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Goldsinny wrasse (*Ctenolabrus rupestris*) have a sex-dependent magnetic compass for maintaining site fidelity

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Abstract

The goldsinny wrasse (*Ctenolabrus rupestris*) is a commercially important fish that inhabits coastal areas across the eastern Atlantic. This species moves from a shallow home territory along the coast into deeper waters in the autumn and winter and then returns to that same territory in the spring. Only male goldsinny wrasse exhibit strong territorial behavior, which may manifest as sexual differences in the ability or motivation to return to home territories. The orientation mechanism underlying the homing migration of goldsinny wrasse males and females is unknown. In this study, we hypothesized that goldsinny wrasse use the magnetic field of the Earth to follow a compass-based path toward their home territory. To test this hypothesis, we collected 50 adult goldsinny wrasse, approximately half males and half females, in a harbor in Austevoll, Norway. Fish were translocated to a magnetoreception laboratory situated north of the site of capture, in which the magnetic field was artificially rotated. In the laboratory, males oriented toward the magnetic south taking a mean direction of 201°, which is the approximate direction that they would have had to take to return to the site at which they were captured. Females oriented in random magnetic directions. There was no difference in swimming kinematics between males and females. These results show that male goldsinny wrasse have a magnetic compass that they could use to maintain site fidelity, an ability that could help them and other coastal fish undertake repeatable short-range migrations.

KEYWORDS
cleaner fish, homing, magnetic sense, orientation

1 | INTRODUCTION

Wrasse (Labridae family) are coastal fish that are widespread in the Atlantic, Pacific, and Indian oceans (Helfman et al., 2009). Wrasse exhibit complex species- and sex-specific social, reproductive, and small-scale movement behavior (Donaldson, 1995; Hilldén, 1981). Some species of wrasse undertake facultative parasite-cleaning behavior when they are near larger fish (Costello & Bjordal, 1990;

Hilldén, 1983). As a result, wild-caught wrasse have been used in salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) aquaculture as cleaner fish to reduce infestations of the copepod ectoparasite *Lepeophtheirus salmonis* (Costello, 2009; Costello & Bjordal, 1990). The demand for wild-caught cleaner fish has driven the development and expansion of a lucrative commercial fishery (Halvorsen et al., 2020; Skiftesvik et al., 2014). Among the wrasse species present in Norway, goldsinny wrasse (*Ctenolabrus rupestris*) is one of the most abundant and is widely used as a cleaner fish (Skiftesvik et al., 2015). Understanding the movement and reproductive ecology of goldsinny wrasse will inform the management of the fishery, in particular the practice of fishers translocating and discarding wrasses that are too small to be used as cleaner fish (Halvorsen et al., 2021).

Goldsinny are among the most territorial of the wrasses, and there are distinct genetic populations in Europe (Jansson et al., 2020), as well as along the Norwegian coast (Sundt & Jørstad, 1998). Goldsinny wrasse typically occupy territories characterized by relatively turbulent water movement (Gjøsaeter, 2010). This is because wave motion and water circulation influence benthic algal cover, which is correlated with the availability of shelters (Gaylord et al., 1994), the benthic invertebrate community, and food supply (Skiftesvik et al., 2015; Smetacek, 1984). Goldsinny wrasse also exhibit sex-dependent differences in behavior. The males occupy a small territory (0.5–10 m^2) in shallow water (0–50 m) with a shelter at its center. Females stay near the territory of the male with which they spawn (Davies & Sheehan, 2019; Hilldén, 1981). Males continuously patrol their territory to defend it from other males and almost never leave it, except for brief forays of a few seconds (Hilldén, 1981).

Goldsinny wrasse vacate their territories in autumn and undertake small-scale seasonal migrations from summer territories in shallow water toward deeper water in the winter (Halvorsen et al., 2021; Hilldén, 1981; Skiftesvik et al., 2015). This vertical movement is associated with seasonal changes in surface water temperature, which is an important driver of vertical distribution in wrasse species located in temperate areas such as the Norwegian coast (Freitas et al., 2021). In situ observations conducted over a period of 3 consecutive years by scuba divers and using observation rafts show that in the spring, the males return to the same territory that they left in the autumn (Hilldén, 1981). Although the general characteristics of their seasonal movements have been described, the orientation mechanism that guides goldsinny wrasse to their home territory during migration or translocation is unknown.

Many species of fish use the Earth's magnetic field as a compass cue to guide their short- and long-distance movements and migration (Bottesch et al., 2016; Cresci, Paris, et al., 2019; Durif et al., 2013; Quinn, 1980). We tested the hypothesis that goldsinny wrasse use a magnetic compass to guide their return to their home territory during seasonal migration or translocation and that this ability underlies their high site fidelity. To explore this hypothesis, we translocated adult goldsinny wrasse and tested their orientation abilities under artificially rotated magnetic fields.

2 | METHODS

2.1 | Experimental animals

Adult goldsinny wrasse ($N = 50$, 10–12 cm total length) were collected in a small harbor (60.085 N, 5.261 E) located in the Austevoll archipelago, Norway (Figure 1). Fish were collected between 19 and 22 October 2020 using standard wrasse pots baited with 40–80 g frozen prawns *Pandalus borealis* (pots were two chambered, 70 × 40 × 28 cm, 11 mm mesh size, 60 × 90 mm elliptical entrances, 12 mm wide escape openings). After capture, fish were maintained in a submerged net in the same location where they were captured. Fish were fed with frozen prawns during the period of captivity (minimum 1 day and up to 4 days). Sex was determined visually as males have distinctive red spots in the abdominal region (Hilldén, 1981). The size of the fish was measured after they were tested using a measuring tape inserted into a halved PVC pipe.

2.2 | Compass orientation experiments in the MagLab

The main hypothesis tested in this study is that goldsinny wrasse translocated from their territories to a new, unfamiliar environment would orient in the direction of their home territory using the magnetic field as an orientation cue. In this experiment, the home territories were located in the harbor where fish were caught, and the fish were translocated to the magnetic field reception facility (MagLab) 4.5 km north of the harbor (i.e., home territories) (Figure 1). Home territories were in a SE direction from the MagLab (142° S). Fish were transported in a 20-L cooler box filled with seawater and dark plastic sheets, which served as shelter. The cooler was transported by car (approximately a 10-min drive).

The experiments conducted in the MagLab followed the same protocol as described in Cresci, Paris, et al. (2017) and Cresci, Paris, et al. (2019). All tests were conducted during daytime under artificial light.

The MagLab is designed to study the magnetic orientation of aquatic animals and to eliminate other possible external cues that could be used for orientation; for example, the animals are not exposed to water flows, odor plumes, sunlight, or any celestial cues. The MagLab is equipped with a triaxial electric coil system (Figure S1a), designed as described by Merritt et al., 1983, that is connected to a multichannel power supply (max. 3 A). In the laboratory, the coil system consists of four double wrapped nested electric coils described in Durif et al., 2013. One was used to cancel out the horizontal component of the ambient field. The other three were used to produce the artificial magnetic field and to reorient the magnetic north. The artificial field had the same total intensity and inclination as the ambient field (48.8–50 μT and 73°, with a deviation of <1°).

At the center of the coils, there is a circular tank made of fiberglass (diameter, 1.40 m; height, 0.90 m; see Figure S1a) filled with seawater, which is pumped from the sea 300 m away. The building (see

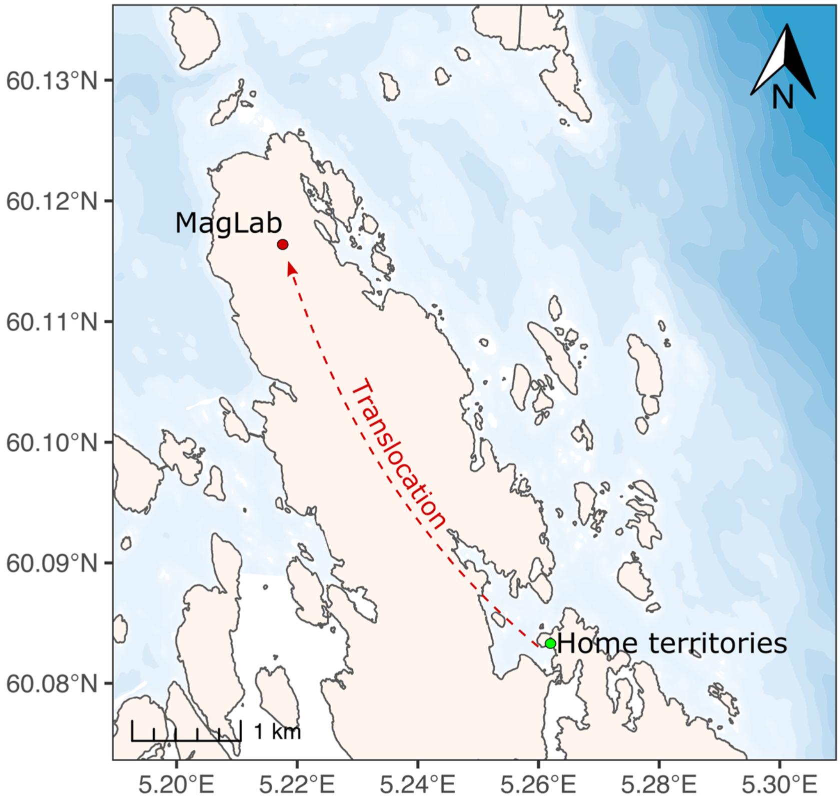

FIGURE 1 Study area. Location of the harbor with the home territories (green circle) of the goldsinny wrasse (*Ctenolabrus rupestris*) used in the study. The red circle shows the location of the magnetic laboratory (MagLab) to which the fish were translocated and in which the experiments were conducted

Figure S1b,c) is constructed of nonmagnetic material and is far from any source of magnetic interference (163 m from the nearest electrical disturbance and 365 m from the closest building; Figure S1c). Light intensity in the tank was low (<0.1 lum/ft^2 as measured by a HOBO light sensor) and water temperature ranged between 8 and 9°C.

Each wrasse was observed for 20 min, with the first 5 min considered as an acclimation period. A small cylinder (20 cm diameter) connected to a string that extended to an adjacent room was placed at the center of the tank. At the beginning of a test, a fish was released into the small cylinder where it was allowed to habituate. After 5 min, the cylinder was lifted upward using the line, and the test began. This protocol was repeated for one fish at a time, and individuals were tested only once.

Each fish was tested under one of the four simulated magnetic field conditions, with the magnetic north reoriented to the Earth's east, south, west, or north (see Figure S2). Each wrasse experienced only one of these four magnetic conditions. Using this approach, it is possible to discriminate between magnetic and topographical orientation cues.

After the experiment was completed, fish were released at the site where they were captured before the experiment started.

2.3 | Data analysis

The behavior of each fish was determined by analyzing videos collected using a GoPro HERO 7 placed above the tank and looking downward. Videos were processed using Tracker 5.1.5. (Copyright © 2020 Douglas Brown, https://physlets.org/tracker). Fish in the videos were manually tracked, and the fish tracks were used to calculate swimming kinematics and orientation behavior for each individual. We tracked the position of each fish, every second, for the 15-min observation period (900 data points per wrasse), as detailed in Figure S3. The angle of each position of the fish with respect to the artificially rotated magnetic north in the laboratory was considered as a bearing (using the center of the arena as a reference). As the magnetic north had a different orientation in the laboratory during each test, we monitored the direction of the north using an analog compass. If the frequency distribution of the 900 bearings for each fish was significantly different from uniform (Rayleigh's $p < .05$), we considered it as evidence of orientation, and we used the mean of the 900 bearings as the orientation direction of the fish (Cresci, Paris, et al., 2019; Irisson et al., 2009; Paris et al., 2008).

To test for male–female differences in orientation, the next step of the analysis was to evaluate whether the wrasse of each experimental group (females; males) were swimming toward a common orientation direction (Figure S3c). To explore that, we used Rayleigh's test of uniformity applied to all of the mean individual bearings of all of the wrasses from each of the experimental groups as data points ($N = 19$ males; $N = 22$ females).

An ANOVA for circular data was applied to test for influence of sex on the orientation directions. Male–female differences in average and maximum swimming speed and acceleration, and differences in total distance covered were tested using the nonparametric Wilcoxon test. Possible confounding effects of body size on speed and acceleration of the fish were assessed with fitting of linear models.

3 | RESULTS

The average total length of the males used in this study was 11.9 ± 1.2 cm (mean ± SD), which was significantly different, but only slightly greater than the total length of females (10.6 ± 1.2 cm; Wilcoxon test, W = 518, *p*-value = .0002). The sex ratio was 46% males (*N* = 23) and 54% females (*N* = 27). Of the 27 female wrasses tested, 22 oriented (81%; Rayleigh test of uniformity applied to the track of each fish; $p < .05$). This proportion was similar in male fish: 82% showed a significant orientation direction (19 out of 23; $p < .05$). Sex had a strong influence on the magnetic field-based orientation of the fish (circular ANOVA; *df* = 1, *F* = 8.123, *p* = .007), with the females that oriented not having a preferred orientation direction with respect to the magnetic field (*N* = 22, *p* = .84; Figure 2). However, on average, males oriented toward the magnetic south (*N* = 19, mean direction = 201°, *r* = .39, *p* = .05; Figure 2). Among the orienting males, there was an outlier, as one fish oriented toward the opposite direction (magnetic northeast) compared to the other males (Figure 2). Without the outlier, the magnetic orientation of the males is highly significant toward the south (*N* = 18, mean direction = 201°, *r* = .47, *p* = .002; Figure 2). A summary of the orientation directions before correction to the artificially rotated magnetic north is in Table S1.

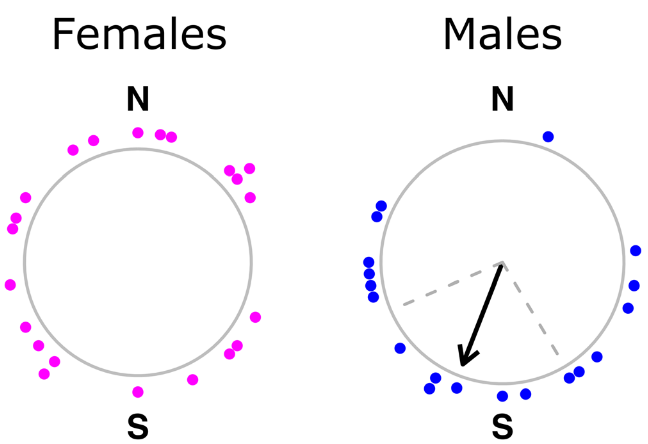

FIGURE 2 Orientation of goldsinny wrasse (*Ctenolabrus rupestris*) in a magnetic laboratory. The orientation of female (*N* = 22) and male (*N* = 19) goldsinny wrasse is presented with respect to the magnetic north (N) and south (S) in the magnetic laboratory. During the experiments, the magnetic north in the laboratory was rotated for each fish (i.e., the magnetic north in the lab had a different direction for each of the magenta and blue data points). The orientation of each fish was corrected to the artificially rotated magnetic north in the laboratory. Each point corresponds to the mean bearing of one goldsinny wrasse (averaged over 900 data points from the video tracks; Figure S3). These figures display the mean bearings of the fish that showed an individual preferred orientation. The black arrow points towards the mean angle of all the individual bearings. Dashed gray lines are the 95% confidence intervals around the mean. Absence of the arrow means that there was no preferred magnetic orientation direction

Males and females had the same swimming kinematics (Table 1). The frequency distribution of both swimming speed and acceleration data had similar shape (Figure 3a,b). The mean speed of the individuals did not differ between the two groups (Wilcoxon test; W = 295, *p* = .81), nor did the mean acceleration (W = 262, *p* = .35) (Figure 3). Furthermore, females and males covered almost the same total distance during the tests (W = 336, *p*-value = .63) (Figure 4). There was no influence of total length on mean speed (linear model, *F* = .29, *p* = .56), maximum speed (*F* = .63, *p* = .43), mean acceleration (*F* = .54, *p* = .46) or maximum acceleration (*F* = .25, *p* = .62).

4 | DISCUSSION

In this study, male and female goldsinny wrasse were translocated from their territories to a magnetic laboratory situated to the north, where their orientation relative to the magnetic field was studied. For each individually tested fish, the magnetic north in the laboratory was rotated by 90°, and their orientation direction with respect to the rotated north was assessed. Goldsinny wrasse exhibited sex-dependent differences in magnetic orientation (Figure 2). Females did not show any preferred magnetic direction, while males oriented to the magnetic south (201°)—the approximate direction of the home territories from which they were translocated (142°).

Several species of both temperate and tropical fish, such as sockeye salmon (*Oncorhynchus nerka*) (Quinn, 1980), Atlantic haddock (*Melanogrammus aeglefinus*) (Cresci, Paris, et al., 2019), European eels (Cresci, Durif, et al., 2019; Durif et al., 2013), and cardinal fish (*Ostorhinchus doederleini*) (Bottesch et al., 2016), use the magnetic field as a compass for orientation. However, whether there are sexual differences in magnetic compass orientation of fish is unknown. Sex differences in orientation and movement behavior are present in other animals, such as natterjack toads (*Bufo calamita*) (Sinsch, 1992) and blenniid fish (Costa et al., 2011), as well as in humans (Boone et al., 2018). Only a small number of studies report sex differences in magnetic field-based orientation behavior. In the fruit fly, *Drosophila melanogaster*, males exhibit strong and consistent magnetic compass response, while females fly in random directions (Phillips & Sayeed, 1993). In deer mice (*Peromyscus maniculatus*), males display better performance in navigation behavior and spatial learning compared to females (Kavaliers et al., 1996), but these differences disappear after a 5-min exposure to weak magnetic fields of 100 μT (Kavaliers et al., 1996). To the best of our knowledge, sex-dependent magnetic compass behavior has not been reported in fish.

Magnetic field-based migration behavior has been documented in many long-distance migrators such as salmon, eels, sharks, and turtles (Durif et al., 2021; Keller et al., 2021; Lohmann et al., 2007; Putman et al., 2014). In these species, the benefits associated with an ability to use a magnetic compass or map to cross hundreds to thousands of kilometers in pelagic water is clear. However, magnetic orientation responses are also exhibited by species performing relatively short-range movements, such as zebrafish, newts, and fruit flies (Cresci, de Rosa, et al., 2017; Phillips, 1986; Phillips & Sayeed, 1993). For marine

TABLE 1 Swimming kinematics of male and female goldsinny wrasse (*Ctenolabrus rupestris*)

	Mean speed (cm/s)	Max speed (cm/s)	Mean acceleration (cm/s^2)	Max acceleration (cm/s^2)	Total distance covered (m)	Mean turning angle (degrees)
Females	4.59 ± 2.77	23.32 ± 14.09	1.27 ± 1.24	12.05 ± 9.26	42.63 ± 20.47	22.87 ± 0.51
Males	4.86 ± 2.91	21.01 ± 11.29	1.44 ± 1.23	10.09 ± 5.60	44.67 ± 20.86	21.20 ± 0.48

Note: Values are reported as mean ± SD.

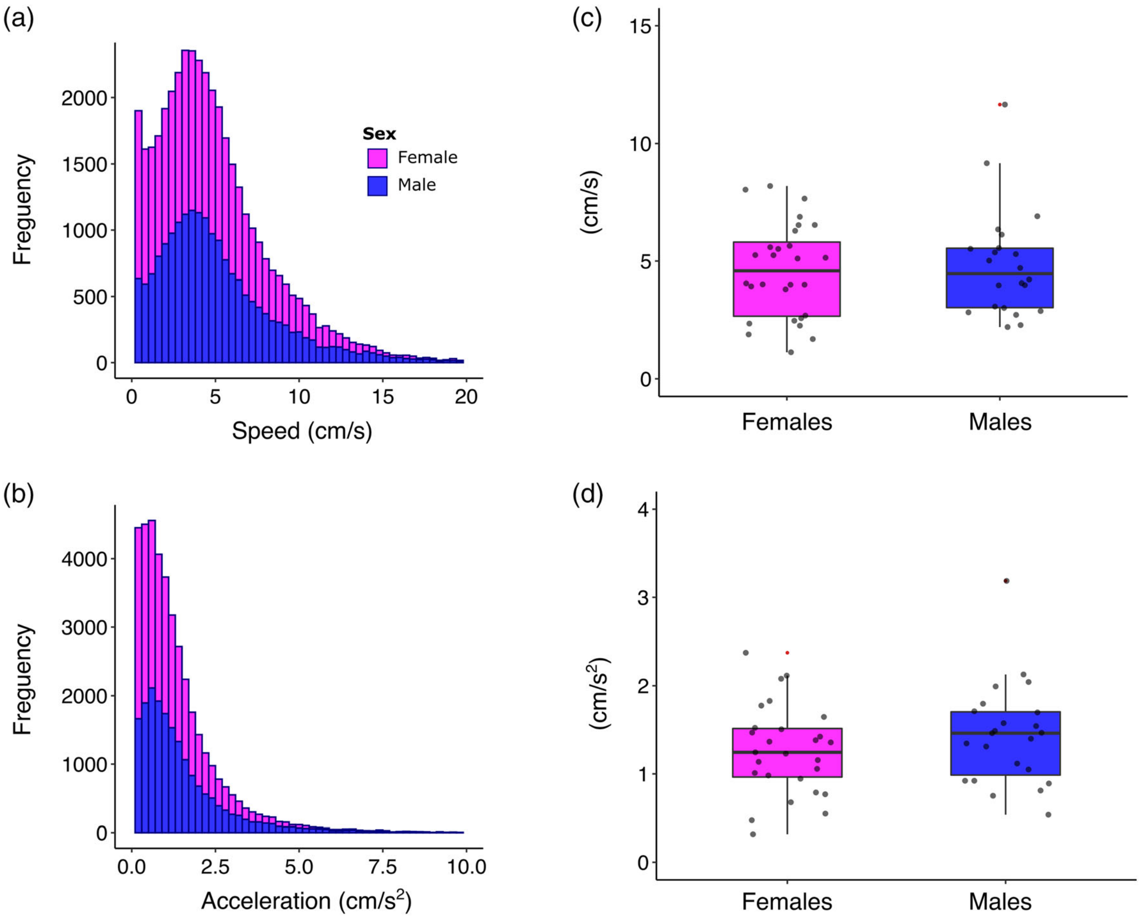

FIGURE 3 Swimming speed and acceleration of goldsinny wrasse (*Ctenolabrus rupestris*) males ($N = 23$) and females ($N = 27$). (a,b) The frequency distributions of swimming speed and acceleration from the video tracks are displayed for males and females. (c,d) Boxplots of swimming speeds and acceleration (with median, 25th, and 75th percentile)

short-distance migrants, magnetic field-based orientation could have several functions: It could help improve accuracy in locating specific nesting or mating areas; it could serve as a frame of reference in flowing water when visual landmarks are absent, or it could help provide the right direction for seasonal migrations such as those undertaken by goldsinny wrasse. Thus, for goldsinny wrasse, a magnetic compass could play an important role in guiding their return to their home territory following overwintering in deeper waters. Goldsinny wrasse live in shallow water (0–50 m) mostly in association with rocky shores and kelp forests (Skiftesvik et al., 2014, 2015), from which they undertake short-range movements (Hilldén, 1981; Sayer et al., 1993). Fish perform short-range orientation behavior by using multiple sensory systems, ranging from visual to tactile and olfactory, and by adopting different orientation strategies (Braithwaite & Burt De Perera, 2006). Fish use beacons (single landmarks), learn geometric relationships between the landmarks, and integrate multiple kinds of spatial information to perform short-range movements (Braithwaite & Burt De Perera, 2006; Hughes & Blight, 1999). Among these orientation mechanisms, magnetic orientation could also be used by fish for short-range migrations, especially when visual cues are unavailable (Cresci, Paris, et al., 2017).

Both male and female goldsinny wrasse appear to perform short seasonal migrations, moving to deeper waters in the winter, while returning to shallow waters in the spring (Halvorsen et al., 2021; Hilldén, 1981; Sayer et al., 1993; Skiftesvik et al., 2015). Our study suggests that males, but not females, have a strong motivation and

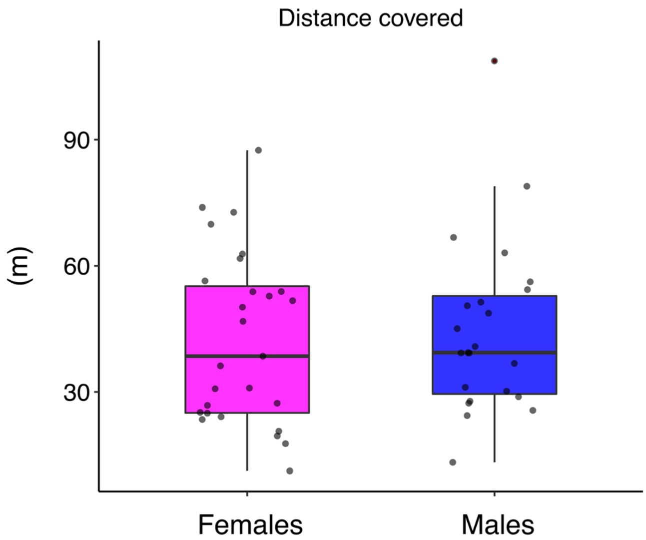

FIGURE 4 Total distance covered and mean turning angle of goldsinny wrasse (*Ctenolabrus rupestris*). Boxplots of total distance (meters) covered by males ($N = 23$) and females ($N = 27$) (with median, 25th, and 75th percentile)

ability to orient toward their home when displaced. This is consistent with previous field observations showing that when males and females are displaced, males return faster to the location from which they were removed than females (Hilldén, 1981). The ability of males to follow a magnetic compass direction toward their home territory likely plays a role in their faster migratory performance compared to females. It is possible that this sex difference in orientation behavior reflects a stronger site fidelity of territorial males, who may be motivated to relocate to their former territory and its properties, where they forage and mate (Hilldén, 1981).

A high-quality territory, which provides shelter and food for females, can increase the chance of male mating success in fishes (Hermann et al., 2014), and, under high densities, the number of suitable territories may be limited (Warner & Hoffman, 1980). Male goldsinny wrasse resolve territorial disputes with a distinct behavior involving boundary displays, mouth fighting, and biting (Hilldén, 1981). In this context, a magnetic compass could help the males trace their route back to their home area and reduce the chance of having to establish new territories, lowering the risk of territorial disputes. The absence of orientation to the magnetic field in females requires additional investigation to explore, for example, (i) whether they lack magnetic field-based orientation entirely or (ii) whether magnetic field-based orientation in females is exhibited during the spawning season but not outside of it.

The male goldsinny wrasse observed in this study had an average S–SW magnetic orientation direction (201°). This was the approximate—but not the exact—direction of their home territories, which are located 142° SE of the MagLab. This difference might be accounted for by the fact that in the MagLab, wrasse were deprived of all cues other than the magnetic field. However, other cues could also play a role, perhaps as a reinforcement of the magnetic compass, in a more complex and integrative orientation mechanism used for homing. This could be particularly important at the end of the seasonal migration, when vision and olfaction are likely to be the main cues allowing males to identify the target territory.

The sex-dependent magnetic compass of goldsinny wrasse is not associated with differences in swimming performance. The latter did not vary with sex even though males were slightly, but significantly, longer than females (in goldsinny wrasse, males reach slightly greater asymptotic length compared to females) (Olsen et al., 2019). Thus, the sex difference in magnetic orientation is not an artifact of differential swimming performance between males and females, but rather is the manifestation of different choices of orientation direction.

This study provides novel evidence that sex can be an important factor in magnetic field-based orientation and movement behavior of coastal fish and that magnetic compass orientation is involved in short-range movement in coastal waters. Future studies on magnetic compass orientation should focus on other species of coastal fish, as this could be an important tool for short- and mid-range movement behavior and for maintaining site fidelity which has been reported in a growing number of species.

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CONFLICT OF INTEREST

The authors declare no competing interests.

ETHICS STATEMENT

The Austevoll Research station has a permit to operate as a Research Animal facility for fish (all developmental stages), under Code 93 from the national Institutional Animal Care and Use Committee (IACUC), NARA. We did not require specific approval for these experiments because they are nonintrusive behavioral observations.

AUTHOR CONTRIBUTIONS

A.C. designed the study, collected, analyzed, and interpreted the data, and wrote the paper; T.L. designed the study and collected and analyzed the data; K.T.H. designed the study, interpreted the data, and wrote the paper; C.M.D. designed the study, collected, and interpreted the data and wrote the paper; R.B. designed the study and interpreted the data and wrote the paper; H.I.B. designed the study, collected and interpreted the data, wrote the paper, and funded the research; A.B.S. designed the study, collected and interpreted the data, wrote the paper, and funded the research.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

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