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Habitat specialisation, site fidelity and sociality predict homing success in coral reef cardinalfish

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ABSTRACT

Species that home demonstrate faithfulness to a particular location, however not all species with high site fidelity can or will home. These movement decisions are often mediated by a species social behaviour and habitat preferences. Here we explored how habitat specialisation, site fidelity and social traits relate to homing behaviour in five species of cardinalfish (Family: Apogonidae). We also compared species' capacity to home across open water versus continuous reefscapes. To track site fidelity and then homing behaviour the precise location of over 1200 tagged cardinalfish on Kimbe Bay reefs (West New Britain, Papua New Guinea) was visually monitored over time. Following experimental displacement, all species homed quickly across ~ 400m of both open water and continuous reef habitats. Incredibly, individuals of one species homed up to five kilometres across multiple reef and inter-reef passages. Homing was not coupled with site fidelity as both low and high fidelity species homed well. However, it was correlated with the degree of habitat specialisation, with specialist species returning in greater numbers than generalist species. Social traits alone did not predict stronger homing behaviours, but gregarious species with high site fidelity homed better than the less social and less specialised species. Hence, both social factors and habitat preferences appear to influence the propensity to home. Generalist species and those that do not form rigid social groups are more likely to be able to settle for new sites and have less need to return to precise locations.

Keywords: homing, behaviour, habitat specialisation, aggregation, coral reef fish, social preferences, Apogonidae.

INTRODUCTION

Many animals exhibit homing behaviour, navigating through complex environments to return to a previously used location (Griffin 1952). Homing (i.e. to “return by instinct to one’s territory after leaving it” Oxford Dictionaries, v.d.) is common in animals that regularly migrate between foraging, breeding and / or resting locations and is widespread in the animal kingdom (reviewed by Papi 1992). The behaviour allows individuals to exploit widely spaced resources while maintaining connections with familiar locations and/or individuals. The distance some species will traverse is extraordinary. For instance, particular species of bees (Pahl et al. 2011), lizards (Jenssen 2002, Huang & Pike 2011), bats (Guilbert et al. 2007) and fish (Ogden & Buckman 1973, Matthews 1990, Yoshiyama et al. 1992, White & Brown 2013) will travel 10 - 200 times further than their usual daily ranges to return home. Homing behaviour, however, is not consistent among similar species or even individuals. The likelihood of homing is often affected by an individual’s age, size, experience and / or reproductive status (e.g. Rau 1929, Wall & Herler 2009; Shima et al. 2012). Some species appear to be more motivated and / or more successful at returning home than others, but the underlying reasons for variation in the propensity to home are not well understood.

There is increasing evidence that species or individuals with particular ecological or behavioural traits are more likely to home than others. Taxa that exhibit strong site fidelity (i.e. repeatedly use the same location) or have a prolonged association with a particular place are more likely to home when displaced. For instance, resident rock pool fish return to the capture pool more than transient species do (White & Brown 2013). In addition, species that migrate between the same foraging, resting or nesting areas, typically home back to their familiar site. For example, nesting turtles (Limpus et al. 1992), migratory birds (e.g. Part 1995, Dell’Ariccia et al. 2015) and various fish species (e.g. Ogden & Buckman 1973, Matthews 1990, Dittman & Quinn 1996, de Perera & Guilford 2008, Morris et al. 2014) all home back to very precise locations. In contrast, taxa that regularly move among locations, switching between multiple breeding or feeding sites, may be less likely to home following displacement. Interspecific differences in the ability and motivation to home may relate to the nature of species' site fidelity and the type of advantages gained by using familiar locations.

The degree of habitat specialisation and the distance a species needs to traverse to return home will have a large effect on their homing success, particularly for small bodied animals. In sub-tidal marine environments, movement of small fish (< 10cm in length) is usually impeded by open water and / or sand gaps larger than five metres in width (Frederick 1997, Overholtzer-McLeod 2006, Feary 2007, Wall & Herler 2009). In contrast, larger fish (> 13cm in length) will home over open terrain from eight kilometres away (Matthews 1990, Carlson et al. 1995, Hartney 1996, Workman et al. 2002). In some cases the habitat may be more of a barrier than the distance. Parrotfish for example will home long distances across continuous reef habitats, but not short distances through open environments (Ogden & Buckman 1973). Yet for highly specialised reef fish living on patchy habitats, homing across any terrain may be necessary to ensure they find suitable habitat.

On coral reefs, species in the cardinalfish family (F. Apogonidae) are known to have impressive homing abilities. Cardinalfish are nocturnal planktivores that rest diurnally in branching corals or caves, and typically form large multi-specific aggregations at these resting sites (Gardiner & Jones 2005). At dusk, they disperse from their aggregations and forage in isolation above sand, rubble, rock or coral substrata, before returning to resting sites at dawn (Chave 1978, Marnane & Bellwood 2002). Their fidelity to diurnal refugia appears to be very high and can persist for at least several months and / or several breeding cycles

(Fukumori et al. 2010, Marnane 2000, Okuda 1999). Marnane (2000) experimentally displaced several species (*Apogon doedoerlini*, *Cheilodipterus artus* and *Cheilodipterus quinquelineatus*) within a shallow, lagoonal environment and observed fish homing returns of 33 - 63% from two kilometres away, and 56 - 81% from one kilometre, all within three days. Since Marnane's (2000) discovery other authors have documented strong homing and site fidelity in several other reef species (Fukumori et al. 2010, Gould et al. 2014, Rueger et al. 2014) and begun to investigate the sensory cues and motivational drivers of homing (Atema et al. 2002, Døving et al. 2006, Gerlach et al., 2007, Fukumori et al. 2010, Rueger et al. 2014, Gould et al. 2015).

For cardinalfish, both social and habitat preferences are likely drivers of their homing responses and their site fidelity. Differences in the interactions of these preferences may explain species-specific differences in their homing responses and site fidelity. Species (and individuals) that live in small cohesive social groups may be more motivated to home than less gregarious species. For instance, site fidelity and homing success is higher in paired individuals of *Ostorhinchus cyanosoma* than in solitary fish, presumably because of the reproductive links (Rueger et al. 2014). The gregarious species *Pterapogon kauderni* also homes, but it appears to be homing to the site rather than to familiar individuals (Kolm et al. 2005). Indeed, individuals within groups are not always faithful to each other, despite the advantages of living among known individuals (Chivers et al. 1995; Grabowska-Zhang et al. 2012). Cardinalfish vary in their habitat specificity (Gardiner & Jones 2005) and, as seen in other small reef fish species, generalists may move more than specialists (Feary 2007). Thus for some species the habitat may be a greater motivator than their social environment.

Here we explore the link between homing and site fidelity for five species of cardinalfish that differ in their apparent social group structure and habitat preferences. We examine whether inter-specific differences in homing success are related to differences in species' degree of site fidelity, habitat specialisation, and sociality. Previous research on coral reef cardinalfish has only evaluated their capacity to home across relatively continuous reef habitats. Here, we also compare homing success across continuous versus open-water environments and test the distance to which inter-reef homing might extend. The following specific questions are addressed: (1) Is homing success higher in species with stronger site fidelity, and is this correlated with their social and /or habitat preferences? (2) Does the type of terrain crossed affect homing success? In particular does homing success in Apogonidae differ between continuous reef and open water (inter-reef) crossings? And (3) to what distance can homing extend?

METHODS

Study site and species

This study was conducted on fringing and inshore platform reef slopes in western Kimbe Bay, Papua New Guinea (5°30´S; 150°05´E. Figure 1). Reefs in this area are separated by 0.2 – 1km of open water and depths of 30 – 60m (Jones et al. 2004, Srinivasan & Jones 2006). Diurnal, multi-specific aggregations of 20 - 1000 cardinalfish fish are easily located on large *Porites cylindrica* branching corals on most reef slopes (Gardiner & Jones 2005). Our study was conducted in 3 – 15m water depth, below which the study species and branching coral habitats are rarely found (Gardiner & Jones 2005). Extensive surveys were conducted on the Tamare - Kilu reefs (Figure 1) to map out all aggregations of cardinalfish species. This familiarity with the study area subsequently enabled us to relocate tagged fish during the project.

We used the five species of cardinalfish most abundant in the area: *Taeniamia zosterophora, Zoramia fragilis, Z. leptacantha, Cheilodipterus artus* and *C. quinquelineatus*. These species vary in their degree of habitat specialisation among diurnal resting habitats (Gardiner & Jones 2005), their apparent social preferences and their site fidelity. The standard length of individuals used in this study were: *T. zosterophora* 33 - 50mm, *Z. fragilis* 31 – 39mm, *Z. leptacantha* 31 – 39mm, *C. artus* 41 – 61mm, *C. quinquelineatus* 41 – 63mm. Only adults were used. All animal handling techniques used in this study followed stipulations of James Cook University animal ethics committee (#A1028).

Habitat specialisation

In Kimbe Bay, all five species preferentially inhabit *P. cylindrica* corals but vary in the breadth of other micro-habitats occupied. Species were categorised by their degree of habitat specialisation at this locality, according to Gardiner & Jones (2005). In order of micro-habitat specialisation, from least to most, the species are *C. quinquelineatus*, *C. artus*, *T. zosterophora*, *Z. fragilis* and *Z. leptacantha.*

Sociality

Inter-specific variation in sociality was explored by comparing species' propensity to aggregate. The dispersion of the five species was recorded across 10 fore and back-reef slopes on the Tamare - Kilu reefs (Figure 1a). This information was collected prior to the experimental aspects of the current paper, in association with habitat use data (Gardiner & Jones 2005). For each observed individual, or group of individuals, we recorded the number of conspecifics in the group. When the number of individuals exceeded 20, accurate counts were visually difficult and an estimated abundance was extrapolated. Variation in species' aggregation tendencies was compared graphically by plotting the observed group sizes as well as the frequency of group sizes that individual fish occurred in. The latter provided a means to compare the probability by which individuals of each species would occur in an aggregation or in isolation.

Site fidelity

To establish each species' degree of fidelity to a home site we conducted a mark-resight study. The home site was the coral colony where fish were captured, tagged, then repeatedly observed resting in. For one species, *T. zosterophora*, we also explored the extremity of its site fidelity by monitoring how consistently individuals used particular sections within the colony. This species was used because it showed the highest site fidelity (see results), and occurred in sufficient numbers within neighbouring aggregations on one reef slope area, allowing for optimal sampling efficiency.

Adult individuals were captured using clove oil anaesthetic (Munday & Wilson 1997), small hand nets and / or a Bincke net (Anderson & Carr 1998). Clove oil was prepared with a 10:5:100 oil, low grade ethanol to seawater ratio and dispersed around the coral colony through hand held spray bottles (500ml volume). The anaesthetic acts to slow fish responses down (within ca. 30 seconds) such that divers can catch them with hand nets. On adult cardinalfish the anaesthetic effect tended to last approximately five minutes. Repeated doses were used if fish were not captured and tagged in that period. While still under the influence of anaesthetic, fish were tagged subcutaneously with fluorescent elastomere (VIE-NorthWest Marine Technology) inserted into dorsal and/or caudal musculature on the right-hand side of the fish. Individuals of each species were uniquely tagged using a combination of five tag colours and five body positions. The tags were relatively long (2 – 4mm long) and in bright colours so that they were easy to see from 1 – 2m away. To minimize handling stress, fish were also tagged whilst at their capture depth, rather than being taken to the surface. Capture and tagging of cardinalfish in this manner does not adversely affect their behaviour or predation mortality (Marnane 2000).

After tagging fish were held in mesh cages near their capture location for at least 30 minutes prior to release. This time was sufficient for effects of the anaesthetic to disperse from the coral colony, and for the affected fish to resume normal swimming behaviour (NMG pers. obs.). Fish were released in a group and most individuals experienced more than 30 minutes recovery (and up to 2 hours). Upon release from the cage, divers monitored the group of tagged fish for any signs of abnormal behaviour, and / or instant predation. Any fish experiencing immediate adverse effects was excluded from future data analysis.

Fidelity to a single coral colony

To investigate fidelity to particular coral colonies and / or movement among adjacent corals, we monitored positions of tagged fish on one reef slope. The chosen area had numerous cardinalfish aggregations on *P. cylindrica* corals allowing for efficient monitoring of multiple species and individuals (Figure 1b). The designated monitoring area was 200m long, approximately 30m wide and extended to a depth of 15m. The area was bordered by large expanses of sand to the south and steep walls to the North, such that there was at least a 50m distance to suitable resting refugia on either side. Comprehensive visual surveys identified all diurnal refuge sites of cardinalfish within the monitoring area, and also around the remainder of Gava Gava reef (Figure 1b). Four aggregations of *T. zosterophora*, and *Z. fragilis* and three aggregations of *C. quinquelineatus* and *C. artus* were selected for tagging and monitoring. Only three groups of the latter species could be found in the study area, limiting their sample size. Within each aggregation, 10 - 16 individuals of the focal species were captured, tagged, and then monitored.

Two to three days after tagging, surveys of focal aggregations were carried out and sightings of tagged individuals were recorded. Surveys proceeded by the same observer (NMG) hovering about two metres from the edge of fish aggregations and passively observing fish at rest. This method was effective because the resting cardinalfish sit on the outer edges of their refuges and are quite easy to watch and count when not panicked. The observer remained at each aggregation site for 30 - 60 minutes to count tagged fish, or longer if the aggregation was particularly large (i.e. > 50 fish). If the fish group were panicked by a predator or a rapid movement by the diver, they typically resumed their relaxed resting posture within 1 – 2 minutes. This behaviour was taken to indicate that the aggregations of cardinalfish do not feel harassed by the passive diver observations and thus we assumed surveys did not affect fish presence / absence at the study sites. To enhance reliability of the visual records per tagged fish, multiple sightings of each tagged fish were taken during the daily observation time. The same search procedures were also used in latter surveys and homing experiments.

Repeat surveys were conducted four times over nine consecutive days and then once more after three months. All known refuge sites of the focal species were surveyed, as well as any suitable refugia (branching corals and large crevices) within the 200m reef area. Only individuals that were re-sighted at least once during the nine day monitoring period were included in analyses. This was to allow for inclusion of any particularly cryptic fish not observed on a single survey. With repeated surveys any fish still present in the study area had a very high chance of being seen more than once. Fish that were never observed after tagging were ‘missing’ and presumed dead due to handling mortalities. The number of excluded or ‘missing’ fish was very low (25 fish) but varied per species (Table 1). To find any fish that had moved long distances, reef wide surveys of the home reef (Gava Gava) and the closest neighbouring reef areas (Figure 1b) were carried out after the initial nine day monitoring period and again three months later.

Aggregations of *Z. leptacantha* were not present on the Gava Gava reef site and so their site fidelity was measured separately at alternate locations. Three aggregations were identified on neighbouring reefs and ~ 20 fish were tagged and monitored from each group (Table 1). The home sites and reef area within 100m of the colonies was surveyed for six days following tagging. Long term (three month) observations were not possible for this species due to logistical constraints.

Tagged fish were recorded as (1) at home, (2) relocated (i.e. found in a different coral colony) or (3) not sighted. Results from each tagging site were pooled for analyses, because of the low sample numbers per site. Site fidelity was compared over time, per species, using the number at home versus the number away (relocated + not sighted). Interspecific comparisons of site fidelity were conducted using data from the third survey (during days 4 - 6). Using this time period allowed a simple comparison of all five species’ fidelity responses and also appeared to be the time period with the most conservative measure of fidelity for all species (see Results). Site fidelity data was statistically analysed with Pearson Chi-squared tests of independence on contingency tables of Location (2) x Time (4), and Location (2) x Species (5).

Fidelity to positions within coral colonies

We explored whether *T. zosterophora* individuals with high fidelity to a single coral colony also had fidelity to particular positions within the refuge. To do this we monitored the positions of tagged *T. zosterophora* fish within their home colonies. 64 fish were tagged from four aggregations (16 – 20 fish tagged per group) and their positions recorded over six days. Positions were grid referenced using a semi-permanent rope grid constructed above the coral colony. Grid cells were 20 x 20cm in size. The rope was 3mm in diameter, did not touch the coral and did not appear to restrict fish movements.

For each fish we calculated the number of times it was observed in the colony (min 0, max 6), the number of grid cells in which it was observed in (min 1, max 6), the minimum and maximum distance between observations and the maximum distance between any observations. Distances were calculated using the distance between centre points of each grid. We determined that each individual's approximate degree of fidelity to specific positions in the coral would be indicated by a combination of how many grid cells they used and how far apart the cells were. A fish with the highest positional fidelity would be seen in one position, with a distance of 0m between observations while a fish with very low fidelity would be observed in a different spot each day and have a higher distance between repeat observations.

As we were only examining individuals with high site fidelity, only fish that were either (1) always observed in the home colony (2) never seen in a different colony, and (3) observed at least four times were included in analyses. This resulted in a total of 38 fish being used in data comparisons. Fish that were only observed in the home colony, seen four times, but missing on 1 – 2 of six occasions were still included as they may have just been extremely cryptic on those missing occasions. Such fish were also usually re-sighted the following day.

26 of 64 tagged fish were excluded from the analyses as they either moved among nearby colonies (N = 7), or were missing on more than three occasions (N = 19).

Position fidelity was only examined on *T. zosterophora*, and not other study species. This species was used because it demonstrated relatively high fidelity to particular coral colonies and because replicate colonies were located on the same reef area allowing for efficient sampling. Replicate home sites for other suitable species (e.g. *Z. leptacantha*) were not all on one reef and the time required to setup and sample additional grids was prohibitive for our study.

Homing

Interspecific comparisons of homing behaviour investigated: (1) whether differences in each species' site fidelity, habitat specialisation and / or sociality were associated with differences in homing success; and (2) whether the environment affects homing success. Homing success was measured by the absolute number of fish that returned to the capture location, per replicate. Displacements were made to locations within the same reef and to locations on neighbouring reefs. Fish would thereby need to home across either continuous reef areas or across open water respectively. A second displacement experiment was conducted to test the distance to which homing might extend across a reef-scape of multiple continuous reef and open water passages.

Experiment 1: Homing within versus between reefs

Here we tested the hypothesis that cardinalfish homing behaviour would be more successful for individuals traversing continuous reef than those returning from neighbouring reefs across deep open-water channels. Three diurnal refuge sites per species were used (Figure 1c).

These ‘home’ sites consisted of *P. cylindrica* coral colonies with high numbers of the focal species. Each replicate site was either on a different reef or separated by more than 250m such that it was considered independent from other replicates. For each home site, and species, two displacement locations approximately 400m away were designated as (1) ‘within reef’ (WR) and (2) ‘inter-reef’ (IR) displacement sites. The direction displaced fish would have to travel home varied among displacement sites (Figure 1c).

At each species’ replicate home site approximately 60 conspecific adults were caught and tagged, as per the previous methods, and displaced. Tagged individuals were haphazardly assigned to one of three groups; (1) control, (2) within reef displacement or (3) inter-reef displacement with about 20 individuals in each (min. 14, max. 25). Groups were identified using unique tag colour combinations. Fish were captured, tagged and transported to displacement locations by day (08:00 – 17:00h) and released from temporary holding containers after dusk (18:30 – 20:00h). Fish were released in groups, but as they do not shoal together at night time we assumed each fish moved independently of other fish. Displacement locations were in the vicinity of branching corals and other cardinalfish aggregations. Control groups underwent the same transport and holding conditions but were released at the capture site. Controls were used to account for any handling and disturbance effects on fish presence at the home site. Fish were released at night during their foraging period, following Marnane (2000), with the assumption that predation risk would be lower and movement success higher in this period. Pre-release mortalities due to tagging and / or transport conditions were minimal and excluded from analyses.

We counted the number of tagged fish at each home site and / or in the surrounding reef matrix for seven days post-displacement. Pilot studies indicated decrease in tagged fish numbers after this period (see also Marnane 2000). No tagged fish was ever seen in the neighbouring reef areas. The displacement site and its surrounding reef area were surveyed the morning after displacement, following Marnane (2000). The mean proportion of tagged fish returning to home sites was compared amongst species and displacement locations using a two-way fixed factor ANOVA. Normality and homogeneity of variances were verified using Levene's test and residual plots. Post-hoc comparisons were conducted with Tukeys Honestly Significant Difference (HSD) tests.

Experiment 2: Long distance homing

Long distance homing capacity of a single species, *T. zosterophora,* was assessed with a two and five kilometre displacement from one home site (Figure 1a). *T. zosterophora* was chosen because of the extreme site fidelity and homing responses it displayed in earlier parts of this study. If any cardinalfish was able to home these long distances, this species was considered the most likely candidate. 30 fish per distance were captured, tagged, and displaced following the above methods and released at displacement locations immediately. Logistical constraints prevented fish release at night as per Experiment 1. The home coral colony, on Gava Gava, was monitored for the next 26 days, looking for any returns of the displaced fish.

Comparison of homing with behavioural traits

To investigate whether homing responses are related to species' specific degree of site fidelity, habitat specialisation and/or social tendencies, we compared the relative strength of each trait to that species' overall degree of homing success. For each trait, species were ranked as low, moderate or high and the concordance of ranks compared across traits. This comparison was done in a qualitative manner, due to the predominantly observational approach taken for assessing trait strength. Importantly the inter-specific comparisons of traits and homing behaviour were made within the guild and not against other organisms. Each species' homing was ranked according to the total percent of fish that returned from displacements. This was the additive value of both homing treatments (i.e. within reef plus inter-reef returns). Site fidelity ranks were based on the percent of tagged fish faithful to the home site after nine days. Habitat specialisation was accorded following the results of Gardiner & Jones (2005) and based on the total number of benthic habitats used (1 – 22 categories of living and non-living benthos). Species that use three or less micro-habitat types as diurnal refugia were called highly specialist, while species that use multiple types of micro-habitats (> 10 living or other substrates) were ranked as low in specialisation (i.e. generalists). Sociality ranks were based on the frequency with which individuals occurred in groups and the modal size of those groups. Pearson correlation tests were conducted between homing response and each other trait, as well as between specialisation and site fidelity. If homing is greater in species with stronger site fidelity, gregariousness and / or habitat preferences we expect a positive correspondence in trait rankings among species.

RESULTS

Sociality

All five cardinalfish species are gregarious, and were seen in aggregations with up to 500 conspecifics in them. However, the frequency to which each species formed aggregations, and the size of these groups varied (Figure 2). Individuals of all species predominantly occurred in groups of either 20 – 50 or 50 – 100 fish. *Zoramia fragilis* was also frequently observed in groups of 100 – 200 fish. The *Cheilodipterus* and *Taeniamia* species appear to have weaker gregarious preferences than the *Zoramia* species. The former were observed as solitary individuals, or in groups of less than 10 fish, 2 – 4 times more often than the latter.

95% of *Z. fragilis* groups had more than 20 fish in them, and 68% of *Z. leptacanthus* groups had more than 50 fish in them. In contrast it was not uncommon to see solitary *Cheilodipterus* and *Taeniamia* individuals. In particular, 100 *C. quinquelineatus* individuals were seen on their own and others were observed in groups of less than ten 300 times.

Site fidelity

Single coral colonies

Site fidelity varied among the five species, but each species' particular level of short-term site fidelity was consistent over the 9-day period. After three months the total number of fish re-sighted, either at home or in another location had halved (Figure 3). At this time some individuals of all the species were still at home, and up to 40% of *C. quinquelineatus* were still there.

The degree of site fidelity differed among species. There were significant species differences in the number of tagged fish sighted in home locations compared to away ($X^2_4 = 55.067$, $p < 0.001$). *Z. leptacantha* and *T. zosterophora* exhibited the highest site fidelity, with more than two thirds of tagged individuals repeatedly sighted in their original coral colonies over nine days (Figure 3). For *Z. leptacantha,* at least 80% of individuals were sighted at home repeatedly and no fish were found in alternate, nearby conspecific aggregations. Only 10% of tagged *T. zosterophora* changed resting sites and the majority of these only switched sites once (Table 2). For *C. quinquelineatus* approximately 50% of individuals used the same home resting site each day (Figure 3) and only two individuals were found switching between alternate sites (Table 2). However, a third of *C. quinquelineatus* were not found on at least one occasion. For *Z. fragilis* and *C. artus* there was relatively low fidelity to their 'home' capture locations. Less than a third of these individuals stayed in the home coral (Figure 3).

Half of the tagged *Z. fragilis* individuals (24) moved to an alternate refuge colony (within the 200m study area) within two days of counting, and eight of these switched sites 2 – 3 times during nine days (Table 2). *C. artus* individuals also moved a lot, but most of the tagged fish were not sighted consistently (Figure 3). Surveys of cardinalfish aggregations outside of the designated study area, around Gava Gava reef, found only one tagged fish (*T. zosterophora*), in a coral colony 157m from its capture site. No tagged fish were found on nearby reefs.

Positions within coral colonies

Of the 38 *T. zosterophora* individuals with total fidelity to singular coral colonies three were always seen in the same position (Figure 4a), and more than two-thirds (71%, 27 fish) used the same spot on consecutive occasions (min distance 0cm: Figure 4b). A large proportion (42%) of fish were restricted to a two cell radius area on their colonies (max. distance ≤ 24cm). Five individuals were in different positions each day (Figure 4a) with the distance between them ranging from 20cm (the neighbouring cell) to 160cm (the other side of colony: Figure 4b).

Homing

Experiment 1: Homing within versus between reefs

All five species demonstrated the capacity to home over both continuous reef and open-water environments (Figure 5a). Homing also occurred quickly with more than half the individuals that homed doing so overnight. While some of each species did home, the degree of homing success (i.e. the number that came back) was quite species specific. There was a significant treatment effect on the number of fish resighted at the home colony (Table 3). This effect was due to the difference between control and displaced fish sightings, with the former consistently higher in all species (Figure 5). No statistical interaction between species and displacement location occurred (Table 3).

T. zosterophora showed the strongest and most consistent homing patterns (Figure 5a). 96 of the 123 displaced *T. zosterophora* fish returned home (i.e. 78%) including 100% of one inter-reef treatment group (n = 20). The fidelity of the control groups was very consistent among replicates (80 - 90% fidelity) and variability among responses of the within reef treatment 2 - 4 fold less than that of other species (st. dev WR returns 0.086; Fig 5a). The lowest homing response was from one of the inter-reef displacement groups, which even then still had 58% of fish home back. *Z. leptacantha* had similarly strong homing behaviour (97 of 132 fish or 73% of displaced fish), with > 60% of displaced fish returning except for one of the inter-reef treatments in which only eight of the 22 fish returned (36%). In general, *T. zosterophora* and *Z. leptacantha* were the most site faithful and strongest homers.

Z. fragilis and *C. artus* had intermediate homing success. Control *Z. fragilis* individuals had high site fidelity (> 77%), but only moderate success at returning 400m when displaced. Only half of all displaced fish returned (53% total). *Z. fragilis* showed the opposite pattern to other species with lower returns from displacements on the home reef (WR: 49.4% ± 18.2 st. error) than from displacements on alternate reefs (IR: 67.3% ± 10.8 st. error). *C. artus* had lower site fidelity than other species with 10 - 20% fewer control individuals resighted than in other species. However homing success was comparable to other species with 49 - 68% of displaced fish returning from within reef and inter-reef treatments respectively.

The weakest homing species was *C. quinquelineatus*. Despite strong site fidelity of control individuals (71 - 95%), only half of the displaced within reef fish returned home and less than a quarter of the inter-reef displacements returned (Figure 5a). The species also had high variability in homing success. No returns occurred from one treatment site and less than 40% from three other sites. Statistical differences in homing strength among species were driven by differences between *C. quinquelineatus* and the strongest homing species: *T. zosterophora* and *Z. leptacantha* (Table 3b).

Of the displaced *C. quinquelineatus* individuals that did not return home, 20-50% were resighted near displacement sites, the morning after relocation (Figure 5b). These individuals were typically found among conspecific aggregations in branching corals. Ad-hoc surveys of inter-reef displacement locations (2 - 8 days later) found that 60 - 80% of those individuals had persisted in their new refuge positions. In contrast to *C. quinquelineatus*, persistence of other species at displacement sites was rare and mirrored their higher frequency of returns (Figure 5b).

Experiment 2: Long distance homing

T. zosterophora homed back to capture locations from both two and five kilometre displacements. 36% of individuals (11 fish) returned from two kilometres within 11 days. One individual returned in the first evening and five more in the second evening. One individual from the 5 kilometre displacement returned home sometime between 8 and 11 days.

Behavioural trait comparison

Behavioural attributes were not consistently related across the guild (Table 4, Figure 6). Different species had different levels of each trait that related variably to homing strength. The only consistent pattern was that the two species with the strongest homing response also had high fidelity, were habitat specialists, and quite gregarious (*T. zosterophora* & *Z. leptacantha*, Figure 6a - c). The converse link between weaker homing, weaker habitat specialisation, and weaker sociality was not evident. For instance, the species with the weakest homing response (*C. quinquelineatus*) was not the one with the lowest site fidelity (*Z. fragilis*).

Homing was statistically correlated to habitat specialisation, but not other traits (Figure 6b). The more specialist species had stronger homing responses than the weaker species (Pearson correlation test: $r^2 = 0.80$, $p < 0.05$). The more specialist species (*T. zosterophora* and *Z. leptacantha*) also had high site fidelity. However, site fidelity and habitat specialisation were not consistent across the guild with the least specialist species (*C. quinquelineatus*) having greater fidelity than moderate specialist species in the guild (Figure 6d). Social tendencies were not very different within the guild and thus not well correlated with differential homing responses (Table 4, Figure 6c). The *Zoramia* species that frequently occurred in larger aggregations had moderate to strong homing success but either weak or high site fidelity. The *Cheilodipterus* species with more solitary tendencies had moderate fidelity and weak homing.

DISCUSSION

Our study confirms that coral reef-dwelling cardinalfish exhibit a remarkable ability to home over long distances and across both open water and continuous reef environments. We found that for most species homing was equally successful across either environment. As predicted, inter-specific differences in the tendency to home appeared to be related to each species degree of sociality and habitat specialisation. The motivation to home, having to navigate through foreign or hostile terrains, appears to be higher for specialised species and those with high fidelity to cohesive social groups. Species with strong specialisation and high site fidelity homed strongly (> 70% success: *Taeniamia zosterophora* and *Zoramia leptacantha*) while moderate and weak specialists had variable homing responses. Homing was stronger in low site fidelity species (*Z. fragilis* and *Cheilodipterus artus*) than in those with moderate site fidelity (*C. quinquelineatus*). Weaker homing in the latter could be related to that species' generalist habitat preferences and its tendency to live alone.

Previous work on cardinalfish demonstrated they could home across continuous reef and shallow lagoon environments from up to two kilometres (Marnane 2000). We extended this work by investigating the effect of terrain on homing success. Unexpectedly, all cardinalfish species were able to home rapidly across deep, open water passages. Furthermore, for one select species, some individuals homed across multiple reef and inter-reef passages from long two and five kilometre distances. Our results demonstrate that the lack of structured habitat is no absolute barrier to cardinalfish movements, nor their ability to cue towards a home location. This degree of homing behaviour, by a very small and poor swimmer (Fisher et al. 2005) surpasses that known for larger reef fish species (e.g. Matthews 1990, Carlson et al. 1995, Hartney 1996).

For most of the cardinalfish studied here, site fidelity appears to be a good predictor of homing success. However, one of the most site faithful species, *C. quinquelineatus,* was the least successful at homing, both in this study and in Marnane (2000). Here, two-thirds of the displaced individuals remained at the displacement location. Perhaps this species was able to establish new 'home' sites because it is less constrained by habitat and social preferences. Insitu observations and aquarium studies have demonstrated the species has weaker social and habitat preferences than other cardinalfish (Gardiner and Jones 2010). The species was physically able to home but generalist habitat preferences and solitary living behaviour may weaken the necessity to quickly get back to a familiar location or group. Such flexibility in resource use could enable *C. quinquelineatus* to adapt quickly to shifts in habitat regimes and adds to evidence that generalist fish species are less vulnerable to extinction than specialists (Munday 2004, Wilson et al. 2008).

Familiarity with a social group and / or a refuge site can increase an individual’s survivorship and reproductive output substantially (Chivers et al. 1995, Brown et al. 2008, Grabowska-Zhang et al. 2012), thereby driving high site fidelity and homing responses. In our study, the species with the highest fidelity to a coral colony (*T. zosterophora*) also had very high fidelity to specific positions within the colony, and could home over long distances. This species appears to form distinct mating pairs, and the individual that came back from five kilometres returned to the same exact branch position and mate that it was with before displacement (NMG pers. obs.). Pair bonding may therefore drive this species’ site fidelity and homing behaviour. Such is the case in another cardinalfish, *Ostorhinchus cyanosoma*, where fidelity depends on whether fish are paired or not (Rueger et al. 2014).

For the two highly aggregative species studied here, much lower site fidelity and homing in *Z. fragilis* than in *Z. leptacantha* could be due to differences in social bonds within the aggregations. For example, if *Z. leptacantha* forms mating bonds within the aggregations but *Z. fragilis* does not, the latter would be more likely to move among aggregations. *Z. fragilis* homing was actually lower within reefs than between reefs, perhaps because displaced fish found conspecific aggregations enroute to the home site. In contrast fish traversing open-water terrain had minimal friendly distractions. Determining whether homing and fidelity is to the social group, to the site or both will require manipulative experiments across multiple species groups.

A high proportion of fish tagged in this study were not re-sighted again. Among control groups, approximately 20% of *Taeniamia* and *Zoramia* individuals were missing from each survey time, and up to 40% of the *Cheilodipterus* individuals. High natural mortality, emigration outside the study area and / or observer error attributes to these missing fish numbers. Tropical cardinalfish probably only live for 1 - 2 years (e.g. Longenecker & Langston 2006, Kingsford et al. 2014) and are highly susceptible to predation (e.g. Kingsford 1992). A 10 - 20% loss of fish due to mortality would be consistent with the percent of natural population decline seen in the guild at this location (Gardiner unpubl. data). Emigration of tagged fish outside of the study area may also account for lower re-sight numbers. Two species had high inter-site movements (*Z. fragilis* and *C. artus*) and it is quite likely that some individuals moved further afield and were not found. Whether un-sighted fish from other species also did this cannot be said. Cardinalfish can be highly cryptic and some 'present' individuals may not have been emergent during our surveys. In general, site faithful fish had a greater chance of being counted than unfaithful fish in our study, and thus the overall proportion of each species fidelity may be exaggerated. Regardless of these factors the inter-specific comparisons of several independent trials herein consistently indicated which species were more likely to be in the home site and which were less.

The exact cues that small, adult coral reef fish use to direct homing across inter-reef areas and especially at distances greater than 500m are not known. The speed in which individuals homed across two kilometre and inter-reef displacements in this study suggests navigational cues are definitely used. Cardinalfish use olfactory cues to discriminate among micro-habitats, water sources, and conspecific locations (Døving et al. 2006). As seen in diurnally migrating parrotfish (Ogden & Buckman 1973) and butterflyfish (Reese 1989), spatial awareness of local landmarks and routes probably assists individuals to navigate between familiar reef areas, such as the fish that homed from within reef displacements. However, the passage of site specific chemical signals or knowledge of routes from other reefs and especially those 2 - 5km away seems unlikely. For the returning fish, directional information at this level may be contributed by magnetic cues, as used by tide pool fish (Jorge et al. 2012) and several larger marine species (Klimley 1993, Walker et al. 1997, Lohmann et al. 2008). The typical distances cardinalfish migrate between diurnal and nocturnal areas have not been measured. Given their abundant food resources, small size, and large population sizes, long or frequent inter-reef journeys do not seem necessary. Thus, how or why adult fish would remember the way back home is mysterious. Perhaps cue orientation used in the larval phase (e.g. Gerlach et al. 2007, Leis et al. 2011) persists in the adult memory.

Reef fish assemblages are threatened by increased fragmentation of reef habitats and shifts in coral species distributions, as a result of climate change, as well as ongoing destructive fishing practices (Bonin et al. 2011, Wilson et al. 2006). Designing effective management systems to combat these changes, such as marine reserve networks, requires a thorough understanding of how fish use space, what their movement and dispersal potential is and how nearby populations are connected to one another (Green et al. 2015). Here we illustrate how habitat, site and social preferences influence a fish’s movement, within and among coral colonies on the same reef, between reefs over a few hundred metres and over several kilometres of reef scape. These behavioural dynamics act to concentrate some species’ populations and increase the dispersal of others into neighbouring populations. Strongly homing species will be more impacted by habitat loss as they are less likely to move to remnant habitats. The future looks brighter for species with a broader versatility in their habitat use.

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FIGURE LEGENDS

Figure 1.

Study sites. (A) Inshore reef scape in proximity to Mahonia Na Dari research centre (MND), Kimbe Bay, Papua New Guinea. Dashed rectangle indicates the Tamare - Kilu reef sector in which the cardinalfish community was surveyed. Labelled points indicate sites used for the long-distance displacements from a home site (Gava Gava), to 2km (Garbuna) and 5km (Kume) sites. (B) Locations of cardinalfish aggregations on Gava Gava reef, where site fidelity was monitored. The dashed lines indicate a magnification of that section of the reef slope. Numbers 1 - 8 indicate home sites of tagged individuals. Rope grids were constructed above sites 1 - 4 to measure fidelity to positions within coral colonies. (C) Locations of aggregations and displacement sites used in the primary homing experiment: Numbers indicate 3 replicate control (C) sites for 5 species and corresponding within-reef (WR) and inter-reef (IR) displacement locations. *Taeniamia zosterophora* and *Zoramia fragilis*; C = 1-4-7, WR = 2-5-8, IR = 3-6-1. *Z. leptacanthus*: C = 9-5-4, WR = 1-4-5, IR = 8-6-6. *Cheilodipterus artus*; C = 9-4-7, WR = 1-5-8, IR = 3-6-1. *C. quinquelineatus*; C = 5-10-11, WR = 4-6-2, IR = 6-4-3. Most reef tops are exposed at low tides, indicated by lighter grey shading.

Figure 2.

Aggregation tendencies of five cardinalfish species. Shown is the number of fish observed in different sized groups (white bars) and the total number of groups observed per size (black bars). The study was conducted on inshore reef slopes of Kimbe Bay, Papua New Guinea.

Figure 3.

Site fidelity of cardinalfish to diurnal refuge sites (branching coral colonies). Bars indicate the percentage of tagged fish located at the initial capture site (‘home’), on nearby coral colonies (‘relocated’) and those not sighted during that survey. ‘n’ indicates the total number of tagged fish used per species. Fidelity responses were consistent over the initial 9 days of monitoring (*T. zosterophora* $X^2{}_3 = 0.521$, $p = 0.914$. *Z. fragilis* $X^2{}_3 = 4.719$, $p = 0.194$. *Z. leptacantha* $X^2{}_2 = 1.007$, $p = 0.605$. *C. artus* $X^2{}_3 = 5.672$, $p = 0.129$. *C. quinquelineatus* $X^2{}_3 = 2.167$, $p = 0.539$). Observations were taken on multiple days over a 9 day period and repeated 3 months later.

Figure 4.

Diurnal fidelity of 38 cardinalfish (*Taeniamia zosterophora*) to positions within coral colonies. (A) Number of positions (20 x 20cm grid cells) that fish were observed in across 4 - 6 days. (B) Distance between positions that fish were observed in. Shown is the upper and lower bounds of distances for each individual fish. Minimum distance, the lower bound, is the distance between the closest points fish were ever observed in on consecutive survey days. Maximum distance, the upper bound, was the distance between the two furthest grid cells that a fish was ever observed in (i.e. greatest distance apart).

Figure 5.

Strength of homing behaviour by five cardinalfish species displaced approximately 400m from home sites. ‘Control’ bars represent fish tagged and released at the home site. ‘Within’ bars represent fish released on the same reef, but at a distance. ‘Inter-reef’ bars represent fish released on a different reef. (A) The mean proportion of tagged individuals that returned to the home site within 7 days. (B) The mean proportion of tagged fish sighted at displacement locations the morning after release. Species are *Taeniamia zosterophora, Zoramia fragilis, Z. leptacantha*, *Cheilodipterus artus* and *C. quinquelineatus.*

Figure 6.

Interspecific comparison of behavioural attributes and homing ability in guild of co-occurring cardinalfish. Values for homing response indicate the total percent of fish, per species, that homed from displacements in this study (i.e. cumulative of both displacement treatments). Values for site fidelity (A and D) indicate the percent of fish fidel to the home site over 9 days. Values for habitat specialisation (B and D) are the number of distinct coral and non-coral micro-habitats used as diurnal refugia, according to Gardiner & Jones 2005. Values for sociality (C) are the modal frequency of aggregation size that fish were found in (see Figure 2). Statistical values indicate Pearson correlation test results with linear relationship plotted when significant at $p < 0.05$.

TABLES

Table 1.

Tagged cardinalfish counts per home site. ‘N tagged’ indicates the total number of tagged fish while ‘N re-sighted’ indicates the number of those that were fish re-observed at least once in the course of the study. ‘N missing’ is the number of tagged fish not seen post tagging, and assumed dead. Fidelity analyses used N re-sighted. Site numbers refer to diurnal refuge locations (branching coral colonies) of cardinalfish aggregations on Gava Gava reef, as shown in Figure 1b. Sites used for *Z. leptacantha*, were located on different reefs (specifically sites 4, 5, 9 on Figure 1c).

Species	**Site**	**N tagged**	**N re-sighted**	**N Missing**
Taeniamia zosterophora	1	16	14	2
	2	16	12	4
	3	16	16	0
	4	16	15	1
	Pooled	64	57	7
Zoramia fragilis	1	16	14	2
	6	16	11	5
	7	17	15	2
	8	16	12	4
	Pooled	65	52	13
Zoramia leptacantha	4	22	22	0
	5	18	18	0
	9	22	22	0
	Pooled	62	62	0
Cheilodipterus artus	1	5	4	1
	2	9	9	0
	4	10	10	0
	Pooled	24	23	1
Cheilodipterus quinquelineatus	1	16	13	3
	2	16	15	2
	5	11	11	0
	Pooled	43	39	4

Table 2.

Frequency of movement by tagged cardinalfish that changed resting sites during a 9 day period. N is the total number of individuals that moved from their original capture site between consecutive observations (per Figure 1b). From these, the ‘Frequency of movement’ is the percent of fish that switched between diurnal refugia once, twice or three times.

		Frequency (%) of movement		
Species	N	1	2	3
Z. fragilis	24	67	17	17
T. zosterophora	11	82	18	0
C. artus	9	44	44	11
C. quinquelineatus	2	0	100	0

Table 3.

Statistical comparison of homing success amongst five cardinalfish species and three displacement locations (control, within reef and inter-reef). (A) Two-way fixed factor ANOVA testing differences in the proportion of tagged fish returning home. (B) Tukey's HSD post-hoc comparison amongst species and locations. Post-hoc comparisons amongst species pairs are shown where significant. Species are *Taeniamia zosterophora, Zoramia fragilis, Z. leptacanthus, Cheilodipterus artus* and *C. quinquelineatus.*

(A)	Source of variation	*df*	SS	MS	F	*p*
	Species	4	0.598	0.149	4.538	**
	Displacement location	2	0.507	0.254	7.694	**
	Species x displacement	8	0.423	0.053	1.606	0.165
	Error	30	0.988	0.033	4.538	

(B)	Source of Variation	Non-homogenous groups		Proportional difference	*p*
	Species	*C. quinquelineatus*	*T. zosterophora*	- 0.301	*
			Z. leptacantha	- 0.287	*
	Displacement location	Control	Within-reef	0.167	*
			Inter-reef	0.255	**
		Within-reef	Inter-reef	- 0.088	0.386

* *p* < 0.05, ** *p* < 0.01

Table 4.

Interspecific comparison of behavioural attributes and homing ability in cardinalfish. The relative strength of each behaviour is ranked (low, moderate, high) in comparison to the other study species. Homing response values indicate the total percent of fish that returned from displacements in this study. Site fidelity values indicate the percent of fish fidel to the home site over 9 days (per Figure 3). Habitat specialisation values are the number of distinct coral and non-coral micro-habitats used as diurnal refugia, according to Gardiner and Jones (2005). Values for sociality are the modal frequency of aggregation size that fish were found in (per Figure 2).

Species	**Homing response** (Total % fish returns)	**Site Fidelity** (% fish fidel)	**Habitat Specialisation** (# habitats used)	**Sociality** (Modal group size)
Taeniamia zosterophora	78% High	68% Moderate	5 Moderate - Uses variety of live coral species	50 Moderate - Seen solitary, and in moderate to large groups
Zoramia fragilis	53% Moderate	23% Low	7 Moderate - Uses variety of live coral species	20 Moderate - Mostly seen in medium to large groups
Zoramia leptacanthus	73% High	91% High	3 High - Predominantly uses 1 coral species	50 Moderate - Mostly seen in medium to large groups
Cheilodipterus artus	58% Moderate	43% Low	12 Low - Uses living and non-living substrata	20 Moderate - Sometimes seen solitary
Cheilodipterus quinquelineatus	34% Low	69% Moderate	20 Very low - Uses living and non-living substrata	50 Moderate - Frequently seen solitary
Source of information:	This study (Figure 5)	This study (Figure 3)	Gardiner and Jones, 2005	This study (Figure 2)

FIGURES

Figure 1

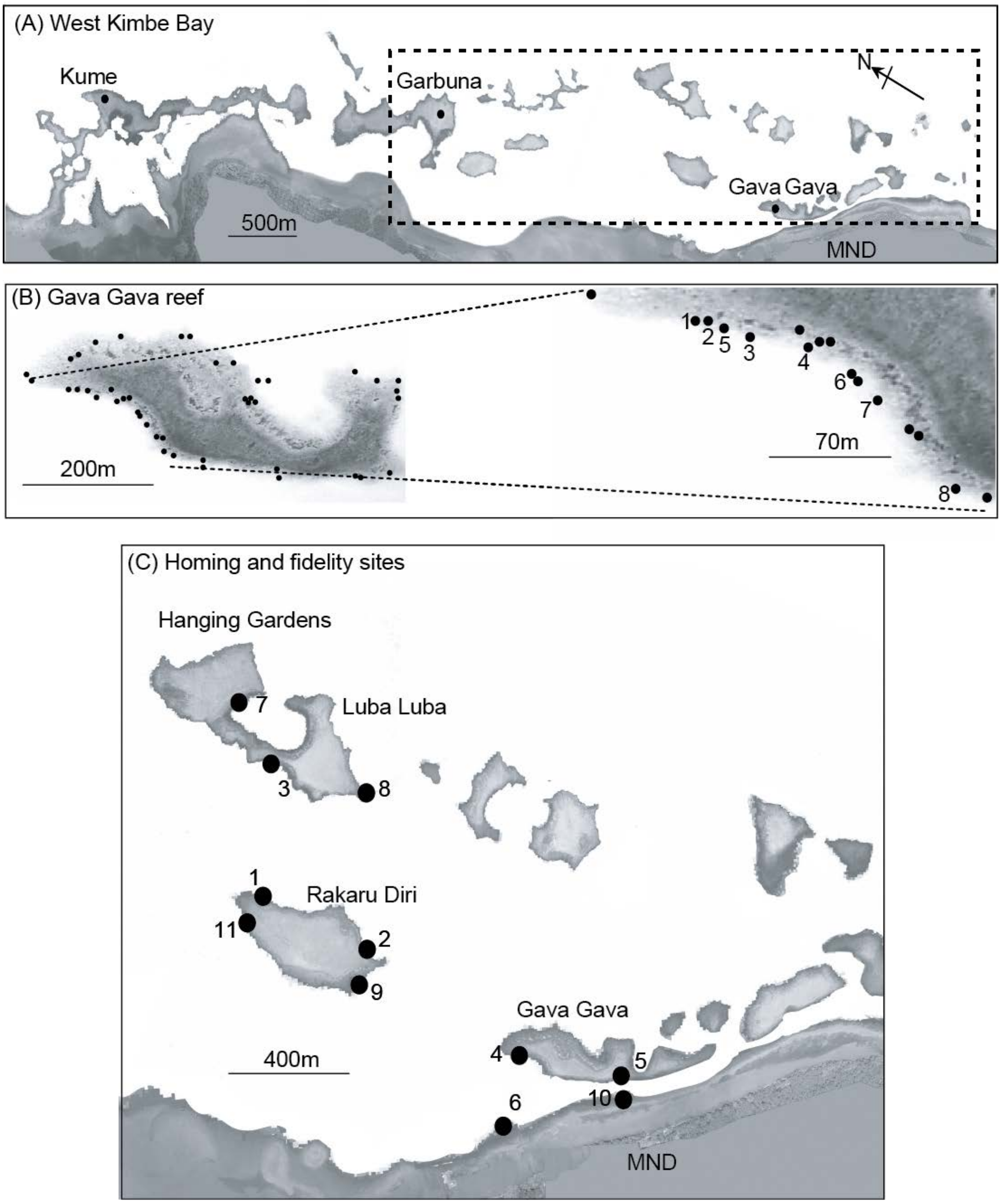

Figure 1. Study sites. (A) Inshore reef scape in proximity to Mahonia Na Dari research centre (MND), Kimbe Bay, Papua New Guinea. Dashed rectangle indicates the Tamare - Kilu reef sector in which the cardinalfish community was surveyed. Labelled points indicate sites used for the long-distance displacements from a home site (Gava Gava), to 2km (Garbuna) and 5km (Kume) sites. (B) Locations of cardinalfish aggregations on Gava Gava reef, where site fidelity was monitored. The dashed lines indicate a magnification of that section of the reef slope. Numbers 1 - 8 indicate home sites of tagged individuals. Rope grids were constructed above sites 1 - 4 to measure fidelity to positions within coral colonies. (C) Locations of aggregations and displacement sites used in the primary homing experiment: Numbers indicate 3 replicate control (C) sites for 5 species and corresponding within-reef (WR) and inter-reef (IR) displacement locations. *Taeniamia zosterophora* and *Zoramia fragilis*; C = 1-4-7, WR = 2-5-8, IR = 3-6-1. *Z. leptacanthus*: C = 9-5-4, WR = 1-4-5, IR = 8-6-6. *Cheilodipterus artus*; C = 9-4-7, WR = 1-5-8, IR = 3-6-1. *C. quinquelineatus*; C = 5-10-11, WR = 4-6-2, IR = 6-4-3. Most reef tops are exposed at low tides, indicated by lighter grey shading.

Figure 2

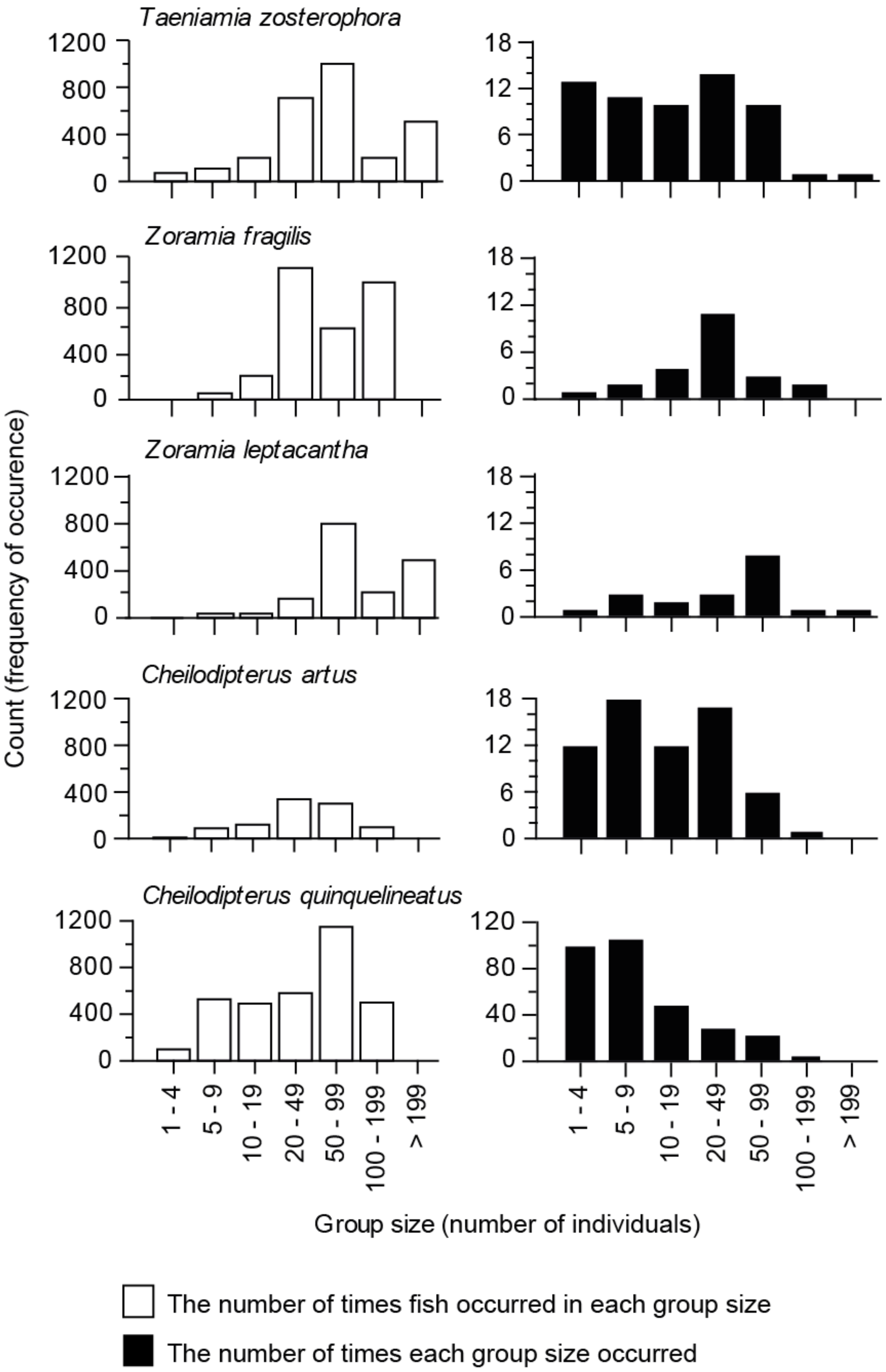

Figure 2. Aggregation tendencies of five cardinalfish species. Shown is the number of fish observed in different sized groups (white bars) and the total number of groups observed per size (black bars). The study was conducted on inshore reef slopes of Kimbe Bay, Papua New Guinea.

Figure 3

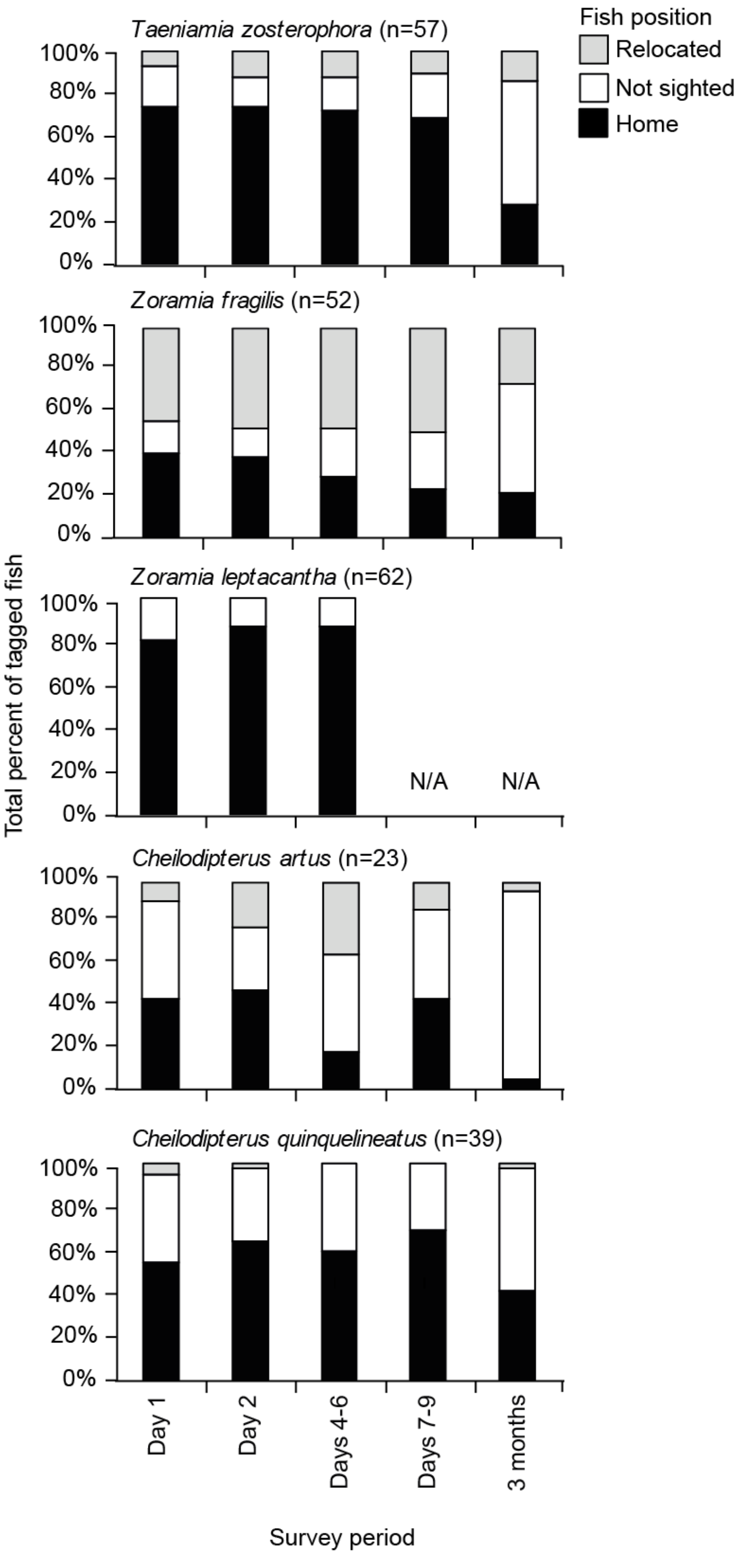

Figure 3. Site fidelity of cardinalfish to diurnal refuge sites (branching coral colonies). Bars indicate the percentage of tagged fish located at the initial capture site (‘home’), on nearby coral colonies (‘relocated’) and those not sighted during that survey. ‘n’ indicates the total number of tagged fish used per species. Fidelity responses were consistent over the initial 9 days of monitoring (*T. zosterophora* $X^2_3 = 0.521$, $p = 0.914$. *Z. fragilis* $X^2_3 = 4.719$, $p = 0.194$. *Z. leptacantha* $X^2_2 = 1.007$, $p = 0.605$. *C. artus* $X^2_3 = 5.672$, $p = 0.129$. *C. quinquelineatus* $X^2_3 = 2.167$, $p = 0.539$). Observations were taken on multiple days over a 9 day period and repeated 3 months later.

Figure 4

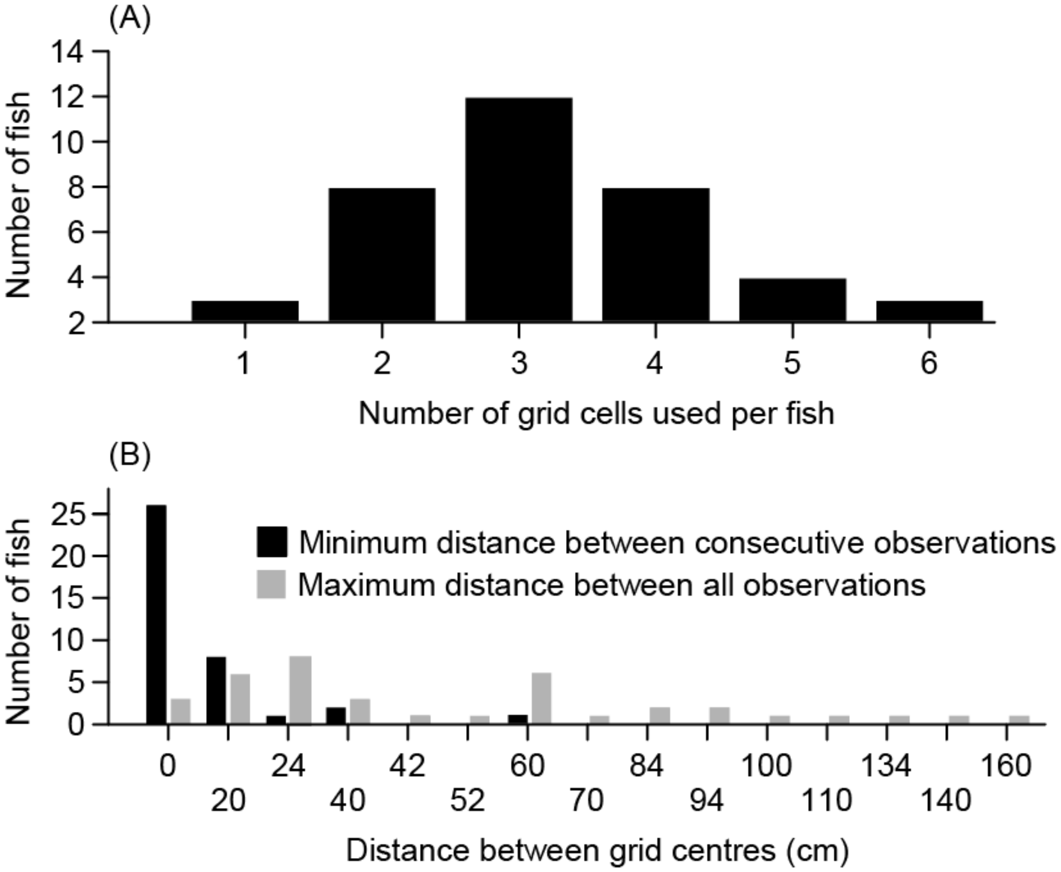

Figure 4: Diurnal fidelity of 38 cardinalfish (*Taeniamia zosterophora*) to positions within coral colonies. (A) Number of positions (20 x 20cm grid cells) that fish were observed in across 4 - 6 days. (B) Distance between positions that fish were observed in. Shown is the upper and lower bounds of distances for each individual fish. Minimum distance, the lower bound, is the distance between the closest points fish were ever observed in on consecutive survey days. Maximum distance, the upper bound, was the distance between the two furthest grid cells that a fish was ever observed in (i.e. greatest distance apart).

Figure 5

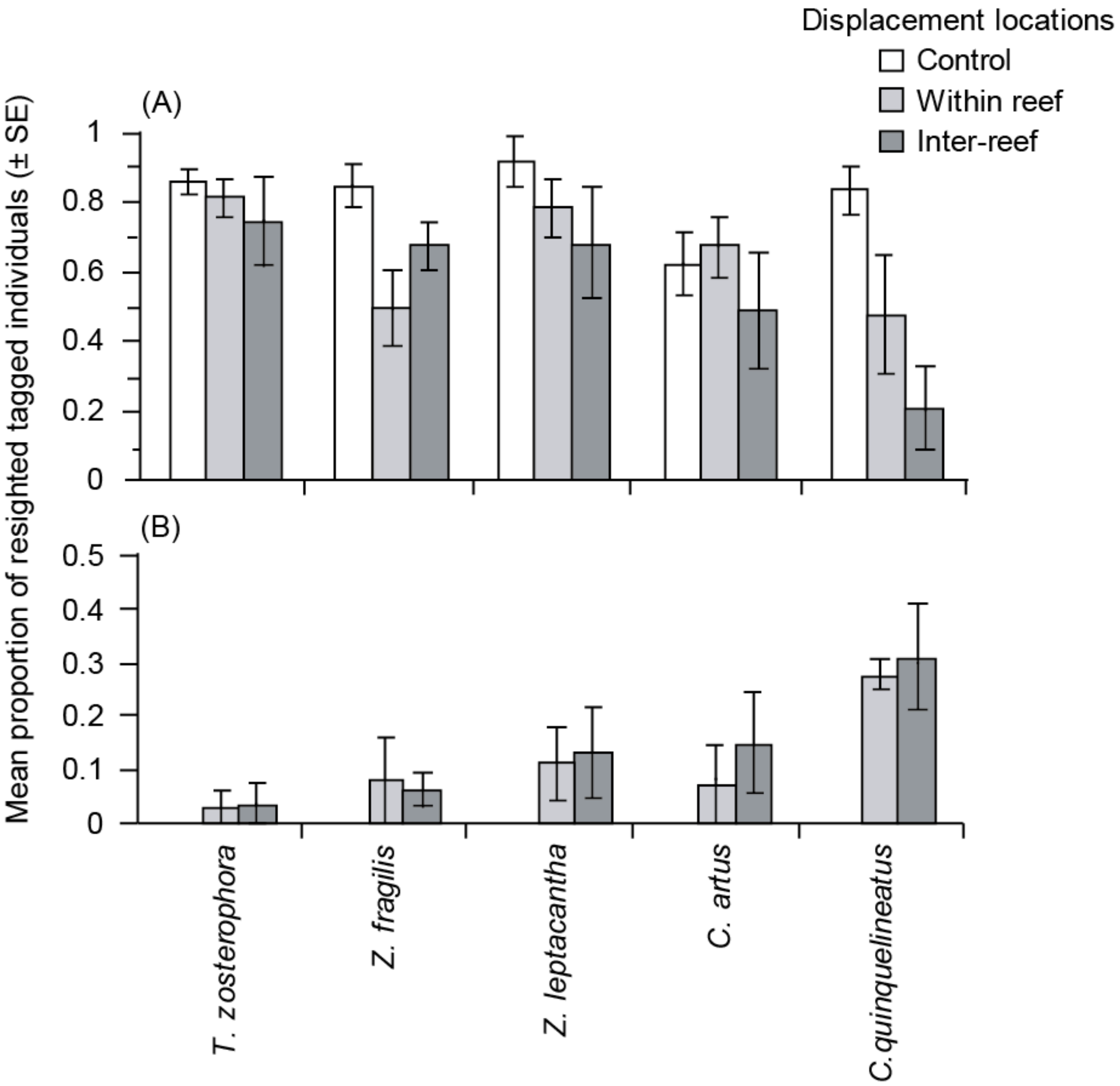

Figure 5.
Strength of homing behaviour by five cardinalfish species displaced approximately 400m from home sites. ‘Control’ bars represent fish tagged and released at the home site. ‘Within’ bars represent fish released on the same reef, but at a distance. ‘Inter-reef’ bars represent fish released on a different reef. (A) The mean proportion of tagged individuals that returned to the home site within 7 days. (B) The mean proportion of tagged fish sighted at displacement locations the morning after release. Species are *Taeniamia zosterophora, Zoramia fragilis, Z. leptacantha, Cheilodipterus artus* and *C. quinquelineatus.*

Figure 6

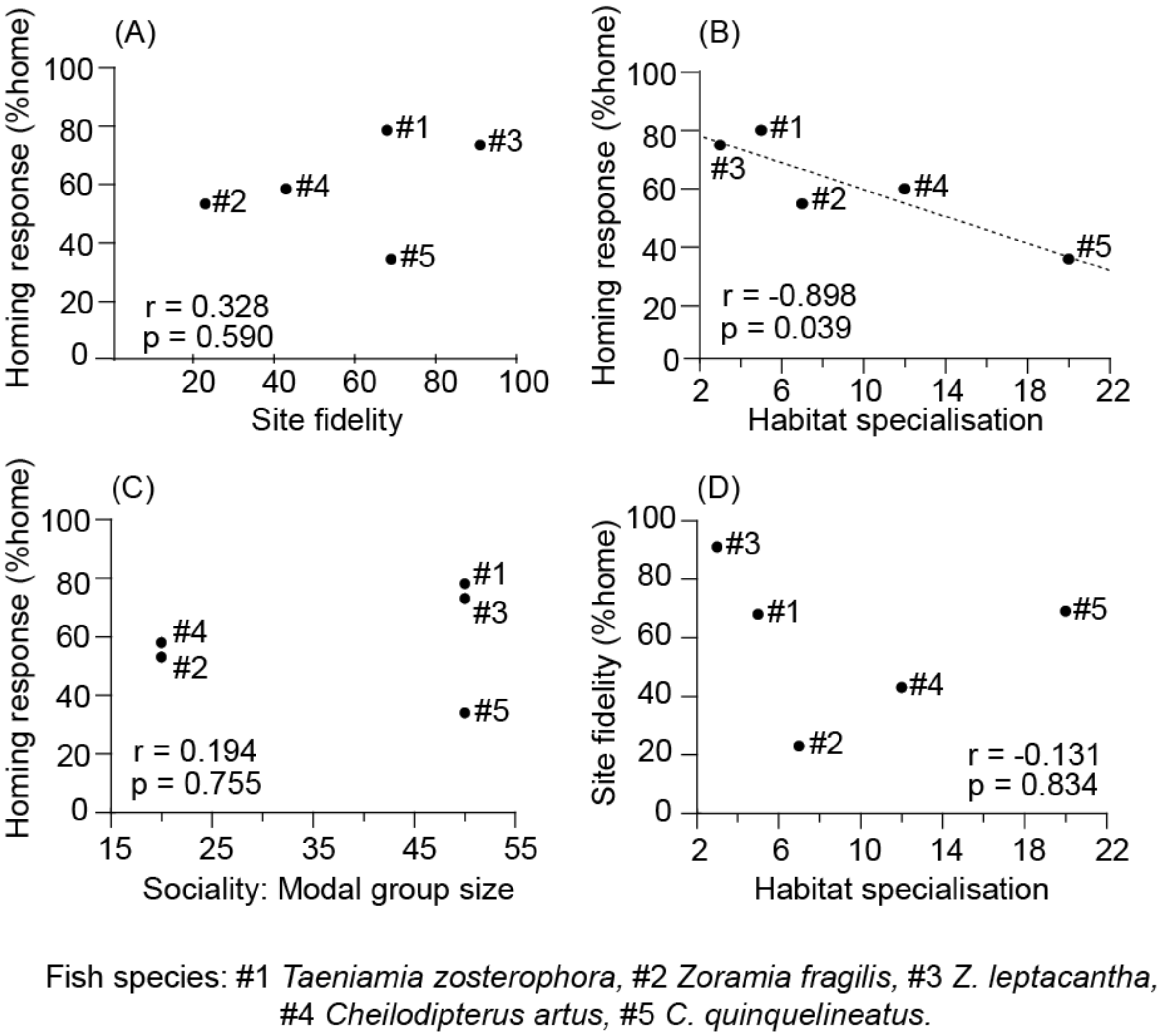

Figure 6.
Interspecific comparison of behavioural attributes and homing ability in guild of co-occurring cardinalfish. Values for homing response indicate the total percent of fish, per species, that homed from displacements in this study (i.e. cumulative of both displacement treatments). Values for site fidelity (A and D) indicate the percent of fish fidel to the home site over 9 days. Values for habitat specialisation (B and D) are the number of distinct coral and non-coral micro-habitats used as diurnal refugia, according to Gardiner & Jones 2005. Values for sociality (C) are the modal frequency of aggregation size that fish were found in (see Figure 2). Statistical values indicate Pearson correlation test results with linear relationship plotted when significant at $p < 0.05$.