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 5 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 locations of over 1200 tagged cardinalfish on Kimbe Bay reefs (West New Britain, Papua New Guinea) were visually monitored over time. Following experimental displacement, all species homed quickly across ~400 m of both open water and continuous reef habitats. Incredibly, individuals of one species homed up to 5 km 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.

KEY WORDS: 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 ('to home' means to 'return by instinct to one's territory after leaving it'; www.oxforddictionaries.com) 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 underly-

ing 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, Burt 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 (<10 cm in length) is usually impeded by open water and/or sand gaps larger than 5 m in width (Frederick 1997, Overholtzer-McLeod 2006, Feary 2007, Wall & Herler 2009). In contrast, larger fish (>13 cm in length) will home over open terrain from 8 km 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 (family 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 they can persist for at least several months and/ or several breeding cycles (Okuda 1999, Marnane 2000, Fukumori et al. 2010). Marnane (2000) experimentally displaced several species (*Ostorhinchus doedoerlini*, *Cheilodipterus artus* and *C. quinquelineatus*) within a shallow, lagoonal environment and observed fish homing returns of 33–63% from 2 km away, and 56–81% from 1 km, all within 3 d. 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 have 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 5 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 a 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 spe-

cific 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?

MATERIALS AND 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; Fig. 1). Reefs in this area are separated by 0.2–1 km of open water and depths of 30–60 m (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 3–15 m water depth, below which the study species and branching coral habitats are rarely found (Gardiner & Jones 2005). Extensive surveys were conducted in the Tamare–Kilu reef sector (Fig. 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 5 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* 33–50 mm, *Z. fragilis* 31–39 mm, *Z. leptacantha* 31–39 mm, *C. artus* 41–61 mm, *C. quinquelineatus* 41–63 mm. 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 5 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 5 species was recorded across the back- and fore-reef slopes of 10 reefs in the Tamare–Kilu reef sector (Fig. 1A). This information was collected prior to the experimental aspects of the present study, 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 (500 ml volume). The anaesthetic acts to slow fish responses down (within ca. 30 s) such that divers can catch them with hand nets. On adult cardinalfish, the anaesthetic effect tended to last ~5 min. Repeated doses were used if fish were not captured and tagged in that period. While still under the influence of anaes-
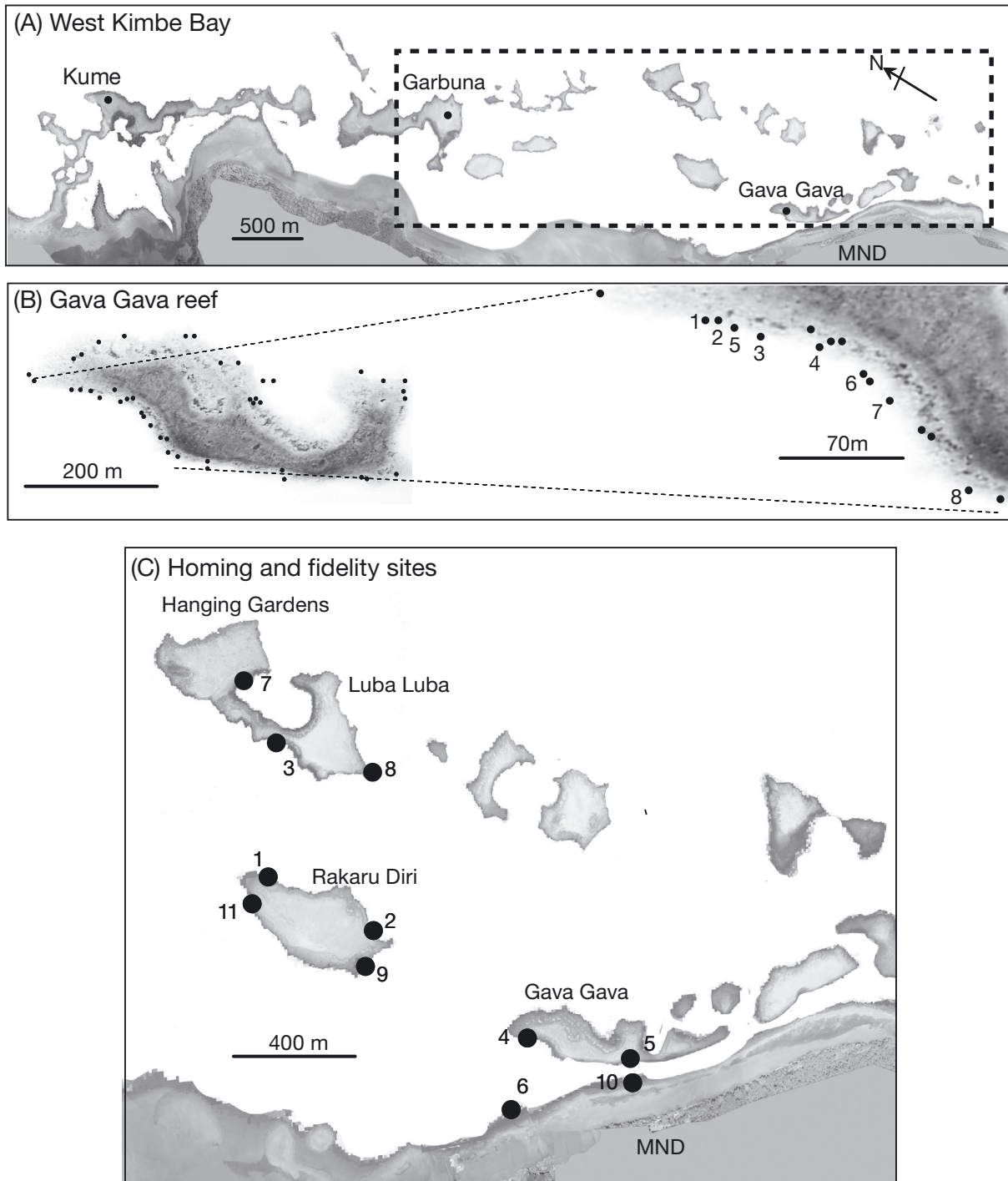
Fig. 1. Study sites. (A) Inshore reef scape in proximity to Mahonia Na Dari research centre (MND), Kimbe Bay, Papua New Guinea. Dashed rectangle: Tamare–Kilu reef sector in which the cardinalfish community was surveyed. Labelled points: sites used for the long-distance displacements from a home site (Gava Gava), to 2 km (Garbuna) and 5 km (Kume) sites. (B) Locations of cardinalfish aggregations on Gava Gava reef, where site fidelity was monitored. Dashed lines: magnification of that section of the reef slope. Sites 1–8: home sites of tagged individuals. Rope grids were constructed above Sites 1–4 to measure fidelity to positions within coral colonies. (C) Aggregations and displacement sites used in the primary homing experiment. Numbers: 3 replicate control home (H) sites for 5 species and corresponding within-reef (WR) and inter-reef (IR) displacement locations. *Taeniamia zosterophora* and *Zoramia fragilis*: H = 1, 4, 7; WR = 2, 5, 8; IR = 3, 6, 1. *Z. leptacanthus*: H = 9, 5, 4; WR = 1, 4, 5; IR = 8, 6, 6. *Cheilodipterus artus*: H = 9, 4, 7; WR = 1, 5, 8; IR = 3, 6, 1. *C. quinquelineatus*: H = 5, 10, 11; WR = 4, 6, 2; IR = 6, 4, 3. Most reef tops are exposed at low tides, indicated by lighter grey shading

thetic, 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 5 tag colours and 5 body positions. The tags were relatively long (2–4 mm) and in bright colours so that they were easy to see from 1–2 m 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 min 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 (N. M. Gardiner pers. obs.). Fish were released in a group, and most individuals experienced more than 30 min recovery (and up to 2 h). 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 (Fig. 1B). The designated monitoring area was 200 m long, ~30 m wide and extended to a depth of 15 m. 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 50 m 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 (Fig. 1B). Four aggregations of *T. zosterophora*, and *Z. fragilis* and 3 aggregations of *C. quinquelineatus* and *C. artus* were selected for tagging and monitoring. Only 3 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 3 d after tagging, surveys of focal aggregations were carried out and sightings of tagged individuals were recorded. Surveys proceeded by the same observer (N. M. Gardiner) hovering about 2 m 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 min to count tagged fish, or longer if the aggregation was particularly large (i.e. >50 fish). If the fish group was panicked by a predator or a rapid movement by the diver, its members typically resumed their relaxed resting posture within 1–2 min. This behaviour was taken to indicate that the aggregations of cardinalfish do not feel harassed by the passive diver observations, and thus we assumed that 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 4 times over 9 consecutive days and then once more after 3 mo. All known refuge sites of the focal species were surveyed, as well as any suitable refugia (branching corals and large crevices) within the 200 m reef area. Only individuals that were re-sighted at least once during the 9 d 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 (Fig. 1B) were carried out after the initial 9 d monitoring period and again 3 mo later.

Aggregations of *Z. leptacantha* were not present on the Gava Gava reef site, and so their site fidelity was measured separately at alternative 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 100 m of the colonies were surveyed for 6 d following tagging. Long-term (3 mo) 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

Table 1. Tagged cardinalfish counts per home site. Tagged: total number of tagged fish; Re-sighted: number of those that were re-observed at least once in the course of the study; Missing: number of tagged fish not seen post tagging, and assumed dead. Fidelity analyses used the number re-sighted. Site numbers refer to diurnal refuge locations (branching coral colonies) of cardinalfish aggregations on Gava Gava reef, as shown in Fig. 1B. Sites used for *Zoramia leptacantha* were located on different reefs (specifically Sites 4, 5, 9 in Fig. 1C)

Species	Site	Tagged (n)	Re-sighted (n)	Missing (n)
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

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 to 6). Using this time period allowed a simple comparison of all 5 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 were statistically analysed with Pearson chi-squared tests of independence on contingency tables of Location (2) × Time (4), and Location (2) × 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. zos-*

terophora fish within their home colonies. A total of 64 fish were tagged from 4 aggregations (16–20 fish tagged per group) and their positions recorded over 6 d. Positions were grid referenced using a semi-permanent rope grid constructed above the coral colony. Grid cells were 20 × 20 cm in size. The rope was 3 mm 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 (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 0 m 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 4 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 4 times, but missing on 1–2 of 6 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. A total of 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 3 occasions (n = 19).

Position fidelity was only examined on *T. zosterophora* and not on 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 reefscape of multiple continuous reef and open water passages.

Expt 1: Homing within vs. 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 (Fig. 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 250 m such that it was considered independent from other replicates. For each home site, and species, 2 displacement locations approximately 400 m away were designated as (1) 'within-reef' (WR) and (2) 'inter-reef' (IR) displacement sites. The direction in which displaced fish would have to travel home varied among displacement sites (Fig. 1C).

At each species' replicate home site ~60 conspecific adults were caught and tagged, as per the previous methods, and displaced. Tagged individuals were haphazardly assigned to 1 of 3 groups: (1) control, (2) WR displacement or (3) IR 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 (08:00–17:00 h) and released from temporary holding containers after dusk (18:30–20:00 h). Fish were released in groups, but as

they do not shoal together at night-time, we assumed that 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 7 d 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 2-way fixed factor ANOVA. Normality and homogeneity of variances were verified using Levene's test and residual plots. Post-hoc comparisons were conducted with Tukey's honestly significant difference (HSD) tests.

Expt 2: Long-distance homing

Long-distance homing capacity of a single species, *T. zosterophora*, was assessed with a 2 and 5 km displacement from one home site (Fig. 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. A total of 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 Expt 1. The home coral colony, on Gava Gava, was monitored for the next 26 d, to investigate whether any of the displaced fish returned.

Comparison of homing with behavioural traits

To investigate whether homing responses are related to species' specific degree of site fidelity, habi-

tat specialisation and/or social tendencies, we com-
pared the relative strength of each trait to that spe-
cies' 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 be-
haviour 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. WR plus IR returns). Site
fidelity ranks were based on the percent of tagged
fish faithful to the home site after 9 d. Habitat special-
isation was accorded following the results of Gar-
diner & Jones (2005) and based on the total number
of benthic habitats used (1–22 categories of living
and non-living benthos). Species that use 3 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 sub-
strates) were ranked as low in specialisation (i.e. gen-
eralists). 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 prefer-
ences, we expect a positive correspondence in trait
rankings among species.

RESULTS

Sociality

All 5 cardinalfish species are gregarious and were
seen in aggregations with up to 500 conspecifics in
them. However, the frequency at which each species
formed aggregations and the size of these groups
varied (Fig. 2). Individuals of all species predomi-
nantly 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 *Tae-
niamia* 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.
Of the *Z. fragilis* groups, 95% had more than 20 fish
in them, and 68% of *Z. leptacanthus* groups had
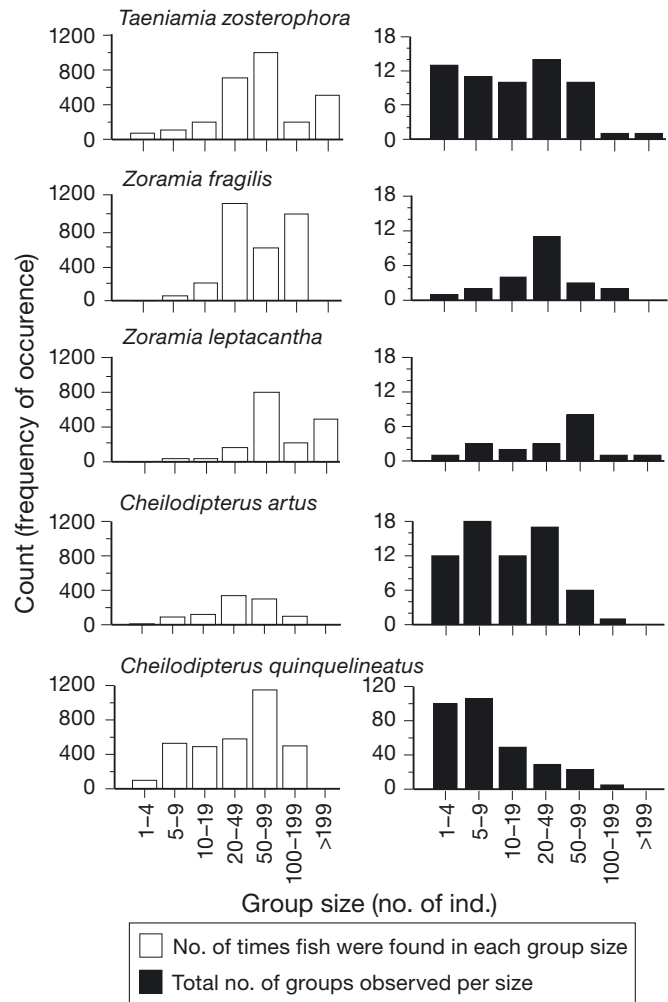
Fig. 2. Aggregation tendencies of 5 cardinalfish species.
Shown is the number of times fish were found in different-
sized groups (white bars) and the total number of groups
observed per size (black bars). Study was conducted on
inshore reef slopes of Kimbe Bay, Papua New Guinea

more than 50 fish in them. In contrast, it was not
uncommon to see solitary *Cheilodipterus* and *Taeni-
amia* individuals. In particular, 100 *C. quinquelinea-
tus* individuals were seen on their own, and others
were observed 300 times in groups of less than 10.

Site fidelity

Single coral colonies

Site fidelity varied among the 5 species, but each
species' particular level of short-term site fidelity was
consistent over the 9 d period. After 3 mo the total
number of fish re-sighted, either at home or in
another location, had halved (Fig. 3). At this time
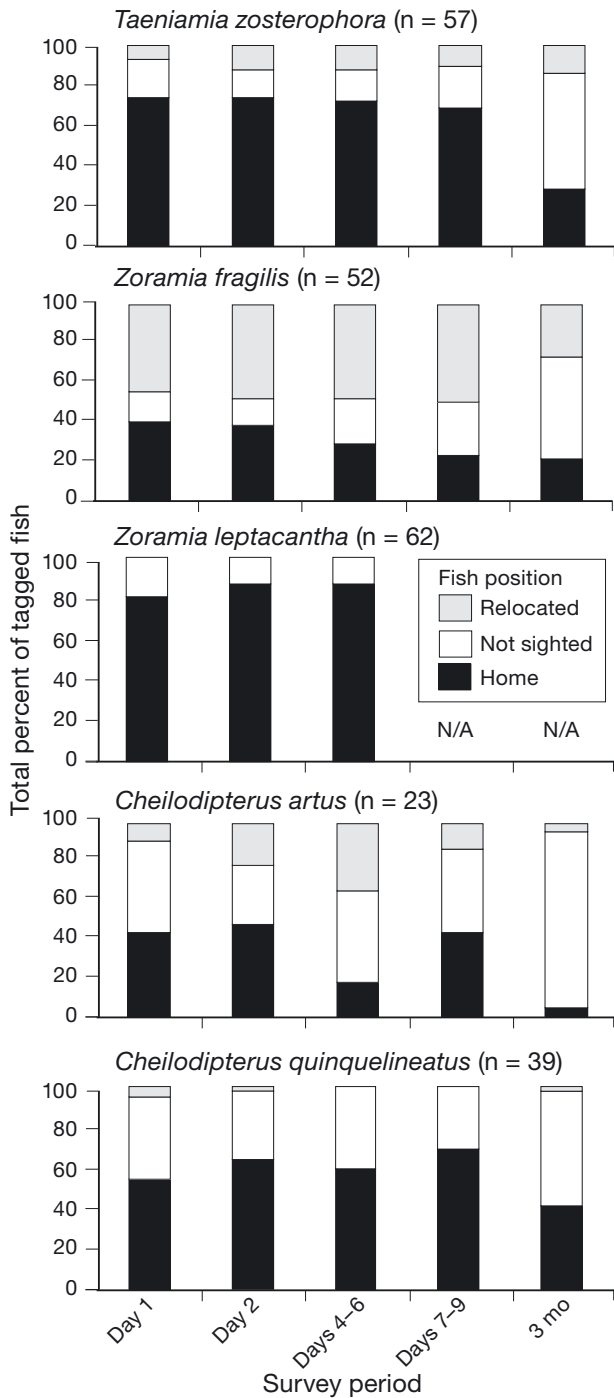
Fig. 3. Site fidelity of cardinalfish to diurnal refuge sites (branching coral colonies). Bars: percentage of tagged fish located at the initial capture site (home), on nearby coral colonies (relocated) and those not sighted during that survey. n: total number of tagged fish used per species. Fidelity responses were consistent over the initial 9 d of monitoring (*Taeniamia zosterophora*: $\chi^2_3 = 0.521$, p = 0.914; *Zoramia fragilis*: $\chi^2_3 = 4.719$, p = 0.194; *Z. leptacantha*: $\chi^2_2 = 1.007$, p = 0.605; *Cheilodipterus artus*: $\chi^2_3 = 5.672$, p = 0.129; *C. quinquelineatus*: $\chi^2_3 = 2.167$, p = 0.539). Observations taken on multiple days over a 9 d period and repeated 3 mo later. N/A: surveys not conducted

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 ($\chi^2_4 = 55.067$, 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 9 d (Fig. 3). For *Z. leptacantha*, at least 80 % of individuals were sighted at home repeatedly, and no fish were found in alternative, 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 (Fig. 3) and only 2 individuals were found switching between alternative 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 (Fig. 3). Half of the tagged *Z. fragilis* individuals (24) moved to an alternative refuge colony (within the 200 m study area) within 2 d of counting, and 8 of these switched sites 2 to 3 times during 9 d (Table 2). *C. artus* individuals also moved a lot, but most of the tagged fish were not sighted consistently (Fig. 3). Surveys of cardinalfish aggregations outside of the designated study area, around Gava Gava reef, found only 1 tagged fish (*T. zosterophora*), in a coral colony 157 m 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 single coral colonies 3 were always seen in the same position (Fig. 4A), and more than two-thirds

Table 2. Frequency (%) of movement by tagged cardinalfish that changed resting sites during a 9 d period. n: total number of individuals that moved from their original capture site between consecutive observations (Fig. 1B). Frequency of movement: percent of fish that switched between diurnal refugia once, twice or 3 times. See Table 1 for full species names

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

(71%, 27 fish) used the same spot on consecutive occasions (min. distance 0 cm; Fig. 4B). A large proportion (42%) of fish were restricted to a 2-cell radius area on their colonies (max. distance ≤24 cm). Five individuals were in different positions each day (Fig. 4A) with the distance between them ranging from 20 cm (the neighbouring cell) to 160 cm (the other side of the colony; Fig. 4B).

Homing

Expt 1: Homing within vs. between reefs

All 5 species demonstrated the capacity to home over both continuous reef and open water environments (Fig. 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 (Fig. 5). No statistical interaction between species and displacement location occurred (Table 3).

T. zosterophora showed the strongest and most consistent homing patterns (Fig. 5A). Ninety-six of the 123 displaced *T. zosterophora* fish returned home (i.e. 78%) including 100% of one IR treatment group (n = 20). The fidelity of the control groups was very consistent among replicates (80–90% fidelity), and variability among responses of the WR treatment 2- to 4-fold less than that of other species (WR returns 0.086 SE; Fig 5A). The lowest homing response was from one of the IR displacement groups, which even then still had 58% of fish return home. *Z. leptacantha* had similarly strong homing behaviour (97 of 132 fish or
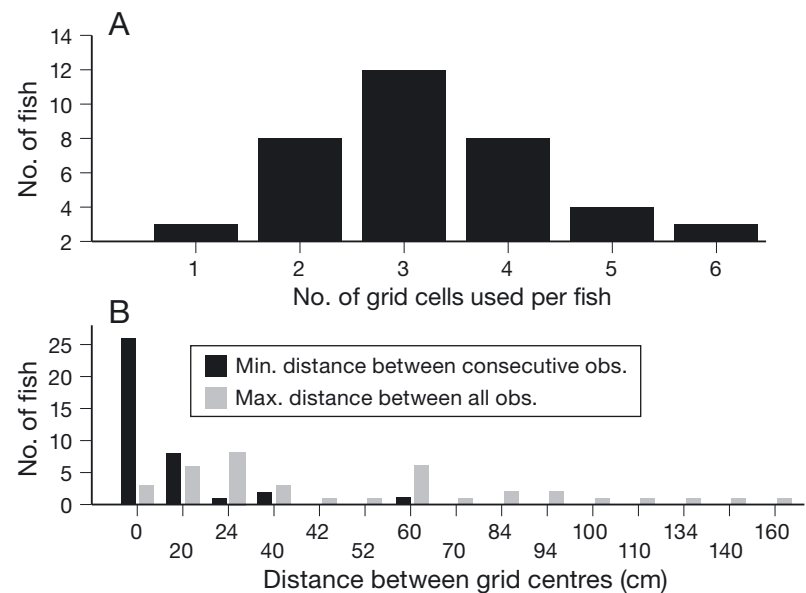
Fig. 4. Diurnal fidelity of 38 cardinalfish (*Taeniamia zosterophora*) to positions within coral colonies. (A) Number of positions (20 × 20 cm grid cells) fish were observed in over 4–6 d. (B) Distance between positions in which fish were observed (upper and lower bounds of distances for each individual fish). Min. distance: distance between the closest points in which fish were ever observed on consecutive survey days. Max. distance: distance between the 2 furthest grid cells in which a fish was ever observed (i.e. greatest distance apart)
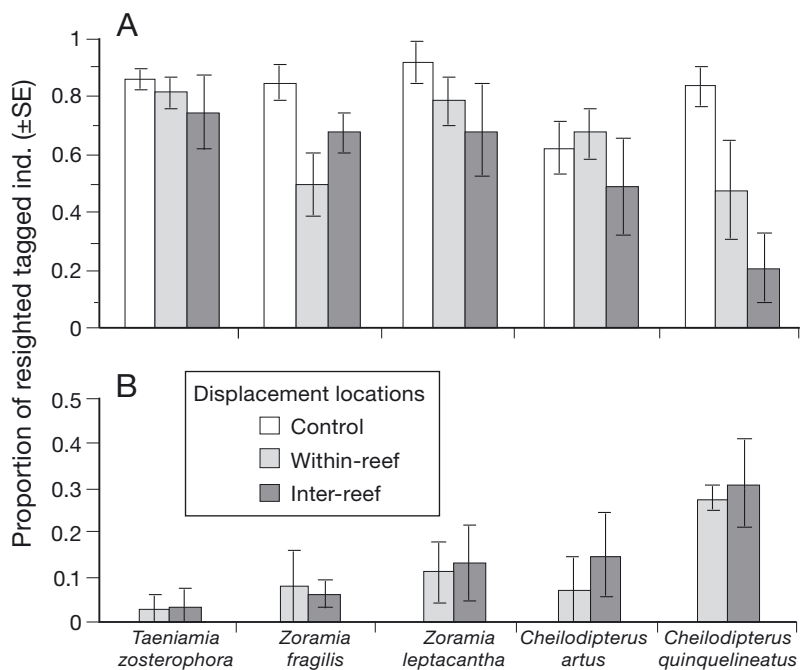
Fig. 5. Strength of homing behaviour by 5 cardinalfish species displaced ~400 m from home sites. Control: fish tagged and released at the home site; Within-reef: fish released on the same reef, but at a distance; Inter-reef: fish released on a different reef. (A) Mean proportion of tagged individuals that returned to the home site within 7 d. (B) Mean proportion of tagged fish sighted at displacement locations the morning after release

Table 3. Statistical comparison of homing success amongst 5 cardinalfish species and 3 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 shown where significant. *p < 0.05, **p < 0.01. See Table 1 for full species names

(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 × 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	

73% of displaced fish), with >60% of displaced fish returning except for one of the IR treatments in which only 8 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 400 m 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% SE) than from displacements on alternative reefs (IR: 67.3 ± 10.8% SE). *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 WR and IR treatments, respectively.

The weakest homing species was *C. quinquelineatus*. Despite strong site fidelity of control individuals (71–95%), only half of the displaced WR fish returned home, and less than a quarter of the IR displacements returned (Fig. 5A). The species also had high variability in homing success. No returns occurred from one treatment site and less than 40% from 3 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 (Fig. 5B). These individuals were typically found among conspecific aggregations in branching corals. Ad hoc surveys of IR displacement locations (2–8 d 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 (Fig. 5B).

Expt 2: Long-distance homing

T. zosterophora homed back to capture locations from both 2 and 5 km displacements. 36% of individuals (11 fish) returned from 2 km within 11 d. One individual returned in the first evening and 5 more in the second evening. One individual from the 5 km displacement returned home sometime between 8 and 11 d.

Behavioural trait comparison

Behavioural attributes were not consistently related across the guild (Table 4, Fig. 6). Different species had different levels of each trait that related variably to homing strength. The only consistent pattern was that the 2 species with the strongest homing response also had high fidelity, were habitat specialists, and quite gregarious (*T. zosterophora* and *Z. leptacantha*, Fig. 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 (Fig. 6B). The more specialist species had stronger homing responses than the weaker species (Pearson correlation test: $r^2 = 0.80$, p < 0.05). The most specialist species (*T. zos-*

Table 4. Interspecific comparison of behavioural attributes and homing ability in cardinalfish. Relative strength of each behaviour is ranked (low, moderate, high) in comparison to the other study species. Homing response: total percent of fish that returned from displacements in this study (Fig. 5). Site fidelity: percent of fish showing fidelity to the home site over 9 d (Fig. 3). Habitat specialisation: number of distinct coral and non-coral micro-habitats used as diurnal refugia, according to Gardiner & Jones (2005). Sociality: modal frequency of aggregation size that fish were found in (Fig. 2)

Species	Homing response (total% fish returns)	Site fidelity (% fish fidelity)	Habitat specialisation (no. of habitats used)	Sociality (modal group size)
Taeniamia zosterophora	High (78)	Moderate (68)	Moderate (5) Uses variety of live coral species	Moderate (50) Seen solitary, and in moderate to large groups
Zoramia fragilis	Moderate (53)	Low (23)	Moderate (7) Uses variety of live coral species	Moderate (20) Mostly seen in medium to large groups
Zoramia leptacanthus	High (73)	High (91)	High (3) Predominantly uses 1 coral species	Moderate (50) Mostly seen in medium to large groups
Cheilodipterus artus	Moderate (58)	Low (43)	Low (12) Uses living and non-living substrata	Moderate (20) Sometimes seen solitary
Cheilodipterus quinquelineatus	Low (34)	Moderate (69)	Very low (20) Uses living and non-living substrata	Moderate (50) Frequently seen solitary

#1: *Taeniamia zosterophora*, #2: *Zoramia fragilis*, #3: *Z. leptacantha*, #4: *Cheilodipterus artus*, #5: *C. quinquelineatus*.
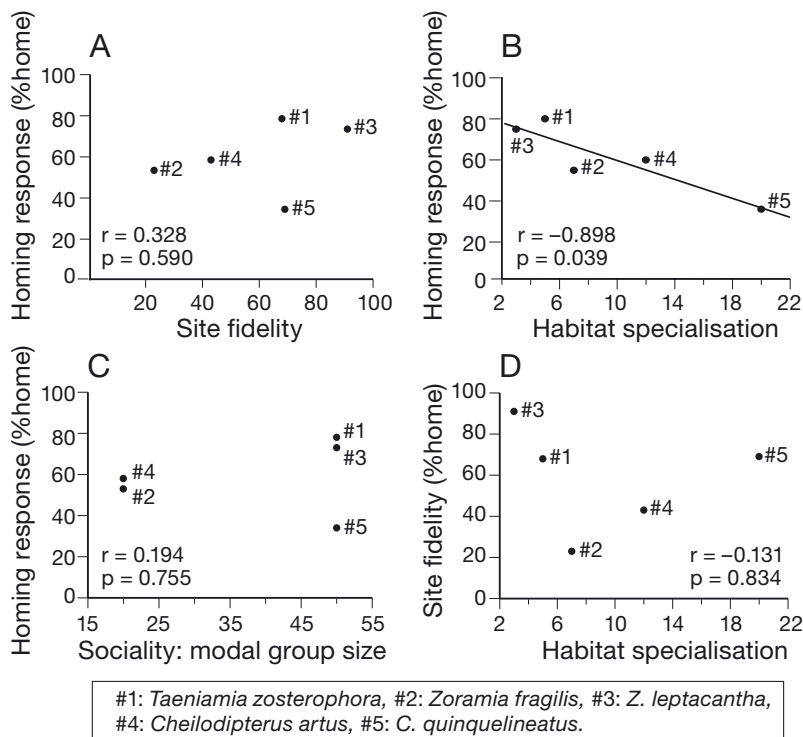
Fig. 6. Interspecific comparison of behavioural attributes and homing ability in guild of co-occurring cardinalfish. Values for homing response indicate the total percent of fish, per species, that homed from displacements in this study (i.e. cumulative of both displacement treatments). Values for site fidelity (A,D) indicate the percent of fish showing fidelity to the home site over 9 d. Values for habitat specialisation (B,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 Fig. 2). Statistical values indicate Pearson correlation test results with linear relationship plotted when significant at p < 0.05

terophora 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 (Fig. 6D). Social tendencies were not very different within the guild, and thus not well correlated with differential homing responses (Table 4, Fig. 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 ten-

dency 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 2 km (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 (*T. zosterophora*), some individuals homed across multiple reef and inter-reef passages from long 2 and 5 km distances. Our results demonstrate that the lack of structured habitat is no absolute barrier to cardinalfish movements or 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). In this study, 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. *In situ* observations and aquarium studies have demonstrated the species has weaker social and habitat preferences than other cardinalfish (Gardiner & 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 5 km returned to the same exact branch position and mate that it was with before displacement (N. M. Gardiner 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 2 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, and up to 40% of the *Cheilodipterus* individuals were missing from each survey time. 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 yr (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 (N. M. 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 likely.

The exact cues that small, adult coral reef fish use to direct homing across inter-reef areas and especially at distances greater than 500 m are not known. The speed with which individuals homed across 2 km 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 2–5 km 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 (Wilson et al. 2006, Bonin et al. 2011). 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.

LITERATURE CITED

Anderson GRV, Carr MH (1998) Bincke: a highly efficient net for collecting reef fishes. Environ Biol Fishes 51:111–115

Atema J, Kingsford MJ, Gerlach G (2002) Larval reef fish could use odour for detection, retention and orientation to reefs. Mar Ecol Prog Ser 241:151–160

Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. Ecology 92:1503–1512

Brown CR, Brown MB, Brazeal KR (2008) Familiarity with breeding habitat improves daily survival in colonial cliff swallows. Anim Behav 76:1201–1210

Burt de Perera T, Guilford TC (2008) Rapid learning of shelter position in an intertidal fish, the shanny *Lipophrys pholis* L. J Fish Biol 72:1386–1392

Carlson HR, Haight RE, Helle JH (1995) Initial behaviour of displaced yellowtail rockfish *Sebastes flavidus* in Lynn Canal, Southeast Alaska. Alsk Fish Res Bull 2:76–80

Chave EH (1978) General ecology of six species of Hawaiian cardinalfishes. Pac Sci 32:245–270

Chivers DP, Brown GE, Smith RJF (1995) Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. Can J Zool 73:955–960

Dell'Ariccia G, Blanc L, Bonadonna F, Sanz-Aguilar A (2015) Mediterranean storm petrels rely on nest position for homing after migration: a test with artificial nestboxes. Anim Behav 107:97–104

Dittman A, Quinn T (1996) Homing in Pacific salmon: mechanisms and ecological basis. J Exp Biol 199:83–91

Døving KB, Stabell OB, Östlund-Nilsson S, Fisher R (2006) Site fidelity and homing in tropical coral reef cardinalfish: Are they using olfactory cues? Chem Senses 31:265–272

Feary DA (2007) The influence of resource specialization on the response of reef fish to coral disturbance. Mar Biol 153:153–1610

Fisher R, Leis JM, Clark DL, Wilson SK (2005) Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. Mar Biol 147:1201–1212

Frederick JL (1997) Post-settlement movement of coral reef fishes and bias in survival estimates. Mar Ecol Prog Ser 150:65–74

Fukumori K, Okuda N, Yamaoka K, Yanagisawa Y (2010) Remarkable spatial memory in a migratory cardinalfish. Anim Cogn 13:385–389

Gardiner NM, Jones GP (2005) Habitat specialisation and overlap in a guild of coral reef cardinalfishes (Apogonidae). Mar Ecol Prog Ser 305:163–175

Gardiner NM, Jones GP (2010) Synergistic effects of habitat preference and gregarious behaviour on habitat use in coral reef cardinalfish. Coral Reefs 29:845–856

Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proc Natl Acad Sci USA 104:858–863

Gould AL, Harii S, Dunlap PV (2014) Host preference, site fidelity, and homing behavior of the symbiotically luminous cardinalfish, *Siphamia tubifer* (Perciformes: Apogonidae). Mar Biol 161:2897–2907

Gould AL, Harii S, Dunlap PV (2015) Cues from the reef: olfactory preferences of a symbiotically luminous cardinalfish. Coral Reefs 34:673–677

Grabowska-Zhang AM, Wilkin TA, Sheldon BC (2012) Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). Behav Ecol 23:322–333

Green AL, Maypa AP, Almany GR, Rhodes KL and others (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev Camb Philos Soc 90:1215–1247

Griffin DR (1952) Bird navigation. Biol Rev Camb Philos Soc 27:359–390

Guilbert JM, Walker MM, Greif S, Parsons S (2007) Evidence of homing following translocation of long-tailed bats (*Chalinolobus tuberculatus*) at Grand Canyon Cave, New Zealand. NZ J Zool 34:239–246

Hartney KB (1996) Site fidelity and homing behaviour of some kelp-bed fishes. J Fish Biol 49:1062–1069

Huang WS, Pike DA (2011) Determinants of homing in nest-guarding females: balancing risks while travelling through unfamiliar landscapes. Anim Behav 82:263–270

Jenssen TA (2002) Spatial awareness by the lizard *Anolis cristatellus*: Why should a non-ranging species demonstrate homing behavior? Herpetologica 58:364–371

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci USA 101:8251–8253

Jorge PE, Almada F, Goncalves AR, Duarte-Coelho P, Almada VC (2012) Homing in rocky intertidal fish. Are *Lipophrys pholis l.* able to perform true navigation? Anim Cogn 15:1173–1181

Kingsford MJ (1992) Spatial and temporal variation in predation on reef-fishes by coral trout (*Plectropomus leopardus*). Serranidae. Coral Reefs 11:193–198

Kingsford MJ, Finn MD, O'Callaghan MD, Atema J, Gerlach G (2014) Planktonic larval duration, age and growth of *Ostorhinchus doederleini* (Pisces: Apogonidae) on the southern Great Barrier Reef, Australia. Mar Biol 161: 245–259

Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry and geomagnetic field. Mar Biol 117:1–22

Kolm N, Hoffman EA, Olsson J, Berglund A, Jones AG (2005) Group stability and homing behavior but no kin group structures in a coral reef fish. Behav Ecol 16:521–527

Leis JM, Siebeck U, Dixson DL (2011) How Nemo finds home: the neuroecology of dispersal and of population connectivity in larvae of marine fishes. Integr Comp Biol 51:826–843

Limpus CJ, Miller JD, Parmenter CJ, Reimer D, Mclachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. Wildl Res 19:347–358

Lohmann KJ, Putman NF, Lohmann CMF (2008) Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proc Natl Acad Sci USA 105:19096–19101

Longenecker K, Langston R (2006) Life history characteristics of a small cardinalfish, *Ostorhinchus rubrimacula* (Percoidei: Apogonidae), from Koro, Fiji. Pac Sci 60: 225–233

Marnane MJ (2000) Site fidelity and homing behaviour in coral reef cardinalfishes. J Fish Biol 57:1590–1600

Marnane MJ, Bellwood DR (2002) Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia. Mar Ecol Prog Ser 231: 261–268

Matthews KR (1990) An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* spp.). Environ Biol Fishes 29:161–178

Morris CJ, Green JM, Snelgrove PVR, Pennell CJ, Ollerhead LMN (2014) Temporal and spatial migration of Atlantic cod (*Gadus morhua*) inside and outside a marine protected area and evidence for the role of prior experience in homing. Can J Fish Aquat Sci 71:1704–1712

Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. Glob Change Biol 10: 1642–1647

Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. J Fish Biol 51:931–938

Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* bloch (Scaridae). Ecology 54:589–596

Okuda N (1999) Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. Anim Behav 58:273–279

Overholtzer-McLeod KL (2006) Consequences of patch reef spacing for density-dependent mortality of coral-reef fishes. Ecology 87:1017–1026

Pahl M, Zhu H, Tautz J, Zhang SW (2011) Large scale homing in honeybees. PLOS ONE 6:e19669

Papi F (1992) Animal homing. Chapman & Hall, London

Part T (1995) The importance of local familiarity and search costs for age-biased and sex-biased philopatry in the collared flycatcher. Anim Behav 49:1029–1038

Rau P (1929) Experimental studies in the homing of carpenter and mining bees. J Comp Physiol 9:35–70

Reese ES (1989) Orientation behavior of butterflyfishes (family Chaetodontidae) on coral reefs: spatial learning of route specific landmarks and cognitive maps. Environ Biol Fishes 25:79–86

Rueger T, Gardiner NM, Jones GP (2014) Relationships between pair formation, site fidelity and sex in a coral reef cardinalfish. Behav Processes 107:119–126

Shima JS, McNaughtan D, Geange SW, Wilkinson S (2012) Ontogenetic variation in site fidelity and homing behaviour of a temperate reef fish. J Exp Mar Biol Ecol 416−417: 162−167

Srinivasan M, Jones GP (2006) Extended breeding and recruitment periods of fishes on a low latitude coral reef. Coral Reefs 25:673−682

Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR (1997) Structure and function of the vertebrate magnetic sense. Nature 390:371−376

Wall M, Herler J (2009) Postsettlement movement patterns and homing in a coral-associated fish. Behav Ecol 20: 87−95, doi:10.1093/beheco/arn118

White GE, Brown C (2013) Site fidelity and homing behaviour in intertidal fishes. Mar Biol 160:1365−1372

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? Glob Change Biol 12:2220−2234

Wilson SK, Burgess SC, Cheal AJ, Emslie M and others (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. J Anim Ecol 77:220−228

Workman I, Shah A, Foster D, Hataway B (2002) Habitat preferences and site fidelity of juvenile red snapper (*Lutjanus campechanus*). ICES J Mar Sci 59:S43−S50

Yoshiyama RM, Gaylord KB, Philippart MT, Moore TR and others (1992) Homing behavor and site fidelity in intertidal sculpins (Pisces: Cottidae). J Exp Mar Biol Ecol 160: 115−130