

RESEARCH ARTICLE

Short-range homing in a site-specific fish: search and directed movements

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SUMMARY

Sedentary and territorial rockfish of the genus *Sebastes* exhibit distinctive homing ability and can travel back to an original location after displacements of metres or even kilometres. However, little is known about the behavioural and sensory mechanisms involved in homing. Although our previous study demonstrated that nocturnal black rockfish *Sebastes cheni* predominantly use their olfactory sense for homing from an unfamiliar area, the possibility of using landmarks in a familiar area cannot be discounted; i.e. site-specific fish are likely to use three-dimensional spatial memory for navigation and orientation. Using high-resolution acoustic telemetry, we investigated whether *S. cheni* exhibit distinctive homing paths. Results show that all of the eight rockfish increased their effort within a small area of an unfamiliar region around the release site just after displacement, suggesting that the rockfish probably searched for the homeward direction. The rockfish showed the search movement in the upstream and/or downstream direction, which did not lead home. Finally, after returning to their familiar area, the rockfish exhibited more directed movements with faster speeds at a shallower depth, which was similar to the depth utilised in daily life as well as that of the fish capture.

Key words: homing, site fidelity, migration, navigation, orientation, behavioural mechanism, olfaction, vision, acoustic telemetry.

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INTRODUCTION

How animals find their original habitat and natal home remains an unsolved mystery of animal behaviour. Homing likely increases the success of reproduction, foraging and predator avoidance, and might have evolved independently in many animals. Homing behaviour has been well studied in terrestrial animals (e.g. insects and birds). However, less is known of homing behaviour in marine animals (e.g. fishes). Some marine fish show strong homing ability and distinct site fidelity to their spawning sites and natal locations. Salmonids are well known to accomplish trans-oceanic navigation and return to their natal rivers for spawning (Hasler and Scholz, 1983; Dittman and Quinn, 1996; Døving and Stabell, 2003). Salmonids use home-stream odour for navigation during their final homing phase. In plaice (flatfish), homing and site fidelity to the spawning grounds have also been well documented. Plaice migrate between feeding grounds and spawning grounds, and selective tidal-stream transport is a key factor in their migratory mechanism (Metcalfé et al., 1990; Metcalfé et al., 1993; Arnold and Metcalfé, 1996). Attempts to explain homing navigation and orientation have spawned a large variety of proposals regarding the behavioural and sensory mechanisms involved. However, the long-distance migrations of fish make it difficult to observe homing behaviours in the sea.

In contrast to fish that show long-distance migration, some fish with a restricted home range exhibit short-range homing to a specific location, such as a shelter hole, burrow or nest (Dodson, 1988; Reese, 1989; Yoshiyama et al., 1992; Kaunda-Arara and Rose, 2004). For

example, butterflyfishes (Chaetodontidae) use coral patches as landmarks to navigate back to their specific location after their daily foraging trip (Reese, 1989). Additionally, the sculpin (*Oligocottus snyderi*, *O. maculosus* and *Clinocottus globiceps*) can return to their original tide pool after artificial displacement (Yoshiyama et al., 1992). Such homing after displacement of even kilometres to an unfamiliar area is well known in many fish species [e.g. rockfishes (Love et al., 2002) and the greasy grouper (Kaunda-Arara and Rose, 2004)]. Homing can occur regularly in natural environments as fish move far away from their habitats when searching for new feeding sites or habitats, and then subsequently return to their original location (Reese, 1989; Matthews, 1990a; Matthews, 1990b).

Rockfish of the genus *Sebastes*, which includes approximately 100 species (Jordan et al., 1930; Kendall, 1991), are well known for homing after displacement. It has been recognised since the 1970s that sedentary and territorial rockfishes can navigate home after being displaced (Carlson and Haight, 1972; Matthews, 1990a; Matthews, 1990b; Percy, 1992; Love et al., 2002; Mitamura et al., 2002; Reynolds et al., 2010). In the northeast Pacific Ocean, the yellowtail rockfish (*Sebastes flavidus*) returned home from as far as 22.5 km even after 6 months of captivity (Carlson and Haight, 1972). Additionally, copper (*S. caurinus*) and quillback (*S. maliger*) rockfishes homed to capture sites after displacements of 500 m (Matthews, 1990b). Rockfishes generally prefer relatively complex and high-relief reefs, and rockfish captured at such reefs tend to home back after displacement to a seemingly less suitable habitat (Matthews, 1990a). Although the homing, site fidelity and habitat

preferences of many rockfish species are well reported (Love et al., 2002; Lowe et al., 2009; Reynolds et al., 2010), less is known about the behavioural and sensory mechanisms that govern short-range homing (Love et al., 2002; Mitamura et al., 2005).

Black rockfish (*Sebastes cheni* Barsukov 1988) in the northwest Pacific Ocean are able to navigate back to their original habitat after 1–4 km displacements (Mitamura et al., 2002). This species grows relatively slowly, is long-lived and abundant in rocky areas, and is a typical site-specific fish that utilises a rock crevice or hole for shelter within a small home range (Mio, 1960; Harada, 1962; Hatanaka and Iizuka, 1962; Yokogawa et al., 1992; Numachi, 1971; Utagawa and Taniuchi, 1999; Mitamura et al., 2009). Our comparative study on the homing behaviour of vision-blocked and olfactory-ablated rockfish revealed that the rockfish primarily used olfaction to navigate back to their original habitat from outside the home range (Mitamura et al., 2005). Many researchers have examined how animals find and track odours (Moore et al., 1991; Zimmer-Faust et al., 1995; Vickers, 2000). Odour plumes are normally dispersed from a source across a large spatial scale, with the highest odour concentration at the odour source and decreasing concentrations with increasing distance from the source (Vickers, 2000). Once an odour plume is detected, an animal will follow the gradient of odour concentration to reach its goal. Therefore, after displacement to an unfamiliar area, animals using olfactory cues would search for an odour plume. At a local scale, odour plumes appear to be distributed along the direction of the water or wind current, even though this direction does not directly lead back to the odour source. Animals tend to show an up-current/upwind movement (Zimmer-Faust et al., 1995; Vickers, 2000) or a back-and-forth movement around their displacement site along a current/wind (Matthews, 1990b). The initial back-and-forth movement would reduce the chances that animals would lose their first position and fail during subsequent navigation and orientation (Matthews, 1990b). Therefore, we hypothesised that rockfish individuals, just after displacement to an unfamiliar area, would show upstream or back-and-forth movements to search for a familiar odour or stimulus. We predicted that during odour-searching behaviour, the rockfish would spend substantial time and effort around the displacement site. However, it is also predicted that site-specific fish species learn landmarks and use three-dimensional spatial memory for orientation and navigation within a familiar area (Dodson, 1988; Reese, 1989). It is thus possible that black rockfish use landmarks to navigate and orient themselves within a familiar area. The use of visual landmarks, in conjunction with olfaction, would allow a rockfish to exhibit better navigation and orientation to its specific location (e.g. shelter) within a familiar area. Therefore, perhaps the rockfish would exhibit more directed homing behaviour with greater speed after recognising a landmark because landmark navigation and orientation do not require the zigzag movement of odour-driven searching behaviour (Zimmer-Faust et al., 1995; Vickers, 2000). This prediction of the homing patterns of site-specific fish after displacement is empirically and theoretically based (Matthews, 1990b). However, to our knowledge, no studies have quantified the homing behaviour of site-specific fish, especially in three dimensions in a natural environment.

Here we aimed to determine whether individual black rockfish show homing behaviour after displacement to an unfamiliar area. Specific hypotheses were as follows: (1) individuals in an unfamiliar area exhibit search movements to detect their homeward direction, (2) the search movements are associated with the direction of the water current and (3) individuals exhibit more directed movements when encountering potential landmarks within their familiar area. We used high-resolution acoustic telemetry to monitor homing behaviour in three dimensions and apply path analyses of individuals.

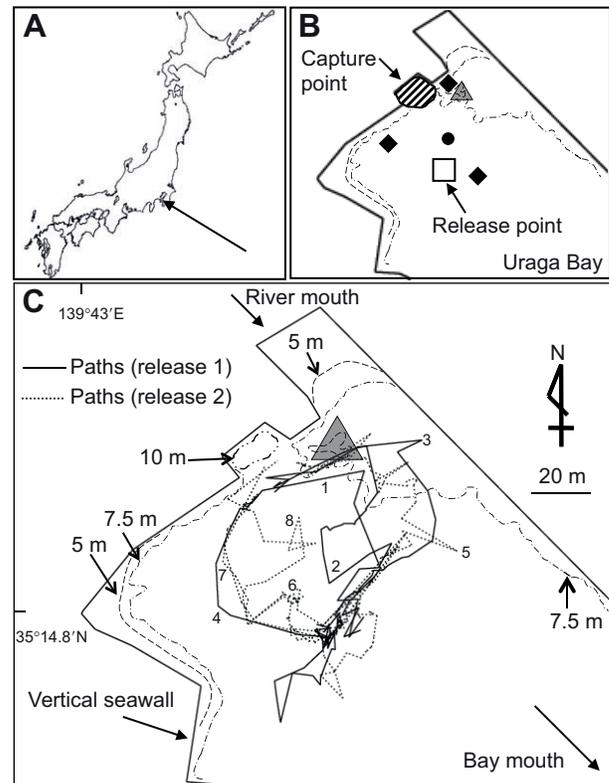


Fig. 1. Study area in Uruga Bay and homing paths. (A) Location of study area in Japan. (B) Shaded area, capture area; open square, release site; black diamonds, radio-linked acoustic positioning system (VRAP) buoy locations; black circle, point where the water current meter and calibration tag were deployed; grey triangle, rocky area. (C) Homing paths monitored by the VRAP system. Solid and dashed paths indicate those monitored in release experiments 1 and 2, respectively. The numbers near the paths indicate fish identification numbers. Dashed lines along the vertical wall in B and C indicate depth contours.

MATERIALS AND METHODS

Study site and water current

This study was conducted in Uruga Bay, Kanagawa Prefecture, Japan; the maximum bottom depth of the study area is approximately 10 m (Fig. 1). The circumference of the bay consists of vertical seawalls with an inlet in the innermost area. The sea bottom is flat and primarily mud, but there was a small rocky area approximately 15 m east of the capture point of *S. cheni* (Fig. 1). The maximum difference between low and high tide was approximately 1.5 m during the study period.

Water current direction and velocity were measured using a miniature electromagnetic current meter (Compact-EM, JFE-Advantech, Kobe, Japan; direction range: 0–360 deg, resolution: 0.01 deg, accuracy: ± 2 deg; speed resolution: 0.02 cm s^{-1} , speed accuracy: $\pm 1 \text{ cm s}^{-1}$ or $\pm 2\%$). The burst mode of the current meter was used to record water current. The burst mode was programmed to record a single datum every 10 min as an average of 30 successive data points at 1 s intervals. The current meter was deployed between the points of fish capture and release, above the sea bottom (Fig. 1).

Fish tagging and monitoring system

The black rockfish, Shiro-Mebaru, was described as *S. inermis* in our previous papers (Mitamura et al., 2002; Mitamura et al., 2005;

Table 1. Tagged black rockfish *Sebastes cheni* descriptive characteristics and homing behaviour

| Fish ID | Total length (mm) | Body mass (g) | Tagging date | Release date | Tag frequency (kHz) | Homing duration (min) | Number of data points |
|---------|-------------------|---------------|--------------|--------------|---------------------|-----------------------|-----------------------|
| 1 | 205 | 155 | 4 June | 5 June | 63 | 27 | 12 |
| 2 | 228 | 202 | 4 June | 5 June | 75 | 67 | 31 |
| 3 | 200 | 136 | 4 June | 5 June | 78 | 132 | 60 |
| 4 | 193 | 116 | 4 June | 5 June | 81 | 76 | 34 |
| 5 | 225 | 186 | 13 June | 16 June | 63 | 308 | 51 |
| 6 | 208 | 146 | 13 June | 16 June | 75 | 149 | 54 |
| 7 | 210 | 166 | 13 June | 16 June | 78 | 49 | 13 |
| 8 | 203 | 146 | 13 June | 16 June | 81 | 68 | 22 |

Mitamura et al., 2009). Recently, however, the species has been separated into three distinct species (Kai and Nakabo, 2008), and our target species has been named *S. cheni*. Black rockfish were collected from depths of 3–7 m by angling on 4 and 13 June 2008 (Table 1). The fish inhabit relatively shallow depths; they were brought to the surface slowly to minimise barotrauma and then moved to a 60 l holding tank 4–5 h before surgery. All of the fish were greater than 190 mm in total length (TL) and were considered to be more than 2 years old and therefore mature (Mio, 1960). The sexes of the fish were unknown because of the difficulty of identifying external sex characteristics.

An ultrasonic pressure-sensitive transmitter (V9P-1H, Vemco, Halifax, NS, Canada; diameter 9 mm, length 40 mm, mass 2.7 g in water, output 150 dB, depth accuracy ± 0.2 m) was used for each fish. The transmitters have four different frequencies (63, 75, 78 and 81 kHz; Table 1), and transmit a signal every 2 s. The transmitter was programmed to stop after 11 days. The transmitter was implanted surgically into the peritoneal cavity of the fish under anaesthesia induced using 0.1% 2-phenoxyethanol (Mitamura et al., 2002). The fish were then returned to a holding tank containing fresh bubbling seawater from the vicinity of their capture site for recovery. A recovery period of 1–3 days was allowed prior to release. No mortalities occurred during implantation. The mass of the transmitter in water was, on average, 1.8% of the fish mass (range: 1.3–2.3%). Preliminary experiments using dummy transmitters demonstrated that intraperitoneal implantation had no discernible effects on feeding or swimming behaviour over a period of approximately 1 month.

All four fish were released at high tide approximately 70 m away from their capture points on 5 and 16 June 2008 (Table 1, Fig. 1). The release site was assumed to be outside of the fishes' home range because the black rockfish normally inhabits complex rocky areas, and the sea bottom at the release site was muddy and flat. There were no apparent potential landmarks around the release site to aid in locating the original capture site. We are confident that the experimental procedure did not disturb the habitat of the fish and that any distress to the fish was minimal.

A radio-linked acoustic positioning system (VRAP, Vemco) was used to monitor the fish after release. The system consists of three acoustic-radio buoys and a base station controlled by a computer. This system accurately provides the horizontal position (accuracy: < 2 m) and the depth of a transmitter (Klimley et al., 2001; Zamora and Moreno-Amich, 2002). The three buoys of the VRAP system were deployed using mooring lines and anchors in a triangular configuration, approximately 90 m apart, surrounding both the capture point and the release site. Tidal currents caused the position of the buoys to change at the surface over the tidal cycle. As the relative position of a transmitter is decided by the relative positions of the buoys at the surface, the relative position of a transmitter shifts with the tidal current. To correct the positions of the

transmitters, a calibration transmitter (V42-9VR, Vemco; frequency 69 kHz, output 164 dB), which transmitted a signal every second, was deployed in a known location on the sea bottom within the study area (Fig. 1). When processing the collected data, the data collected from the calibration transmitter were used to adjust the positions of the fish transmitters.

Outliers and spurious points were removed from the data recorded by the VRAP system. The data set was filtered using the maximum swimming speed of the fish (Parsons et al., 2003). A conservative value of 10 times the steady speed (1 TL s^{-1}) of each fish was defined as the limitation for outliers in this study. This algorithm was able to remove a small number of outliers and spurious points distorted by background noise and/or a multi-path acoustic signal.

The VRAP system was programmed to automatically search (listen) for each transmitter frequency every 10 s, and took approximately 50–60 s to listen for all five transmitters, including the single calibration transmitter. Theoretically, for each listening period, at most five pulses from each transmitter (at 2 s intervals) were detected by the VRAP system. However, the number of recorded pulses varied (0–5) because the acoustic and radio signals between the buoys and the base station were blocked or distorted by background noise. The positions of the pulses detected for each listening period were converted to an average position. Thus, an average position for each listening period was fixed every 1 min at most. The mean number of fixed positions was $37 \pm 11\%$ of the total listening periods during the homing period (Table 1). For example, the number of recorded positions for fish ID 1 was 12 (44%) during its 27 min homing. The mean distance between two successive average positions (data points) for all fish was 7.9 ± 2.8 m. Homing paths were created based on the data points, and the distances travelled and movement speeds were calculated. The significance level was established at $P < 0.05$ for each test type. The data are presented as means \pm s.d.

Analysis of movement patterns just after release

We predicted that fish would increase the time and effort spent searching for the direction of their original habitat immediately after displacement from the capture point. To test this hypothesis, the search effort within a given area along the path was measured using a first-passage time (FPT) analysis following Fauchald and Tveraa (Fauchald and Tveraa, 2003). The FPT analysis is based on calculation of the time required for an individual to cross a circle of a given radius. Calculations of FPT are repeated along each movement path by moving the circle at a given distance, and for increasing radii. Then, FPT can represent a scale-dependent measure of search effort. Furthermore, the analysis allows us to determine the spatial scale, called the area-restricted search (ARS) zone, at which an individual increases search effort. The analysis does not assume any specific movement and can be applied to any animal's movement path. In the analysis, all paths were

systematically discretised with a constant step length of 5 m because the original data might have included errors in horizontal position (<2 m). This was performed to represent the paths as sequences of steps with an equivalent weight (Bovet and Benhamou, 1988). FPT was calculated at every point along each path for radii ranging from 5 to 40 m in 5 m increments. The relative variance $S(r)$ in FPT was calculated as a function of radius r . This variance is given by $\text{Var}\{\log[t(r)]\}$, where $t(r)$ is the FPT for a circle of radius r and is log-transformed to let the variance $S(r)$ be independent of the magnitude of the mean FPT (Fauchald and Tveraa, 2003). $S(r)$ in relation to values of r ranging from 5 to 40 was then plotted. A peak in the relative variance $S(r)$ indicates the scale at which an animal exhibits an ARS.

The movement direction of each fish in relation to the tidal current just after release was investigated. Six (75%) of eight fish exhibited ARS patterns, and the mean FPT was $78 \pm 9.2\%$ of the homing duration. Therefore, the movement directions of all eight fish within the first 25, 50 and 75% of each homing period were analysed. Data for the water current direction during the first 90 min after each release were used, because all of the fish were likely to be within the zones during this time period (Table 2). The null hypothesis that the tidal current direction was normally distributed was evaluated using a Rayleigh test (Zar, 1996). Subsequently, the distribution of step orientation for each fish was computed for each period. We tested the null hypothesis that, for each duration, the movement direction relative to the current direction was normally distributed (Zar, 1996). The data were normalised such that the water current direction was 0 deg. The Rayleigh test was used if the distribution was monomodal; otherwise, the Rao spacing test was used (Zar, 1996). The distribution was monomodal if the fish oriented down-current (e.g. ID 3), whereas it was not monomodal if the fish showed back-and-forth movements along the water current direction while gradually moving towards the goal (e.g. ID 2).

Analysis of final directed homing

A fish is able to show more straight-line homing to its original location if it is able to find a known and familiar landmark with which to orient itself. Thus, whether the particular point at which a fish started to exhibit directed movement is located inside its home range – and furthermore, near a rocky area with a distinctive feature – is crucial to understanding fish homing mechanisms. In this study, a backward path analysis was used to define a straight-homing start point during the homing behaviour (for details, see Girard et al., 2004). This individual path analysis uses a straightness index: as the fish moves backward along the movement path from the end point (in this study, the goal in the original location), the backward beeline distance (BD) between the goal and the present point is measured at any given location of the fish. The backward path length (BL), the path length between the goal and the present point, is also measured. Then, the straightness index is computed as the ratio $\text{BD}:\text{BL}$ measured at any location. If an animal orients itself, the evolution of the straightness index while moving backward should show a linear relationship. In contrast, if an animal moves at random, the evolution should, on average, fit a square-root relationship (Bovet and Benhamou, 1988). For this analysis, the interpolated data for the FPT analysis were used. The point at which the curve shifted from a linear to a non-linear relationship was visually determined (Girard et al., 2004), and was defined as a straight-homing start point. The slope of the linear relationship measures the orientation efficiency during straight homing. There appears to be some subjectivity in determining this particular point. Therefore, to

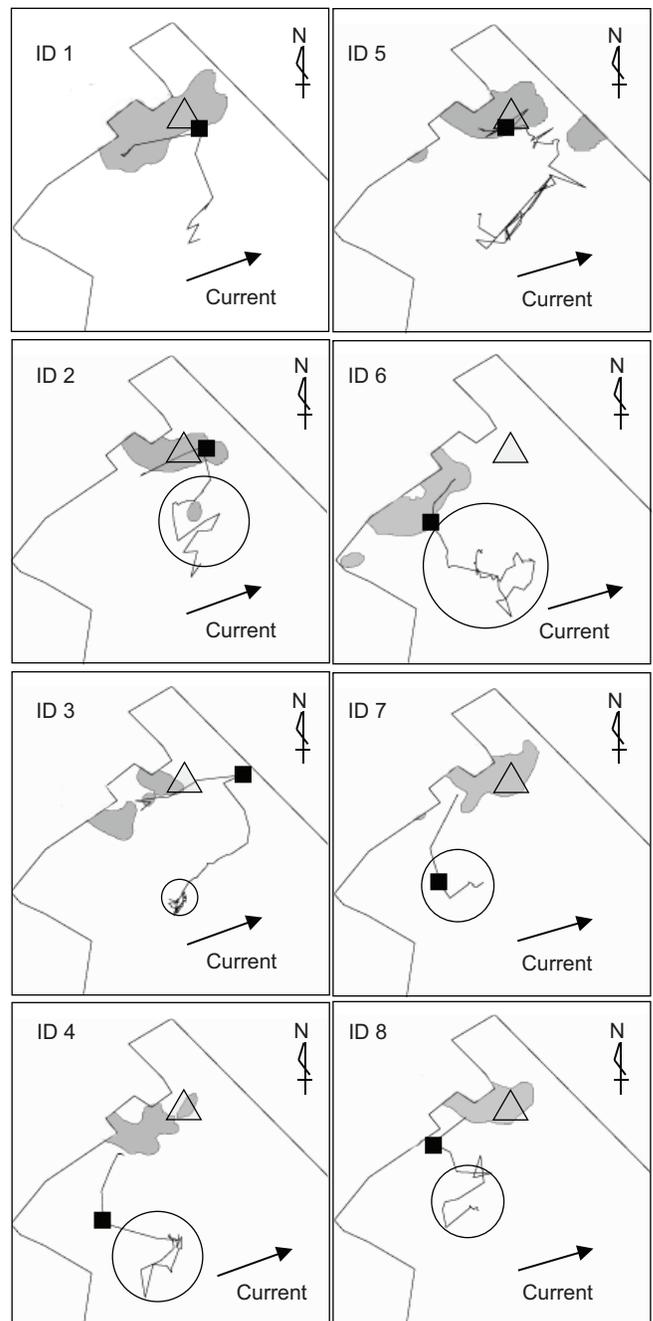


Fig. 2. Homing paths of eight black rockfish. Six circles on homing paths indicate the areas where the rockfish exhibited area-restricted search (ARS) patterns, determined by the first-passage time (FPT) analysis. Nested ARS patterns were not detected. The ARS zones were within a muddy area and were outside the home range. The eight black squares on the homing paths indicate the straight-homing starting points as determined by the backward path analysis. Shaded polygons along the vertical wall indicate the home range (95% usage) of each rockfish, estimated by the fixed kernel density method. Triangles indicate rocky areas.

validate our analysis, the sums of the residual squares in the regression analyses with an intercept fixed at 0 (linear *versus* square-root relationship, least-square method) were used to evaluate which relationship fitted the movement during straight homing. This analysis suggested that no orientation mechanism was involved (Benhamou and Bovet, 1992).

Table 2. Homing behaviour of *S. cheni* analysed by first-passage time (FPT) analysis and backward path analysis

| Fish ID | Radius of ARS zone (m) | Frequency of FPT (%) | Swimming depth in ARS zone (m) | Orientation distance (m) | Orientation efficiency | Distance travelled (m) |
|---------|------------------------|----------------------|--------------------------------|--------------------------|------------------------|------------------------|
| 1 | n/a | n/a | 10.2±0.2 | 45 | 0.97 | 148 |
| 2 | 25 | 76 | 10.5±1.0 | 40 | 0.99 | 208 |
| 3 | 10 | 64 | 10.6±0.5 | 60 | 0.98 | 301 |
| 4 | 25 | 83 | 10.9±0.4 | 45 | 0.93 | 219 |
| 5 | n/a | n/a | 5.6±3.4 | 15 | 0.98 | 504 |
| 6 | 35 | 91 | 9.0±2.2 | 40 | 0.94 | 258 |
| 7 | 20 | 82 | 10.7±0.2 | 60 | 0.92 | 94 |
| 8 | 20 | 74 | 10.0±0.9 | 20 | 0.97 | 178 |
| Mean | 23±8.2 | 78±9.2 | 9.7±1.7 | 41±16 | 0.96±0.03 | 239±125 |

ARS, the area restricted search calculated by the FPT analysis.

For the two fish that showed no ARS pattern, swimming depths during the first 75% of homing duration are provided.

The frequency of FPT indicates the frequency of time spent within the ARS zone relative to the homing duration.

Orientation distance indicates the distance between the original location and where the fish began straight-homing measured *via* backward path analysis.

Home range estimation

Knowledge of whether fish visited a straight-homing start point and release site is crucial when evaluating the homing mechanism of the fish. The home range after homing for each fish was estimated using smoothed location data with the fixed kernel density method utilising animal movement (US Geological Survey, Reston, VA, USA) and ArcView version 3.1 geographic information system software (ESRI, Redlands, CA, USA). Fixed kernel home ranges were calculated with least-squares cross validation as the bandwidth. The kernel utilisation distribution is a probability distribution that represents the area where there is a 95% chance of detecting a monitored fish. A 95% utilisation distribution was used to estimate the overall home range.

RESULTS

All of the rockfish homed to the capture site after their displacement, and we monitored around the capture point until the end of each monitoring period. The mean homing time was 110±90 min ($N=8$). None of the rockfish exhibited a straight-line homing pattern (Fig. 1). Immediately after release, the rockfish moved in the downstream or upstream direction around the release site, then appeared to determine the goal direction, and eventually reached their original location. The home ranges of the fish after homing were restricted and were associated with the vertical wall and the rocky area (Fig. 2). Black rockfish generally inhabit rocky areas, which they rarely leave (Harada, 1962; Shinomiya and Ezaki, 1991; Mitamura et al., 2009). These results suggest that the release site was indeed outside the home ranges of the fish, or at least was rarely visited by the rockfish.

According to FPT analysis, peaks of $S(r)$ plotted as a function of r indicated that six (75%) of the fish exhibited an ARS pattern (Table 2), and nested ARS patterns were not observed. The mean spatial scale at which an ARS pattern was exhibited was 23±8.2 m ($N=6$; Fig. 3). The ARS zones were located in muddy areas. The ARS zones were either located in or close to the release site (Fig. 2). The rockfish spent a mean of 78±8.2% ($N=6$) of their homing duration within the ARS zone. No rockfish exhibited active vertical movement, as all fish stayed near the bottom around the release site (Table 2). The mean swimming depth was 10.3±0.7 m for the six rockfish within the ARS zones (Table 2). These results indicate that the intensive effort of the rockfish was near the muddy bottom around the release site.

The rockfish showed movements in relation to the water current within the ARS zones after release (Figs 2, 4). The water current appeared to be directed with low velocity (release 1: mean angle, 70 deg, Rayleigh test: $z=3.2$, $r=0.6$, $N=9$, $P<0.05$, mean velocity,

1.4±0.3 cm s⁻¹; release 2: mean angle, 74 deg, Rayleigh test: $z=0.83$, $r=0.3$, $N=9$, $P=0.45$, mean velocity, 1.7±0.3 cm s⁻¹; Fig. 4). For 25, 50 or 75% of each homing duration, seven (88%) of the eight fish exhibited directed movement in relation to the water current (Rayleigh test: $P<0.05$; Rao spacing test, $P<0.05$; Table 3).

The fish finally homed in a straight line to the original location from a particular point. The evolution of the BD in relation to the BL showed a linear relationship for each fish. This indicates that the fish oriented themselves to the goal from a particular point. The particular point at which the fish started straight homing was on average 41±16 m ($N=8$) away from the location of the original capture point (Fig. 2, Table 2). The regression analysis showed that the sum of the residual squares for each fish was much smaller for a linear regression than for a square root regression. This indicates that the fish movement was directed and not random. The linear regression analysis also showed that the coefficient of determination (r^2) for the linearity was 0.99. This high value further suggests that

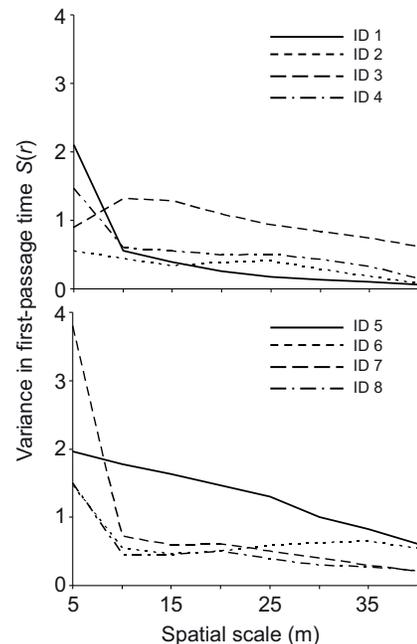


Fig. 3. Variance in FPT analysis, $S(r)$, as a function of radius r for the homing paths of eight black rockfish. Six of eight rockfish exhibited ARS patterns.

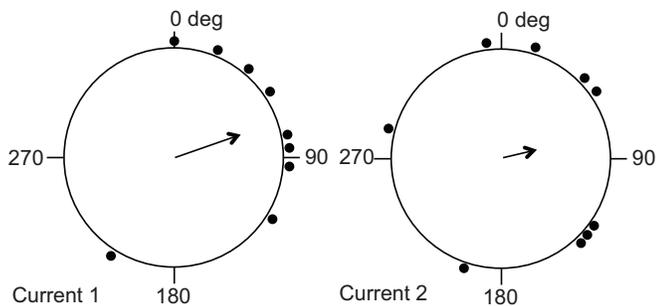


Fig. 4. Circular distributions of water current directions for the first 90 min after fish release. Black circles indicate the water current direction for each 10 min interval. Currents 1 and 2: currents in release experiments 1 and 2, respectively. Mean angles (arrows): 70 deg in experiment 1 (Rayleigh test, $P < 0.05$) and 74 deg in experiment 2 (Rayleigh test, $P = 0.45$).

the fish exhibited active orientation to the original location for the final phase of their homing. The mean orientation efficiency was 0.96 ± 0.03 ($N = 8$). Five (63%) of the eight straight-homing start points were clearly associated with the rocky area or the vertical wall (Fig. 2). The three remaining points were located in a muddy area.

In addition to the differences in movement tortuosity, the fish exhibited different movement speeds and swimming depths around the straight-homing start point. The fish swam at a significantly shallower depth after passing through the straight-homing start point (after: 5.8 ± 2.3 m, range: 1.7–8.5 m; before: 9.4 ± 1.6 m, range: 5.6–10.8 m; paired t -test: $t = 7.1$, $N = 8$, $P < 0.05$; Fig. 5). The fish also showed significantly faster movement after the straight-homing start point (after: 0.36 ± 0.2 TL s^{-1} ; before: 0.21 ± 0.08 TL s^{-1} ; paired t -test:

$t = 2.0$, $N = 8$, $P < 0.05$; Fig. 5). The fish primarily utilised relatively shallow depths after their homing in this study area (Fig. 6). These are similar to the swimming depths after the straight-homing start point during their homing and to the depth of capture.

DISCUSSION

The black rockfish exhibited homing behaviour to the original location from an unfamiliar area. The homing paths are consistent with our hypotheses. Our first specific hypothesis was that individuals in an unfamiliar area would exhibit search movements to detect their homeward direction. The rockfish increased their effort in searching for their original location just after release. Six of the eight rockfish showed ARS patterns, and the ARS zones were located either in or close to the release site. These six rockfish spent an average of 78% of their homing duration within the ARS zones, and the two remaining rockfish that did not exhibit ARS patterns also spent most of their time around the release site just after release. These observations suggest that the rockfish probably did not locate their goal just after release, and spent much time and effort searching for their homeward direction. The spatial scale of the ARS zones was relatively small (23 m on average), and within this small space, the rockfish increased their effort and roughly determined the homeward direction. This ability to detect the homeward direction within the small space of an unfamiliar area was surprising. Carlson et al. (Carlson et al., 1995) suggested that behaviour just after displacement plays a key role in rockfish homing. Using both acoustic telemetry and SCUBA observations, they found that yellowtail rockfish exhibited 3-m-wide circling behaviour immediately after displacement, which is similar to observed circling behaviour in avian homing (Carlson et al., 1995).

Within the ARS zones, the rockfish showed upstream, downstream and back-and-forth movements. These initial

Table 3. Distributions of horizontal movement directions relative to water current direction during the first 25, 50 and 75% of the homing duration

| Fish | Duration | Mean angle (deg) | Length (r) | Test statistic | P | No. of data points |
|------|----------|------------------|------------|----------------|------------------|--------------------|
| ID 1 | 25% | n/a | – | – | – | 3 |
| | 50% | 298 | 0.52 | RS, $u = 218$ | < 0.01 | 7 |
| | 75% | 287 | 0.71 | R, $z = 7.1$ | < 0.01 | 14 |
| ID 2 | 25% | 253 | 0.25 | RS, $u = 170$ | < 0.05 | 15 |
| | 50% | 263 | 0.39 | RS, $u = 167$ | < 0.05 | 19 |
| | 75% | 279 | 0.35 | RS, $u = 160$ | $0.1 > P > 0.05$ | 21 |
| ID 3 | 25% | n/a | – | – | – | 3 |
| | 50% | 73 | 0.18 | RS, $u = 92$ | > 0.5 | 7 |
| | 75% | 339 | 0.46 | R, $z = 3$ | < 0.05 | 14 |
| ID 4 | 25% | n/a | – | – | – | 2 |
| | 50% | 122 | 0.66 | RS, $u = 141$ | > 0.1 | 5 |
| | 75% | 147 | 0.05 | RS, $u = 186$ | < 0.01 | 19 |
| ID 5 | 25% | 11 | 0.14 | RS, $u = 232$ | < 0.01 | 38 |
| | 50% | 316 | 0.17 | RS, $u = 213$ | < 0.01 | 63 |
| | 75% | 298 | 0.13 | RS, $u = 209$ | < 0.01 | 75 |
| ID 6 | 25% | n/a | – | – | – | 1 |
| | 50% | 45 | 0.50 | R, $z = 2$ | > 0.1 | 8 |
| | 75% | 78 | 0.37 | R, $z = 2.3$ | $0.1 > P > 0.05$ | 17 |
| ID 7 | 25% | n/a | – | – | – | 1 |
| | 50% | n/a | – | – | – | 1 |
| | 75% | 171 | 0.88 | R, $z = 3.8$ | < 0.05 | 5 |
| ID 8 | 25% | n/a | – | – | – | 0 |
| | 50% | n/a | – | – | – | 2 |
| | 75% | 292 | 0.34 | RS, $u = 177$ | < 0.05 | 13 |

The data were normalised such that the water current direction was 0 deg in each release.

n/a indicates that there were too few data points to test.

Length indicates the length of the mean vector, measured as r, the concentration of movement directions relative to the water current direction.

The Rayleigh (R) test was used when the distribution was monomodal. The Rao Spacing (RS) test was used when the distribution was not monomodal.

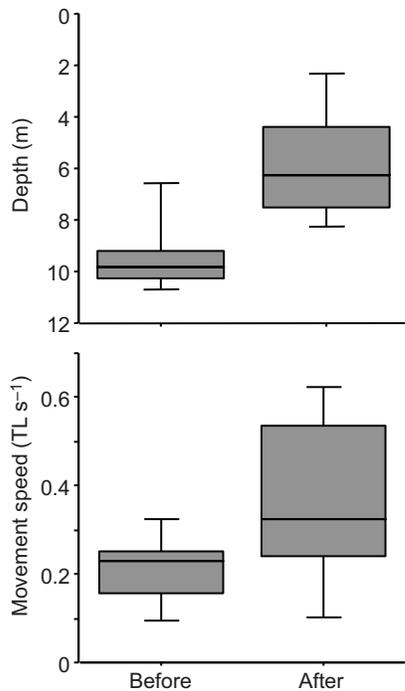


Fig. 5. Box plots of swimming depths and movement speeds around the straight-homing start point. Before and after indicate the periods before and after fish visited the straight-homing start point, respectively. Box plots represent the median (horizontal line), 10th and 90th percentiles (bar), and 25th and 75th percentiles (box).

movements were not random, but were oriented to the water current, which did not lead directly home. The back-and-forth movements would prevent the rockfish from losing track of their first position and therefore making errors in subsequent navigation and orientation (Matthews, 1990b). These results are consistent with our second hypothesis, that the initial search movements are associated with the direction of the water current. Our previous study showed that olfaction-ablated rockfish that were displaced to an unfamiliar area either did not home or strayed, suggesting that in an unfamiliar area rockfish use olfactory cues for homing (Mitamura et al., 2005). Homing salmon using olfactory cues move up and down in depth across the halocline to search for the odour plume of their natal river (Døving et al., 1985). However, in the present study, the rockfish spent their time near the sea bottom (9.4 ± 1.6 m in depth) around the release site because they did not inhabit the river but areas surrounding the sea wall, and the freshwater of the river did not play a role as a homing cue. Odour plumes are normally dispersed from a source across a large spatial scale, with the highest odour concentration at the odour source and decreasing concentrations with increasing distance from the source (Vickers, 2000). However, at a local scale, odour dispersal is complicated and there may be several local-scale currents. Around the release site, odours are probably distributed along the water current. Either upstream movement or back-and-forth movement in the current direction would maximise the likelihood of detecting an odour plume. If the rockfish find another local-scale current with higher odour concentration while moving downstream, they would follow the gradient and eventually reach the goal. Thus, in this study, the rockfish may have been searching for odours that indicated the homeward direction as they showed upstream and downstream movements. The water current velocity in both release experiments

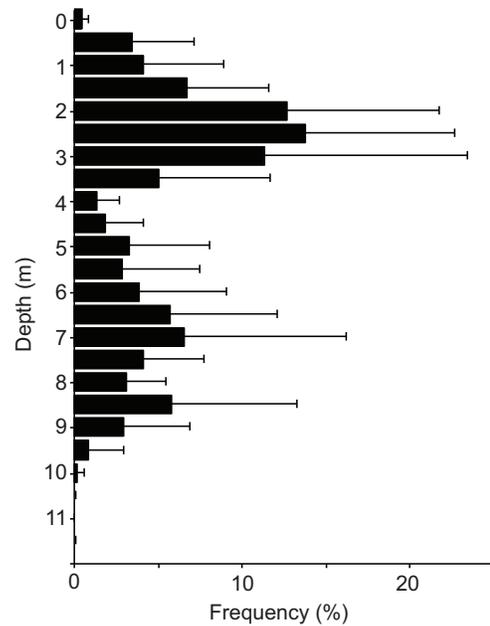


Fig. 6. Distribution of swimming depths for eight rockfish after homing. Error bars indicate standard deviation.

was low; however, the rockfish were still able to detect the homeward direction. Matthews reported that copper and quillback rockfishes were found along the water current after displacement of 500 m (Matthews, 1990b). Another study reported that black rockfish were distributed along the water current soon after displacement by 1–4 km (Mitamura et al., 2002). Our findings are consistent with these previous studies, although the direction and velocity of the water current were not directly measured in the previous studies. The use of olfaction to identify a location has been demonstrated in site-specific fishes (Sweatman, 1988; Døving et al., 2006). For example, in cardinalfish, a conspecific olfactory signal can be used for homing (Døving et al., 2006). However, it is unclear what olfactory cues the black rockfish uses. We previously hypothesised three types of olfactory cues for site-specific fish: a characteristic habitat olfaction, a substance olfaction (for example, urine used as individual markers), and an olfactory cue provided by conspecifics inhabiting the same habitat (Mitamura et al., 2005). However, the possibility remains that the rockfish uses topography or magnetic coordinates, as has been shown in other fish species (Walker et al., 1997). During the final phase of homing, the rockfish exhibited a different behavioural movement: all rockfish demonstrated directed movement to the original location during the final phase, which was in contrast to the initial movements. According to the backward path analysis, most (63%) of the rockfish showed directed movement after encountering the rocky area or the vertical wall, whereas the remaining rockfish (37%) started to home in a straight line within the muddy areas. The orientation efficiency of all fish during the final phase calculated by the backward path analysis was 0.97 on average, suggesting that homing behaviour during the final phase involved relatively linear movement. These results are consistent with our third hypothesis, that individuals exhibit more directed movements within their familiar area.

In this study, all rockfish moved relatively quickly and at relatively shallow depths after the straight-homing start point. The high speeds and linear movements indicate that the rockfish showed

much better navigation and orientation after the straight-homing start point. The rocky area and the vertical wall probably triggered better navigation and orientation of the rockfish. Site-specific fish are likely to learn visual landmarks because they inhabit a restricted area with distinctive features (Dodson, 1988; Reese, 1989), and many fish species are able to use landmarks as goal-directing cues (Braithwaite et al., 1996; Odling-Smee and Braithwaite, 2003). For example, butterflyfish are capable of spatial cognition, and can follow coral outcrops while foraging (Reese, 1989). The sedentary black rockfish probably learn distinctive features as landmarks within a restricted home range and use them as visual cues for returning to their original location in daily life. The straight-homing start points of three rockfish were within muddy areas. These three rockfish might have continued to rely primarily on olfaction cues even during the final phase of homing. It is also possible that there were small landmarks that we did not recognise, which enabled the fish to locate home. In this study, four of eight straight-homing start points were outside the estimated home ranges. In general, black rockfish inhabit small, rocky areas (Harada, 1962; Shinomiya and Ezaki, 1991). The home ranges predicted here were characterised as rocky areas with a vertical wall. However, the home ranges were estimated with data comprising up to 10 days of monitoring, which may be insufficient. Rockfish occasionally exhibit exploratory movement to an unfamiliar area far from their home range to search for new feeding sites or habitats (Matthews, 1990b). During exploratory movement, rockfish may memorise landmarks in the area adjacent to their home range. Such landmarks, which are rarely used in daily life, may have helped the rockfish to find home in this study.

The rockfish changed swimming depth during homing. Just after release, intensive search efforts were made near the bottom, where the probability of finding landmarks is higher than in the middle and surface layers. We also cannot discount the possibility that the rockfish avoided predation risk by staying near the bottom. The rockfish then moved to shallower depths during the final phase of homing. Generally, black rockfish feed on small pelagic fish at shallow depths as well as on benthic crustaceans near the bottom (Harada, 1962; Yokogawa and Iguchi, 1992). The shallower swimming depth during the final phase was consistent with the depth utilised in daily life and the depth of the fish capture (Fig. 6). Indeed, during the study period, rockfish with external identification tags were occasionally observed swimming between the surface and depths of a few metres. These observations suggest that rockfish home to an original location using a familiar depth, and may also follow a familiar path. The average orientation distance was 41 m. Even in such a large area, black rockfish appear to have a three-dimensional spatial map and use visual landmarks for navigation and orientation. However, it is also possible that vision is restricted under low light conditions at night. Therefore, a combination of vision and olfaction, which can be used in the dark, may have evolved for homing in nocturnal sedentary black rockfish.

We found that black rockfish spent much time and increased effort within a small area of an unfamiliar region around release sites just after displacement, suggesting that the rockfish were searching for the homeward direction. The search movement was related to the water current, the direction of which did not directly lead to the goal. The rockfish eventually exhibited relatively quick, directed homing at somewhat shallow, familiar depths. Therefore, it is likely that rockfish effectively use both olfaction and vision for short-range homing. Little attention has been paid to the behavioural and sensory mechanisms involved in site-specific fish homing. Our findings provide the first quantitative support of the homing behaviour of site-specific fish.

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