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Site Fidelity and Homing in Tropical Coral Reef Cardinalfish: Are They Using Olfactory Cues?

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Abstract

A number of tropical coral reef fish hold station and display restricted home ranges. If artificially displaced, they will return to their home site. We questioned if marine fish are using the same mechanisms for home site detection as many freshwater fish, that is, by olfactory sensing of chemical signals deposited on the substrate by conspecific fish. Behavioral experiments were conducted on Lizard Island Research Station, Queensland, Australia, in 2001 and 2002. Five-lined cardinalfish (*Cheilodipterus quinquelineatus*) were tested in groups with split-branded cardinalfish (*Apogon compressus*) as a reference species and individually against *Apogon leptacanthus* as well as conspecifics of another reef site. The group tests showed that both species preferred artificial reef sites that had previously been occupied by conspecifics. Individual *C. quinquelineatus* preferred scent of conspecifics from their own reef site to that from another site. They also preferred the scent released by artificial reefs previously occupied by conspecifics of their reef site to that of similar reefs previously occupied by conspecifics of another reef site. No discrimination between species from the same reef site was obtained in experiments with individual fish. Our data suggest that cardinalfish are keeping station and are homing by use of conspecific olfactory signals.

Key words: chemical cues, conspecific detection, preference behavior, substrate marking

Introduction

On tropical coral reefs a number of fish species hold territories, display restricted home ranges, and return to home sites after displacements (Sale, 1978). Adult cardinalfish (apogonids) have been shown to exhibit strong home fidelity by sharing restricted resting habitats by day and to move into a range of feeding habitats at night. In two studies on apogonids, each carried out on three fish species, individuals were found to move on average less than 5 m from their initial resting positions during daytime in one study and less than 80 cm in the other. These restricted movements were found over a timescale of up to 90 days and 16 months in the two studies, respectively (Kuwamura, 1985; Marnane, 2000). At night, however, cardinalfish have been found spatially segregated, both horizontally and vertically in the water column, with a horizontal distribution of up to 30 m (Marnane and Bellwood, 2002). Furthermore, displacement experiments carried out with cardinalfish demonstrated that between 56% and 81% of the fish returned within 3 days after being displaced 1 km from their original resting site, and 33%–63% of the fish returned when displaced 2 km (Marnane, 2000). These returns occurred despite the presence of numerous suitable habitats between resting and displacement sites and demonstrated a quite remarkable homing behavior in this group of fish.

The sensory basis for homing behavior in cardinalfish is not known, but chemical signatures and sound have been suggested as being important orientation cues for reef fish in general (Stobutzki and Bellwood, 1997; Marnane, 2000). Sweatman (1983, 1985) demonstrated an enhanced settlement of pomacentrid larvae on coral heads where conspecific adult fish predominated. Later, he also found that damselfish settlers preferred experimental corals supplied with water from resident conspecifics and suggested that dissolved chemical cues from fish are used to select settlement sites (Sweatman, 1988). Further support to this view comes from the work by Lecchini (2004), who found that coral reef

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fish larvae detect their settlement location due to the presence of conspecifics. If fish larvae in the marine environment are using chemical cues from conspecifics to detect suitable living sites, it seems reasonable to assume that adult fish can make use of similar detection mechanisms to locate their home areas. In comparison, substrate marking by conspecific odors has been demonstrated in salmonid fish and might also play a key role in homing behavior of these species of fish (Døving *et al.*, 1980; Foster, 1985; Stabell, 1987; Døving and Stabell, 2003).

From an evolutionarily point of view, it should be expected that the same set of functional tools are used by fish in general with regard to site fidelity and homing. Accordingly, we speculated that cardinalfish may keep station, return at dusk from feeding dispersal during night, and display homing behavior after enforced displacement, by essentially the same set of behavioral mechanisms that has previously been demonstrated in other species of fish. That is, by chemical marking of their living environment (i.e., bottom substrate) by conspecific odors secreted within fecal material, followed by appropriate behavioral responses for orientation and keeping station. We aimed at answering some of the following basic questions related to participation of the chemical senses in the behavioral occurrences described in reef fish. 1) Can cardinalfish discriminate between chemical signals of conspecific fish from its own site and conspecifics of another site? 2) Can cardinalfish recognize a substrate they have previously occupied from an identical substrate occupied by another fish species? 3) Do the fish rely on the olfactory sense in the discrimination tasks? To our knowledge, this is the first study aimed at exploring the sensory basis for stationary behavior and homing of a marine fish species.

Material and methods

Experimental fish and sites of capture

The experiments were carried out at the Lizard Island Research Station (14°40′ S, 145°28′ E) on the northern Great Barrier Reef, Australia in November 2001 and 2002. Fish were collected from different sites in the Lizard Island Blue Lagoon, at depths between 4 and 6 m. The fish were anesthetized with clove oil by scuba divers (Munday and Wilson, 1997), captured, and transported to the Research Station. In the laboratory, the fish of each species and site were kept in separate tanks with running seawater during both years.

In 2001, a pilot experiment was carried out with split-banded cardinalfish (*Apogon compressus*) and five-lined cardinalfish (*Cheilodipterus quinquelineatus*), both species collected at the same two sites. Site 1 was largely composed of *Porites cylindrical* habitat, and site 2 was composed largely of *Acropora nobilis*, the sites being situated approximately 2 km apart (Figure 1). In the experiments carried out in 2002, five-lined cardinalfish and threadfin cardinalfish (*Apogon leptacanthus*) were used, with individuals of both species being captured at two new sites (denoted 3 and 4, Figure 1) approximately 1 km apart. Site 3 consisted of a large *Acropora* coral (diameter > 3 m), and site 4 was mainly represented by *P. cylindrical*. In both years, following termination of the experiments, surviving fish were brought back to their respective lagoon sites and released.

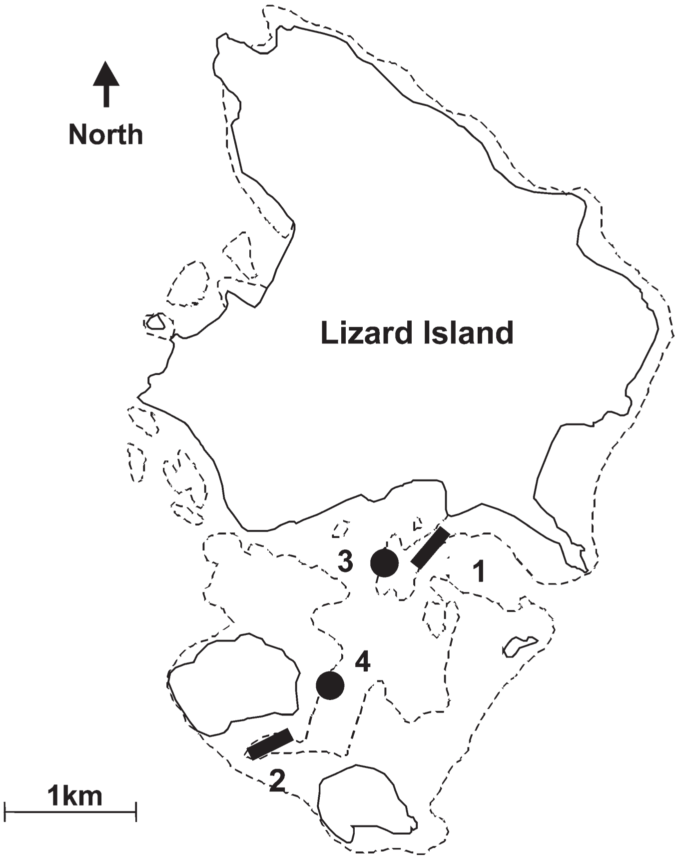

Figure 1 Fish were taken from sites 1 and 2 in 2001 (rectangles) and from sites 3 and 4 in 2002 (dots) in the Blue Lagoon just south of Lizard Island.

Preferences of fish in groups

For the experiments in 2001, adult *A. compressus* (total length, TL: 7–11 cm) and adult *C. quinquelineatus* (TL: 6–8 cm) were tested in conspecific groups of fish from their respective sites. The groups consisted of five fish from site 1 and six fish from site 2 of each species, and each of the groups were tested once a day during 4 days. Before, and in between tests, each group was kept in their respective holding tank with a set of identical artefacts. The artefacts consisted of a bottom lined with a 1-mm mesh size plastic net, upon which was placed two longitudinal halves of polyvinyl chloride (PVC) tube (diameter: 15 cm, length: 25 cm) together with a concrete building block (9 × 19 × 39 cm) with two oval holes (3.5 × 16.5 × 19 cm). These structures appeared to provide adequate shelter for the fish. The fish were fed *ad lib* every evening with small shrimps collected by light traps, and all fish were observed feeding within 1 day of capture.

The behavioral experiments were performed between 0800 and 1400 during four consecutive days, with all four groups of fish tested each day. At the start of each day, the set of artefacts from each holding tank were placed into a circular observation tank supplied with seawater. The observation tank was 2.8 m in diameter with a 40-cm water depth. The four sets of artefacts were placed in the periphery of the tank (North, East, South, West), with each building block on the mesh and the two half PVC tubes placed standing in front of the block. For the human eye, the four sets of artefact arrangements appeared indistinguishable. All four groups of fish were tested separately on the same day, each day in a randomized sequence, with all individuals of a group released simultaneously from the same position in the observation tank. Each group of fish was then left undisturbed in the observation tank for 1 h while being monitored. After each test series, the fish were returned to their holding tanks, followed by their respective artefacts at the end of the day. The relative positions of the four sets of artefacts in the observation tank were changed daily, thereby testing each group of fish with four different positions of their shelters. The first test series were carried out after the fish had been in their respective holding tanks for 2 days.

Distribution of fish during light and dark hours

In 2002, *C. quinquelineatus* from site 3 were tested with regard to dispersal from an occupational site during light and dark hours. This approach was included to control for normal diurnal rhythm in captivity. Four fish were released into a 2-m circular observation tank with a water depth of 50 cm at noon. The tank contained two beds of live corals placed opposite to one another in the periphery of the tank. Within a few minutes, the fish had selected permanent cover among the corals in one of the beds. The position of individual fish in relation to neighbors was subsequently monitored for 4 h the following evening. Photographs were taken from above every 30 min for 2 h before and 2 h after sunset, using flashlight during dark hours. Individual distances were measured from a scale on the tank bottom.

Preferences of individual fish

Test system and experimental procedures

For the experiments in 2002, adult *C. quinquelineatus* from site 3 (TL: 8.2 ± 0.7 cm) were individually observed in a two-choice test system during daytime (0900 and 1600) for 7 days over a period of 2 weeks. *Cheilodipterus quinquelineatus* from site 4 (TL: 7.2 ± 0.4 cm) and *A. leptacanthus* (TL: 4–6 cm) from site 3 were used as odor donors in competitive tests. The tests were carried out in a randomized sequence. Four arenas were made from green polypropylene trays (Epoque 1,000 mm, art. no. 2802, Hammar, Sarvis, Sweden), each measuring 93 × 12.5 cm in bottom area. A wall made from perforated PVC plates were placed vertically 4 cm from both ends of the trays to produce inlet chambers for test solutions, giving test arenas of 85 × 12.5 cm in the center. Each tray was filled with 8 liters of seawater to a level of 6.6 cm. Tests were performed in still water, and test solutions (i.e., water conditioned with chemical cues) were introduced by gravity to both ends of the arenas from separate tanks or beakers into the inlet chambers via polyethylene catheters, each providing a flow rate of 14.5 ml/min. The spread of test solutions in the test system was verified using a diluted solution of milk in seawater. This solution dispersed evenly in the trays and reached the middle of each arena within 15 min. Test periods of 10 min was accordingly chosen to ensure side specificity of stimulants, giving a total volume of approximately 290 ml of stimulus waters added to each arena during tests.

The four trays, each containing one fish, were placed side by side on the floor in a separate part of the laboratory facilities and left undisturbed during the observation period. Movements of fish were monitored with a video camera situated above the test chambers, and a black thread stretched across the top of each tray visually divided the trays into two halves from above. A set of four fish was replicated four times to constitute a series (n = 16), and each time the inlet sides of test and control waters were switched to level out any unbalanced disturbances that could influence the behavior. No fish was used more than once in each series. Between each run, aquaria and tubing were washed twice with a methanol/ethanol mixture and then thoroughly rinsed with freshwater followed by seawater.

A run was initiated by introducing the flow of test waters to the end chambers, followed by transfer of experimental fish to the middle of each test arena and starting of the video recording within 1 min. The fish immediately started to move in the arenas. Following their behavioral performances, the fish were returned to a duplicate holding tank for the group.

Experimental protocol

To test for discrimination ability of *C. quinquelineatus*, altogether six types of experiments were carried out. In all test series, *C. quinquelineatus* from site 3 was used as the focal fish. Choices between chemical cues of different origins were tested as follows: 1) waters conditioned by conspecific fish from the two reef sites, 2) scent deposited on shelters by conspecifics from the two reef sites (i.e., substrate marking), 3) anosmic fish given the choice between waters conditioned by conspecifics from different reef sites, 4) waters conditioned by conspecifics and heterospecifics from the same reef site, 5) scent released from fecal material of conspecifics and heterospecifics of the same reef site, and 6) water conditioned by conspecific fish from their own reef site versus seawater.

Water conditioned by fish. To test for possible discrimination between scents of conspecifics from different reef sites (series 1) or between conspecifics and heterospecifics of the same site (series 4), water was collected in beakers from the holding tanks containing the species and reef group in question.

In test series 6, with water conditioned by conspecifics versus seawater, water was taken from the holding tank with conspecifics of the same reef site.

Substrate marking. Each holding tank was equipped with four artefacts made of plastic tubes, 11 cm in outer diameter and 14.5 cm long. The inside of the tubes was lined with polyethylene brush mats (Astroturf, Southwest Recreational Industries, Inc., Leander, TX) to increase surface area. These artefacts provided shelter for the fish, as shown by the positioning of *C. quinquelineatus* inside the artefacts (Figure 2). The artefacts were used as reservoirs of scents for testing possible substrate marking by fish (series 2). For that purpose, two artefacts from each tank containing *C. quinquelineatus* were lightly rinsed in running seawater and placed in separate tanks with seawater for 2 h before the test waters were applied to the choice chambers.

Scent of fecal material. Fecal material of *C. quinquelineatus* and *A. leptacanthus* was sampled by siphoning the bottom of the two holding tanks containing fish from reef site 3. The material was allowed to precipitate in small beakers, and surplus water was poured out. Equal volumes of precipitate from the two samples were transferred to funnels with filter paper, washed with approximately 100 ml of seawater, and the filtrates diluted to 1 liter in beakers. The fresh extract was subsequently used in preference tests with *C. quinquelineatus* (series 5).

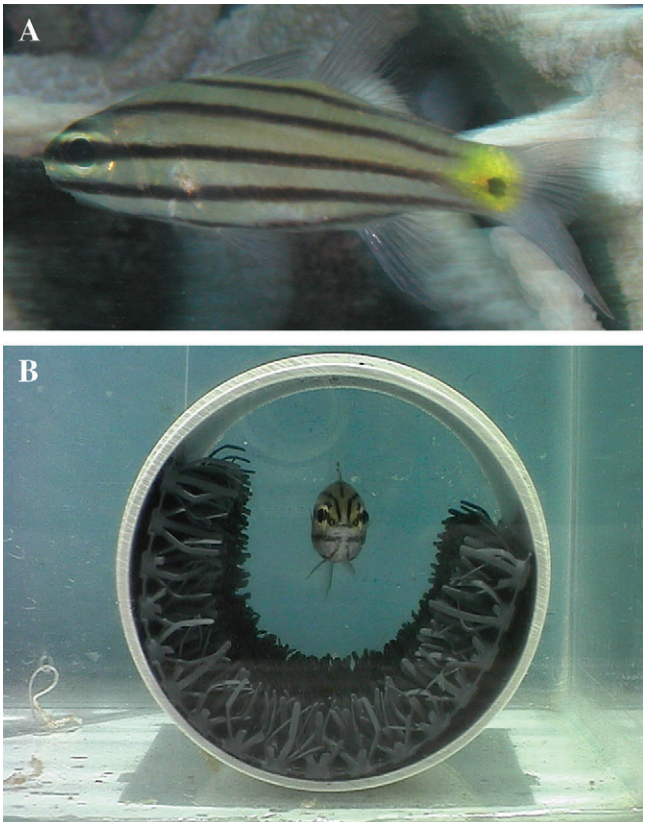

Figure 2 Five-lined cardinalfish (*Cheilodipterus quinquelineatus*): **(A)** side-view (photo G. Nilsson) and **(B)** common position in shelters. Shelters were made from pieces of plastic tubes lined with Astroturf brush mats. Several fish could occupy a shelter simultaneously.

Experiments with anosmic fish. *Cheilodipterus quinquelineatus* were made temporary anosmic by filling the olfactory cavity with Vaseline (Chesebourgh-Pond's Inc., New York, London, Paris). Fish were anesthetized with clove oil before handling and were allowed to recover for at least 2 h before being used in the experiments (series 3). Vaseline was injected into the posterior naris of the fish by using a modified 1-ml plastic syringe which had been melted and extended in the tip to a fine tube. Visual inspection showed that the Vaseline remained in the olfactory cavity for at least 2 days. Test waters for this series were taken from the holding tanks containing conspecifics from the two reef sites, that is, similar to series 1.

Data analysis

The data on group performance of fish were treated by the binomial test, assuming equal probability for final selection of artefacts belonging to conspecifics and heterospecifics as the null hypothesis (Siegel and Castellan, 1988). For the individual choices, the position of each fish in relation to the two halves of the choice chamber was noted after start for every 10 s during a period of 10 min, giving a summated side ratio from 60 observations of each fish. The side ratio for all fish (n = 16) was treated by the one-sample t-test, applied two-tailed, assuming no side preferences as the null hypothesis (i.e., 30/30 distribution). Calculations were carried out by the use of the computer programme Statistics7 (Analytical Software, Tallahassee FL).

Results

Group experiments in 2001

Following the initial release of fish groups in the round observation tank, the fish generally stayed in a dense school and moved slowly along the periphery of the tank. In some cases, the fish would encircle an artefact and move on to the next. The final choices were made within 30 min, and in all cases the fish remained at the shelter, mostly inside the concrete blocks, for the rest of the observation time. Altogether, 10 groups selected a site with artefacts from a tank previously occupied by conspecifics. Only one group of fish (*C. quinquelineatus*) selected an artefact from a tank of the other species (*A. compressus*), while five groups made no choice. Of the 10 groups that selected artefacts belonging to conspecifics, five selected their own site and five selected the other site. No significant difference in choice pattern between the two fish species appeared from the results.

Assuming equal probability for each of the three possible choices, that is, shelters belonging to conspecific, shelters belonging to heterospecifics, and no choice, the probability of the total distribution observed is 0.022. If only the 11 trials where choices of site were made are considered, the probability of the total observed choices is 0.0054.

Distribution patterns during light and dark hours (2002)

During the day, the four *C. cinquelineatus* stayed close to one another and did not move far from one of the corals. The behavior after dark was dramatically different as the interindividual distances increased from a mean of about 10 cm to more than 100 cm (Figure 3). This result demonstrates that *C. quinquelineatus* in captivity follows a normal diurnal rhythm.

Individual preferences (2002)

In the preference experiments with single individuals of *C. quinquelineatus*, the fish made slow explorations to both ends of the choice chambers during the observation periods. Accordingly, recording the position of fish in relation to the midline of the arena every 10 s appeared to be a useful illustration of the actual behavior.

Conspecific discrimination

In the test with water conditioned by conspecifics of their own site versus water conditioned by conspecifics from the other reef site, individual *C. quinquelineatus* from site 3 demonstrated a preference for the scent of conspecific from their own site. The percent of choices toward conspecific scent from reef site 3 was 68.1 (SD = 28.9, $P = 0.024$, Figure 4a).

Substrate marking

In order to investigate if the fish had marked the substrate of the living environment with their chemical signatures, the artefacts from the holding tanks were used alone for conditioning the waters used for testing. The results from the choice tests revealed that *C. quinquelineatus* preferred the scent released by artefacts previously held with fish from their own site to that released by artefacts of the tank with conspecifics from the other site. The percent of choices toward conspecific scent from reef site 3 was 65.5 (SD = 27.2, $P = 0.037$, Figure 4b).

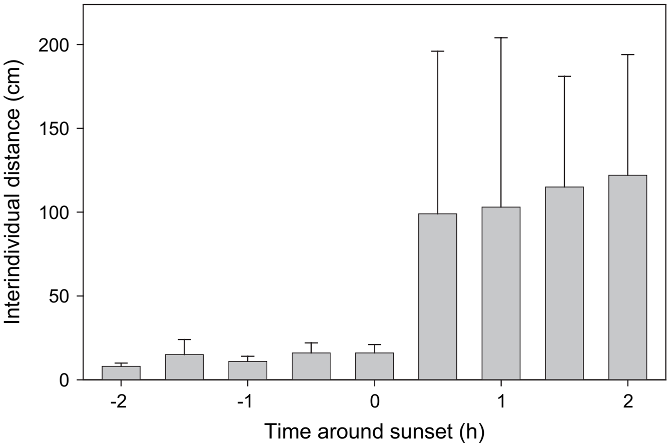

Figure 3 Interindividual distances between four *Cheilodipterus quinquelineatus* around dusk. Observations were carried out with camera at 30-min intervals from 2 h before until 2 h after sunset.

Experiments with anosmic fish

When the olfactory cavities of the test fish had been occluded with Vaseline, no preference was displayed for any of the tank waters conditioned with *C. quinquelineatus* from the two reef sites. The percent of choices toward conspecific scent was 53.8 (SD = 39.6, $P = 0.7104$, Figure 5a). This result indicates that the olfactory sense is responsible for the preference shown by *C. quinquelineatus*.

Interspecific discrimination

When *C. quinquelineatus* was tested for preferences of water conditioned by conspecifics from their own site versus water conditioned by another species (*A. leptacanthus*) of the same site, the results revealed no preferences for either water. The percent choices toward conspecific scent was 68.12, with an SD of 53.8 (SD = 39.6, $P = 0.7104$, Figure 5a).

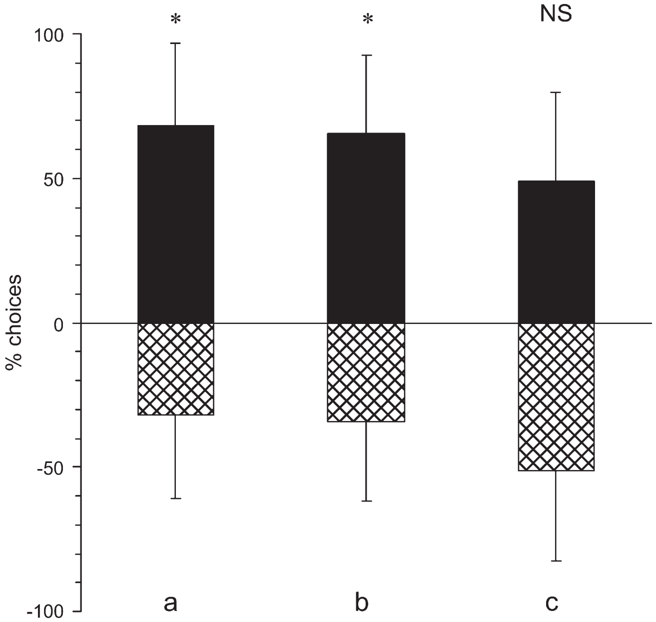

Figure 4 Preference experiments with *Cheilodipterus quinquelineatus* from site 3 ($n = 16$), given the choice between chemical cues of two different sources (±SD). Filled bars denote preferences toward cues released by conspecific fish from reef site 3 (home site), whereas hatched bars denote preferences toward cues released by conspecific fish from site 4. (a) Water conditioned by conspecifics from site 3 versus water conditioned by conspecifics from site 4. (b) Chemical cues released from artificial shelters previously kept with conspecific fish from site 3 versus shelters kept with conspecifics from site 4. (c) Water conditioned by conspecifics from site 3 versus water conditioned by conspecifics from site 4—with performing fish rendered anosmic. NS: not significant, $^{*}P < 0.05$.

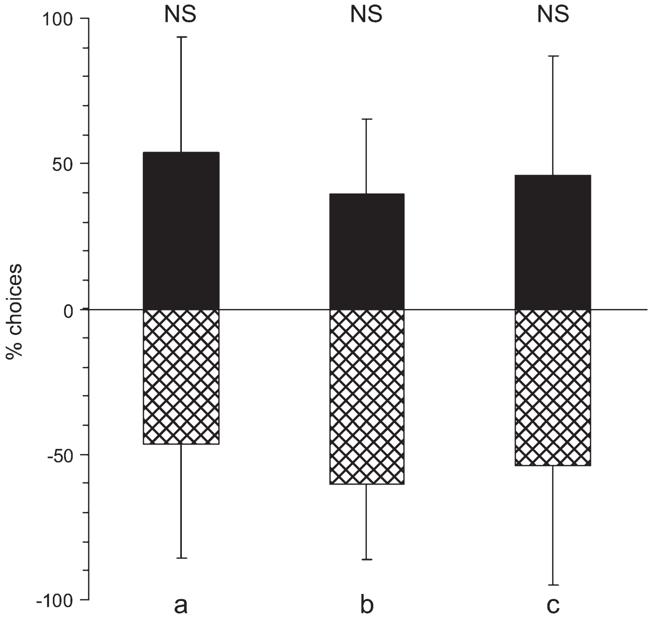

Figure 5 Preference experiments with *Cheilodipterus quinquelineatus* from site 3 (*n* = 16), given the choice between chemical cues of two different sources (±SD). Filled bars denote preferences toward cues released by conspecific fish from reef site 3 (home site), whereas hatched bars denote preferences towards cues released by heterospecific fish from the same site or water. (a) Water conditioned by conspecifics versus water conditioned by *Apogon leptacanthus*, with all fish from site 3. (b) Aqueous extracts of fecal material from conspecifics versus similar extract from *A. leptacanthus*, sampled from the rearing tanks with fish from site 3. (c) Water conditioned by *C. quinquelineatus* from site 3 versus seawater. NS: not significant.

Fecal material

When *C. quinquelineatus* was tested for preferences of water scented by fecal material of conspecifics versus water scented by fecal material of another species (*A. leptacanthus*), the results revealed no preferences for either water. The percent of choices toward conspecific scent was 39.7 (SD = 25.8, *P* = 0.131, Figure 5b). All material used in the tests was sampled from tanks containing fish from site 3, that is, from the same site as the performing fish.

Conspecific scent versus seawater

When *C. quinquelineatus* was tested for preferences of water scented by conspecifics from their own site versus seawater (i.e., blank), the results revealed no preferences for either water. The percent of choices toward conspecific scent was 46.2 (SD = 40.9, *P* = 0.7117, Figure 5c).

Discussion

Cardinalfish display a remarkable ability to home after being displaced from their home site. Authors have proposed different sensory cues as the basis for this behavior. The present study suggests that chemical cues might be a key factor in the homing behavior, supporting the conclusions by Atema *et al.* (2002) that larval reef fish (primarily apogonids) uses chemical cues to orient toward lagoon water after dispersal. Our work, however, does not support their proposal that fish may be imprinted to some general reef odors. We present data indicating that individuals of *C. quinquelineatus* can differentiate between chemical cues of conspecifics from two different sites on the coral reef, suggesting that an ability of intraspecific discrimination may be present in apogonids. The results obtained further suggest that cardinalfish are using their olfactory sense for this performance. Our study also suggests that the fish odorants are deposited on the substrate of their dwelling because water scented by artefacts previously occupied by fish released the same preferences as water from tanks containing fish.

In the choice experiments, *C. quinquelineatus* did not show any preference for odors of their own species to that of another species (*A. leptacanthus*) from the same site. Neither did they show any preference for fecal material of conspecifics compared to similar material from *A. leptacanthus*. According to kin recognition theory, conspecific preferences should presumably have been obtained in the two tests where chemical cues from heterospecifics where involved (i.e., Figure 4a,b). Because, however, no discrimination between conspecific odor and seawater (blank—Figure 5c) was either revealed, alternative explanations ought to be sought.

A factor that hampers plausible interpretations of data comes from the fact that the heterospecific choice in the individual tests (*A. leptacanthus*) was another than used in the prior group test. The split-banded cardinalfish (*A. compressus*) used in 2001 is of similar size, display colorful appearance, and disperse evenly on the reef in close contact with the corals in a similar manner to the focal fish, the five-lined cardinalfish (*C. quinquelineatus*). Threadfin cardinalfish (*A. leptacanthus*), on the other hand, are smaller, display transparent appearance, congregate in shoals, and are commonly observed in a short distance (20–100 cm) away from the corals. However, *A. compressus* were not found in sufficient numbers in 2002, and *A. leptacanthus* was therefore chosen as the alternative species.

A possible explanation for the seemingly contradictory results may be that the test fish associated the odor of the other species with odors of their own site. Associative learning (Clark and Sutterlin, 1985; Wisenden, 2001) of coexisting heterospecific fish from the native reef site may possibly explain the results presented in Figure 4a,b. This is based on the assumption that fish odors are to be found also in fecal material (Selset, 1980; Selset and Døving, 1980; Foster, 1985; Stabell, 1987; Olsén, 1987; Courtenay *et al.*, 1997). Still, an explanation for the lack of discrimination between conspecific cues and seawater is missing. We feel, however, that future ecological studies may eventually clarify these seemingly contradictory results. Support to our trust in the data comes from the fact that even in captivity *C. quinquelineatus* seems to follow a normal diurnal activity pattern. In summary, our data seem to display the problems facing researchers in environments where animals are scarce or protected.

We have no evidence on the nature of the odorants used in the process of intraspecific discrimination. In salmonids, however, bile salts derivatives are potent olfactory cues (Døving *et al.*, 1980). Those substances may be deposited on the substrate with the fecal material where they adhere, to be subsequently released from such deposits over time to serve as signposts in the aquatic environment. Bile salts have been shown to function as homing and sex pheromones also in sea lamprey (Li *et al.*, 1995, 2002; Bjerselius *et al.*, 2000; Fine and Sorensen, 2005; Sorensen *et al.*, 2005). Although no such compounds have hitherto been identified in the marine environment, bile salt derivatives appear to be potential candidates also among fish inhabiting tropical coral reefs.

It should be realized that an odorant as a sensory cue, whether in air or water, does not have a vector and will not give information about the origin or the direction from where the odorants are coming. Salmon are known to rely on the olfactory sense for homing behavior, both in freshwater (Stabell, 1984) and in the sea (Westerberg, 1982; Døving *et al.*, 1985). However, the detailed observations of the salmon moving in the sea demonstrate that the layering of the water is of importance (Westerberg, 1982). The ability of the fish to detect infrasound or linear acceleration (Sand and Karlsen, 1986) can provide the sensory cue necessary for detecting the difference in currents of the layers. Thus, the auditory system may give the fish information about the relative direction of flow in neighboring layers. The combined information gained via the olfactory and the auditory systems has been suggested to be the basis for the homing ability of salmon (Døving and Stabell, 2003). It seems plausible that such a combination can also provide the sensory cues for fish homing in tropical reefs.

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References

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

Bjerselius, R., Li, W., Teeter, J.H., Seelye, J.G., Johnsen, P.B., Maniak, P.J., Grant, G.C., Polkinghorne, C.N. and **Sorensen, P.W.** (2000) *Direct behavioural evidence that unique bile acids released by larval sea lamprey (Petromyzon marinus) function as a migratory pheromone.* Can. J. Fish. Aquat. Sci., 57, 557–569.

Clarke, L.A. and **Sutterlin, A.M.** (1985) *Associative learning, short-term memory, and colour preference during first feeding by juvenile Atlantic salmon.* Can. J. Zool., 63, 7–14.

Courtenay, S.C., Quinn, T.P., Dupuis, H.M.C., Groot, C. and **Larkin, P.A.** (1997) *Factors affecting the recognition of population-specific odours by juvenile coho salmon.* J. Fish Biol., 50, 1042–1060.

Døving, K.B., Selset, R. and **Thommesen, G.** (1980) *Olfactory sensitivity to bile acids in salmonid fishes.* Acta Physiol. Scand., 108, 123–131.

Døving, K.B. and **Stabell, O.B.** (2003) *Trails in open waters: sensory cues in salmon migration*. In Collin, S.P. and Marshall, N.J. (eds), Sensory Processing in Aquatic Environments. Springer-Verlag, New York, pp. 39–52.

Døving, K.B., Westerberg, H. and **Johnsen, P.B.** (1985) *Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, Salmo salar, to hydrographic stratification.* Can. J. Fish. Aquat. Sci., 42, 1658–1667.

Fine, J.M. and **Sorensen, P.W.** (2005) *Biologically relevant concentrations of petromyzonol sulfate, a component of the sea lamprey migratory pheromone, measured in stream water.* J. Chem. Ecol., 31, 2205–2210.

Foster, N.R. (1985) *Lake trout reproductive behaviour: influence of chemosensory cues from young-of-the-year by-products.* Trans. Am. Fish. Soc., 114, 794–803.

Kawamura, T. (1985) *Social and reproductive behaviour of three mouthbrooding cardinal-fishes,* Apogon doederlini, A. niger *and* A. notatus. Environ. Biol. Fishes, 13, 17–24.

Lecchini, D. (2004) *Experimental assessment of sensory abilities of coral reef fish larvae in the detection of their settlement location.* C.R. Biologies, 327, 159–171.

Li, W., Scott, A.P., Siefkes, M.J., Yan, H., Liu, Q., Yun, S.S. and **Gage, D.A.** (2002) *Bile acid secreted by male sea lamprey that acts as a sex pheromone.* Science, 296, 138–141.

Li, W., Sorensen, P.W. and **Gallaher, D.D.** (1995) *The olfactory system of migratory adult sea lamprey (Petromyzon marinus) is specifically and acutely sensitive to unique bile acids released by conspecific larvae.* J. Gen. Physiol., 105, 569–587.

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

Marnane, M.J. and **Bellwood, D.R.** (2002) *Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia.* Mar. Ecol. Prog. Ser., 231, 261–268.

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

Olsén, K.H. (1987) *Chemoattraction of juvenile Arctic charr (Salvelinus alpinus (L.)) to water scented by intestinal content and urine.* Comp. Biochem. Physiol. A, 87, 641–643.

Sale, P.F. (1978) Reef Fishes and Other Vertebrates: A Comparison of Social Structures. John Wiley, New York.

Sand, O. and **Karlsen, H.E.** (1986) *Detection of infrasound by the Atlantic cod.* J. Exp. Biol., 125, 197–204.

Selset, F. (1980) *Chemical methods for fractionation of odorants produced by char smolts and tentative suggestions for pheromone origins.* Acta Physiol. Scand., 108, 97–103.

Selset, R. and **Døving, K.B.** (1980) *Behaviour of mature anadromous char (Salmo alpinus L.) towards odorants produced by smolts of their own population.* Acta Physiol. Scand., 108, 113–122.

Siegel, S. and **Castellan, N.J.** (1988) Nonparametric Statistics for the Behavioral Sciences, 2nd edn. McGraw-Hill International Editions. Statistics series, New York.

Sorensen, P.W., Fine, J.M., Dvornikovs, V., Jeffrey, C.S., Shao, F., Wang, J.Z., Vrieze, L.A., Anderson, K.R. and **Hoye, T.R.** (2005)

Mixture of new sulfated steroids functions as a migratory pheromone in the sea lamprey. Nat. Chem. Biol., 1, 324–328.

Stabell, O.B. (1984) *Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon.* Biol. Rev., 59, 333–388.

Stabell, O.B. (1987) *Intraspecific pheromone discrimination and substrate marking by Atlantic salmon parr.* J. Chem. Ecol., 13, 1625–1643.

Stobutzki, I.C. and **Bellwood, D.R.** (1997) *Sustained swimming abilities of the late pelagic stages of coral reef fishes.* Mar. Ecol. Prog. Ser., 149, 35–41.

Sweatman, H.P.A. (1983) *Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (Dascyllus aruanus and D. reticulatus) on coral reefs.* Mar. Biol., 75, 225–229.

Sweatman, H.P.A. (1985) *The influence of adults of some coral reef fishes on larval recruitment.* Ecol. Monogr., 55, 469–485.

Sweatman, H.P.A. (1988) *Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues.* J. Exp. Mar. Biol. Ecol., 124, 163–174.

Westerberg, H. (1982) *Ultrasonic tracking of Atlantic salmon (Salmo salar L.)*—II. Swimming depth and temperature stratification. Rep. Inst. Freshw. Res. Drottningholm, 60, 102–115.

Wisenden, B.D. (2001) *Learned recognition of novel predator odour by zebra danios, Danio rerio, following time-shifted presentation of alarm cue and predator odour.* Environ. Biol. Fishes, 61, 205–211.

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