interval (Δt)	All Fish		Migrated Fish	
	Number of records	Mean migration rate (M, 0 -1)	Mean migration distance (D)	Mean longest distance (L)
3	6	0.000	-	-
6	49	0.082	0.36 ± 0.28	0.36 ± 0.28
8	8	0.250	0.43 ± 0.11	0.35 ± 0.21
9	6	0.000	-	-
16	11	0.273	0.55 ± 0.00	0.55 ± 0.00
50	10	0.300	0.70 ± 0.35	0.52 ± 0.06
66	5	0.000	-	-
72	1	0.000	-	-
206	4	0.000	-	-
215	8	0.000	-	-
218	1	0.000	-	-
222	20	0.250	0.58 ± 0.63	0.48 ± 0.71
224	6	0.500	0.05 ± 0.01	0.05 ± 0.01
231	8	0.625	0.67 ± 0.32	0.38 ± 0.03
237	10	0.500	0.32 ± 0.16	0.78 ± 0.96
247	2	0.000	-	-
347	12	0.583	1.84 ± 1.48	0.81 ± 0.63
358	10	0.000	-	-
363	33	0.515	0.98 ± 0.77	0.83 ± 0.54
594	1	0.000	-	-
600	1	1.000	5.00 ± 0.00	1.60 ± 0.00

The relationship between the dependent variable rate of migration (M) from a host habitat and the independent variables survey interval (Δt) and distance to the nearest habitat to the host (A) was estimated by multiple regression analysis which was weighted for the number of observations in each survey interval.

Migration rates (0 - 1) from a habitat can best be predicted by the multiple linear least square regression model:

$$M = 0.262 - [(8.52 \times 10^{-2}) \times A] + [(7.14 \times 10^{-4}) \times \Delta t]$$
Equation 1 ($n = 22$; $r^2 = 0.702$; $P<0.001$)

(where; M = mean rate of migration from an habitat; t = time between surveys in days; and A = distance to nearest habitat from host habitat in meters)

This indicates that the variable M significantly decreases as A increases and increases as Δt increases.

A general linear model was used to identify the relationship between the dependant variable, D, and the independent variable, Δt, with the inclusion of a dummy variable to distinguish between fish which had migrated (S=1) and those which had not (S=0). The model can be expressed as:

$$D = 0.777 - (0.898 \times S) + [(8.58 \times 10^{-4}) \times t]$$
Equation 2 ($n = 211$; $r^2 = 0.412$; $P<0.001$)

(where; D = distance moved between habitats in meters, and Δt = time between surveys in days)

A general linear model was also used to identify the relationship between the dependant variable, L, and the independent variables, A and Δt. The dummy variable, S, was again included to distinguish between fish that had migrated and those which had not.

$$L = 0.538 + (-0.585 \times S) - [(3.64 \times 10^{-4}) \times A^{-2}] + [(4.35 \times 10^{-2}) \times t]$$ Equation 3
($n = 211$; $r^2 = 0.566$; $P<0.001$)

where L = longest necessary distance moved between habitats in meters, and A = distance, in meters, to the nearest habitat from host habitat.

The mean initial lengths ($\overline{G_{ti}}$) of fish that migrated (S=1) and those which did not (S=0) was compared using an independent t-test. The $\overline{G_{ti}}$, values of migrating (56.6 ± 18.0 mm) and non-migrating fish (56.5 ± 18.4 mm) were not significantly different (t-test, $P>0.05$).

An arbitrary social status rating, SS (where the largest individual in a habitat = SS1; 2nd largest = SS2; all others = SS3), was adopted (following Nelson et al., 1996) in an attempt to further explain migration rates of fish. The mean change in social status rating ($\Delta SS = SS_{ti} - SS_{ti+1}$) of fish which had migrated and those which had not was compared using an independent t-test. The $\overline{\Delta SS}$ of migrating (S = 1: $\overline{\Delta SS}$ = -0.036 ± 0.769) and non-migrating fish (S = 0: $\overline{\Delta SS} = 0.000 \pm 0.505$) was not significantly different (t-test, $P>0.05$).

Discussion

As *A. ocellaris is* dependent on its host anemone for protection, it is hardly surprising to find that migration between anemones is restricted by the distance between anemones. The three variables generated in this study demonstrate the restrictions on *A. ocellaris* migration in different ways.

For instance, from an individual's viewpoint, the distance to adjacent anemones (A) is presumably the limiting factor in migration. This is reflected in the variation observed in the extent of migration between anemones at the three sites. In particular, the site TPB comprised of anemones either together (< 10 cm apart, which was initially assumed to be a distance where the oral discs of the adjacent anemones could be continuous) or distant (> 5 m apart), and no inter-habitat migration was observed. This is in contrast to the other two sites, RL and Kl, where the distance between anemones was smaller and migration was possible.

The variable L, which represents the longest distance moved by an individual between two anemones, perhaps best

reflects the maximum distance that *A. ocellaris* can migrate under local conditions. It is noted here that in many circumstances L was indistinguishable from A (i.e. an individual migrated to the nearest adjacent anemone). However, to consider the variable A alone would be misleading as it would ignore migration of an individual into other anemones.

The third variable, D, which represents the total migration distance over the survey period, is useful as an indication of the extent of migration under local conditions. The high values of D, relative to L, suggest that inter-anemone migration can occur in a stepping-stone manner. In this way, migration of an individual between a number of close anemones can lead to the observation of a fish, a considerable distance from its starting place.

The next step in our analysis was to consider additional factors, other than simply distance between anemones, which could limit inter-anemone migration. There was no significant variation in the mean initial length (G_{ti}) of fish which had migrated and those which had not. However, length of a fish may not be an accurate representation of its social standing within a habitat. Arbitrary social status ratings (SS) for *A. ocellaris* have proved useful in previous studies, and have provided albeit circumstantial evidence regarding the social interactions of the individuals within a habitat (Nelson *et al.*, 1996). However, in this study SS ratings were unable to account for variation in the migration rate of fish.

Furthermore, the regression analysis, where linear relationships were observed between the variables, suggest that migration of fish is a continuous event. In other words, the rate of migration (M) was directly proportional to time. For those fish that did migrate, they migrated a greater distance (D) and between anemones further apart (L) over a longer survey interval. These apparent linear relationships may themselves indicate the insignificance of other variables (i.e. length or social status) as they account for large proportions of the

variation in the data (i.e. high r^2 values).

The results presented here appear to contradict the observations of Ross (1978), where no migration of *A. melanopus* between colonies of *Physobrachia douglasi* was reported. Ross suggested that this was due to high levels of predation away from the host (Eibl-Eibesfeldt, 1960; Fricke, 1976).

More in accordance with the results presented here, Hattori and Yanagisawa (1991a) observed migration of both mature *A. clarkii* females and males between colonies of *Parasicyonis maxima*. In that study, an equally complex state was described where, following the removal of a female from a pair, sex change of the male in the colony was suppressed by the immigration of neighbouring females. Only where individual males were free from the influence of neighbouring females was sex change observed.

In another report (Hattori and Yanagisawa, 1991b) they noted that *A. clarkii* moved between *P. maxima* and has no social unit typical of tropical anemonefishes. They hypothesised that this could be due to higher densities of host anemones in temperate waters off Japan compared to the tropics (Ochi, 1986, 1989a, b; Yanagisawa & Ochi 1986). It was also reported that sub-adults held home ranges outside the territories of breeding pairs and could form breeding pairs with either breeders or non-breeders.

Moyer and Sawyers (1973) observed large female *A. xanthurus (A. clarkii)* territories, encompassing up to two or three male territories. These observations were made at a site (also in Japanese waters) which was entirely covered by *Cymbactis actinostoloides*. The females constantly migrate between male territories, while immature fish are restricted to the periphery of the territories.

Direct comparisons with these previous studies may be misleading. Allen (1975) suggested that, compared to other *Amphiprion* species, *A. ocellaris*, being a member of the percula complex was

relatively distantly related to *A. clarkii* (clarkii complex) and *A. melanopus* (ephippium complex). Differences in the behaviour of species have been previously documented, notably, the apparent reduced dependence of *A. clarkii* on its host anemones than that of other anemonefishes (Allen, 1972). Spatial behavioural differences have also been recorded, such as seasonal variation in the activity of anemonefish in temperate waters (Moyer and Sawyers, 1973). It is therefore unrealistic to assume correspondence of behaviour between species or even within a species at different locations.

The results presented here do not attempt to map the movement of specific individuals between anemones over time. Although individuals can be confidently identified (Nelson *et al.,* 1994) sexual dimorphism of *A. ocellaris* is unpronounced, compared to *A. clarkii,* and this would in turn limit the relevance of such an approach.

Therefore we stop short of suggesting that there is no different rationale behind the movement of fish of different length and social status. Indeed, whilst both large and small fish (and presumably juveniles and mature females and males) all migrate between anemones at similar rates, they may be doing so for very different reasons. In this context, many reports on other *Amphiprion* species are not contradicted, such as the movement between male habitats of female *A. clarkii* (Hattori and Yanagisawa, 1991a), and the lack of individual territories of *A. clarkii* juveniles (Moyer and Sawyers, 1973).

However, the traditional view, that following the death of the female in a habitat, the dominant male undergoes sex change and the highest ranking non-breeding individual becomes the dominant male (Fautin & Allen, 1992), can be questioned.

Both the studies by Hattori and Yanagisawa (1991a, b) and this investigation have provided evidence that anemonefish social structure at sites of high host density is not typical of other areas. In that study,

Hattori and Yanagisawa (1991a, b) commented that host density at their study sites was high compared to tropical waters. From personal observations (unpublished data) we believe that high densities of *H. magnifica,* probably due to cloning, are also common in certain tropical regions such as Singapore and Malaysia, which is similar to other reports (Fautin & Allen, 1992).

Densities of anemonefish within a habitat in Singapore are similar to those in areas where clones in not observed. A comparison with the density of *A. percula* (a species closely related to *A. ocellaris,* Allen, 1975) with the host *H. magnifica,* in Papua New Guinea, revealed similarities (Fautin, 1992). The noticeable difference between the study sites was that *H. magnifica* in Papua New Guinea were solitary, compared to the clumped anemones (<10 cm apart) commonly observed in this study. Even so, calculating oral disc area (πr^2) from the mean anemone diameter reported by Fautin (47.8 cm ± 12.2) suggest that mean habitat areas of H. *magnifica* in the two studies are of the same order (Table 2). Other density variables reported by Fautin also fell within the ranges recorded at the three sites in this study ($\overline{H}_{f}$: this study = 3.3 ± 2.8, Fautin = 3.5 ± 1.1; $\overline{H}_{c}$ this study = 156.0 ± 134.5, Fautin = 169.4 ± 57.4)

The rate of inter-habitat migration of *A. ocellaris is* likely to influence the effective population size. Allen (1972) suggested that *A. clarkii is* less dependant on host sea anemones than other anemonefishes. In our experience, *A. ocellaris is* restricted to the immediate surroundings of its host anemone habitat, from which it is thought to obtain protection. This is reinforced by our results which indicate that inter-anemone migration occurred mainly between adjacent habitats.

Migration of anemonefishes will almost certainly have some effect on the population ecology of *A. ocellaris.* For example, protandry in anemonefishes has been regarded as an adaptation to low population density of hosts and high predation pressure

outside their hosts (Moyer & Nakazono, 1978; Fautin & Allen, 1992). A traditional approach to the population ecology of *A. ocellaris* individuals in a habitat would suggest that mate replacement, following the death of one of the reproducing pairs in a habitat, is achieved by sex change of the male fish and/or maturation of one of the sub-dominant individuals. In a site such as TPB, where habitats are distant and inter-habitat migration is not observed, this concept should exist.

However, at sites of host density higher than TPB, such as Kl and RL, migration could exist as another means of mate replacement. This point has been made by Hattori and Yanagisawa (1991 b) where new mating pairs were made up of previously matured individuals. Migration may also exist as a mode of mate separation. Hattori and Yanagisawa also reported that 14 mating pairs of *A. clarkii* either separated or disappeared but did not elaborate on their data. Paired individuals that were both identified in subsequent surveys were regularly found in separate habitats. Whether or not the pair was originally a reproducing pair or whether they would have returned to reproduce is unknown, but such separations cast doubt on the monogamy of *A. ocellaris* in such populous environments.

From the perspective of the fisheries biologist our findings indicate that host habitat density will significantly effect the extent of inter-habitat *A. ocellaris* migration, and therefore presumably the effective population sizes following exploitation. The absence of migration from habitats more than 1.65 m from other habitats suggests that pelagic larval recruitment will limit the stock sizes at sites where habitats are widely dispersed, such as at TPB. The effect of *A. ocellaris* exploitation from a habitat in a site of high host anemone density, such as Kl and RL, is complicated by considerable migration of individuals from adjacent habitats. Whether inter-habitat migration of *A. ocellaris* allows faster recovery of the effective population size following

exploitation or whether the complicated social structure in fact decreases the effective population size is unknown. A specific comparative study into the reproductive rates of the two systems is necessary to fully understand the phenomenon.

Acknowledgements

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