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A comparison of spatial learning and memory capabilities in intertidal gobies

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KEYWORDS

gobies, habitat complexity, homing, spatial, learning and memory

ABSTRACT

For the majority of animals, the ability to orient in familiar locations is a fundamental part of life, and spatial memory allows individuals to remember key locations such as food patches, shelter, mating sites or areas regularly occupied by predators. This study determined if gobies collected from rocky platforms and sandy beaches differ in their ability to learn and memorise the locations of tide pools in a simulated rocky intertidal zone. Intertidal rock pool gobies show acute homing abilities and, therefore, should be expected to display superior learning and memory capabilities. In contrast, it is unlikely that natural selection would favour similar learning skills in sandy shore fishes because they simply shift back and forth with the tides. The learning abilities of gobies were tested using small replica rock platforms, containing four tide pools that retained varying depths of water at simulated low tide. Gobies were categorised as having learnt the task if they were able to consistently locate the tide pool that retained the most water at simulated low tide as the pool with the most favourable conditions. Rock pool species were able to locate the deepest pool to wait out low tide for ~95 % of the trials, while species from sandy shores were found in the deepest pool ~10 % of trials. Despite repeated stranding, sandy shore fish continued to follow the tide out. We propose that rock pool species memorised the location of rock pools during simulated high tide enabling them to relocate the best refuge for low tide.

Introduction

Learning is utilised by many animals living in complex and changing habitats, enabling them to adapt their behaviour to suit contemporary, local environmental conditions. The ability to learn and remember allows animals to draw on previous experience when faced with challenging decisions so that they can make the appropriate response (Giraldeau 1997; Braithwaite and Girvan 2003; Dall et al. 2005). Spatial learning and memory is one area of behavioural research that has generated a large amount of interest recently because of its broad applicability, making it ideal for comparative studies (Healy 1998). The main aim of this type of behavioural research is to understand how animals navigate around their local habitat using learning and memory to aid in the relocation of food sources, shelter, and mates and to avoid potential dangers such as predators (Braithwaite and Girvan 2003). However, the majority of work on spatial cognition has focused on terrestrial vertebrates, in particular mammals and birds (Healy 1998, 2005; Shettleworth 2010). These studies used a comparative approach to explore the differences in learning

abilities and strategies of closely related species found in different environments to elucidate how natural selection shapes spatial learning abilities (Krebs et al. 1990; Brodbeck 1994). For example, Clark's Nutcracker can memorise and relocate the locations of thousands of caches up to 9 months after caching, even when buried under a metre of snow (Balda and Kamil 1992). Comparative analyses with closely related corvids show that Clark's Nutcracker has enhanced spatial learning abilities as well as a larger hippocampus (Sherry et al. 1992).

Numerous fish species live in complex and changing habitats; thus, it is expected that they should display sophisticated spatial learning and memory capabilities. In fact, recent research has shown that many fish species are capable of creating long-term memories (Teyke 1989; Warburton 2003), learning complex cues (Odling-Smee and Braithwaite 2003a; Odling-Smee et al. 2008; Burt de Perera 2004a) and employing flexible learning strategies (Laland et al. 2003; Lopez et al. 1999). For example, fish can locate shelter when under threat of predation (Aronson 1951; Markel 1994), identify different food patches using visual landmarks (Braithwaite et al. 1996; Salas et al. 1996; Lopez et al. 1999, 2000; Hughes and Blight 2000) and regain their bearings after disorientation using geometric features of the environment (Sovrano et al. 2003), and they can even encode order into a cognitive map (Reese 1989; Rodriguez et al. 1994; Burt de Perera 2004b).

Furthermore, the spatial learning abilities of some fish species are fine-tuned to enhance survival in their local habitat (Mackney and Hughes 1995; Odling-Smee and Braithwaite 2003a, b). For example, the blind cave fish (*Astyanax fasciatus*), lives in caves of Mexico, where the lack of light has made vision unnecessary. Burt de Perera (2004b) found that blind cave fish use their lateral line organ to gather information about the order, sequence and three dimensional relationships of objects in their environment and then encode this information into a spatial map to aid in orientation. Burt de Perera and Guilford (2008) demonstrated that the shanny (*Lipophrys pholis* L), an intertidal fish, was capable of successfully locating the previous position of a refuge when it had been removed, showing that they are able to learn and remember cues from their surroundings and use this information to orientate. Studies by Odling-Smee et al. (2008) explored the spatial learning abilities of lake-dwelling "benthic" and "limnetic" sympatric species of three-spined stickleback (*Gasterosteus aculeatus*). Benthic species feed mainly on mud-dwelling invertebrates within the vegetated littoral zone and thus require better spatial memories, while limnetic species feed predominately on plankton in the comparatively homogeneous open water column. When fish were trained in a T-maze to locate a reward, benthic individuals learned the task almost twice as quickly and with fewer errors than did limnetics, consistent with the suggestion that differential demands are made by differential lifestyles on spatial learning ability.

Wickler (1957) observed that individuals of the family Gobiidae are capable of learning very quickly and have an exceptional memory, especially when it comes to remembering the topographic features of their surroundings. However, to our knowledge, only three studies have explored the spatial learning abilities of gobies to date, none of which have been comparative in nature. Experiments by Aronson (1951, 1971) demonstrated the ability of the frillfin goby, *Bathygobius soporator*, to use acquired memories of the local topography to jump from their home tide pool to an adjacent pool with impressive accuracy when threatened. If pursued by a threat, the gobies were able to perform a series of jumps leading them from one pool to the next until they reached the open sea. Markel (1994) tested spatial memory in black eye gobies (*Coryphopterus nicholsi*) by measuring the time that naive and experienced captive individuals required to locate an artificial burrow when threatened with a simulated predator attack. Fish that had greater experience (given longer exploration time) were quicker to relocate the burrow than naive fish. However, when the burrow was moved to a new position, the less-experienced group found the burrow faster than the experienced fish. This indicates that the fish had learned and remembered the spatial location of the burrow rather than its actual appearance. To date, there has been no attempt to determine

how intertidal gobies are able to relocate a specific tide pool at low tide and if this ability varies depending on the habitat the fish are collected from.

In this study, the spatial strategy that two intertidal rock pool gobies, Cocos frillgoby (*Bathygobius cocosensis*) and Krefft's goby (*Bathygobius krefftii*), use to home to a familiar rock pool was investigated using a behavioural assay. This assay was designed to simulate the conditions faced by these fish in the wild. Gibson (1967, 1999) and White and Brown (2013) suggest that these intertidal fishes forage over the rock platform at high tide and consistently return to a particular rock pool to seek refuge from the adverse conditions of low tide. Such behaviours are well suited to the use of spatial learning and memory for orientation. For comparative purposes, we tested two sand-dwelling goby species, eastern longfin goby (*Favonigobius lentiginosus*) and Hoese's sandgoby (*Istigobius hoesei*), in the spatial task. Individuals of these species leave the intertidal zone during low tide only to return when conditions are more favourable at high tide (Gibson 1999). Gobies can be broadly broken up into a number of lineages which broadly correspond to the habitats that they occupy (Thacker and Roje 2011). Two such lineages include species that occupy sandy shores and those that inhabit rock pools on rocky reefs (GEW & CB unpublished data). These groups show extensive behavioural, habitat and life history differences that likely have deep phylogenetic origins (Thacker and Roje 2011; GEW & CB unpublished). The ecological cognition hypothesis (Healy and Braithwaite 2000) would predict that natural selection would favour the evolution of enhanced spatial cognition in rock pool-dwelling goby species so they can avoid the risk of becoming stranded in unsuitable areas due to the retreating tides. Whereas, gobies found on homogenous and dynamic sandy beaches would not be subject to the same level of selection for enhanced spatial memory relative to rock pool dwelling species because they have little need to revisit refuges. Using these four species, we addressed three primary questions: (1) Do intertidal gobies have the capability to learn and memorise the spatial position of rock pools at high tide so that they can be revisited at low tide? (2) Is learning ability and visual cue use modified in response to differences in ecological conditions? (3) Compared to sand-dwelling gobies, do rock pool gobies rely more on visual landmarks when revisiting refuges during low tide?

Methodology

Study animals

A total of 53 fish (12–15 individuals of each species; 26 rock pool gobies and 27 sand gobies) were captured at low tide from a number of beaches and rock platforms in Sydney, New South Wales, Australia. Rock pool-dwelling gobies were collected from their home pools at a range of rock platforms using small handheld nets. Sand-dwelling gobies were collected via snorkel and hand nets at several sandy beaches at a water depth of 1.5–3 m. These beaches and rock platforms were chosen for their relative ease of access, relatively sheltered nature of the bays and abundance of rock pools, respectively. Only two fish were collected for testing on any one occasion; thus, collections were performed regularly once every 9 days for a period of 1.5 years.

Captured pairs of fish were transported by car to Sydney Institute of Marine Science (SIMS) at Chowder Bay using a large aerated bucket. Upon arrival, the fish were lightly anaesthetized using a solution of 50 mg/l MS222 buffered with sodium bicarbonate (fish placed in a bucket containing 1.5 L solution until subdued), their total length was measured using calipers and they were marked using Visible Implant Fluorescent Elastomer (VIE) tags (North-West Marine Technology Inc.). VIE tags were implanted beneath transparent scales in a combination of six sites along the fish's dorsal surface so they were visible to an overhead observer. This entire procedure took roughly 2–3 min to perform on each fish and has no obvious effects on behaviour (White and Brown 2013).

After tagging, each fish was housed individually in one of two large flow-through seawater tanks (1.2 m × 1.2 m × 1 m) each containing an artificial rock platform with four tide pools (see “Apparatus” for more detailed description; Fig. 1 and supplementary S1) complete with places to hide much like their natural environment. Both tanks were maintained at the same seawater flow rate (1 L/1/min) and temperature (18 to 22 °C) and were illuminated for 12 h each day with full spectrum UV lights and 12 h with infrared light, enabling fish positions to be observed during low tides occurring in night hours. Fish were fed a combination of live brine shrimp (*Artemia franciscana*) and live black worms (*Lumbriculus variegates*) at high tide every other day.

Upon the completion of the 8-day experimental period, fish were returned to their original beach area or pool of capture during low tide. Tagging fish ensured that the same fish was not captured and tested twice.

Apparatus

Two sloping artificial rock platforms each with four tide pools were constructed from fibreglass and were suspended in the two square experimental tanks (1.2 m × 1.2 m × 1 m). Two small circular pools (tide pools 1 and 2) separated by a low ridge 10-cm wide were built on the highest level, and 15 cm down on the lowest level a further two pools (tide pools 3 and 4) separated by a low ridge 10-cm wide were constructed. Tide pools differed in depth and appearance; tide pool 1 consisted of a deep depression that retained water to a depth of 10 cm at simulated low tide. Tide pools 2 and 3 consisted of shallow depressions that retained water to a depth of 1.5 cm at simulated low tide. Lastly, tide pool 4 consisted of a deep depression with a drain that reduced the water level to 1.5 cm during simulated low tide (Fig. 1a, b). The base of each tide pool was lined with a layer (1.5-cm thick) of small rocks and sand in which the fish could hide or bury. Tide pool 1 was also made more attractive to fish because it had a small shelter constructed from three rocks within the pool itself, two rocks formed the base positioned 4 cm apart with the third rock placed on top to form a roof and no shelter was provided for tide pools 2–4. Rocks and sand remained in the same positions trial after trial, and if any of the rocks or sand was moved during tide changes or due to fish digging, we reposition them in their correct positions (i.e. any holes dug were covered before the next low tide). Lastly, tide pools 1 and 2 had a uniquely shaped rock landmark positioned over their top left corner which the fish could also find refuge under at high tide. Rock landmarks also served as possible cues to identify the location of each pool, i.e. rocks were submerged during high tide (underwater cue) and became exposed and overhanging (terrestrial cue) during low tide (Fig. 1a, b and supplementary material 1).

A small flow of fresh sea water ran constantly into the tank from ten small entry holes on the wall above the highest level of the artificial rock platform; thus, water trickled into pools 1 and 2 first and slowly overflowed from there into the two lower pools. Tide flow was controlled by a custom-built tide regulator (METS 2010). To achieve a “high tide”, the rotating arm lifted the outflow pipe above water level contained within the tank and caused the water level to rise to within 5 cm of the tank rim. To achieve a “low tide”, the arm lowered the outflow pipe below water level contained within the tank, allowing water to exit the tank via drainage holes. At low tide, the tank was drained almost entirely of water except for the tide pools. The tide regulator was programmed to mimic the naturally occurring tide cycles; thus, there was 6.5 h between each high and low tide, two high tides and two low tides occurred daily, time of high and low tides changed daily according to natural tide cycles and water levels increased or decreased gradually. During low tide cycles, pools lower on the rock platform (i.e. tide pools 3 and 4) were exposed to the air for approximately 2 h, while pools higher up on the rock platform were exposed for approximately 4 h. Sea water supplied to the tanks was sourced directly from Chowder Bay using SIMS flow-through sea water system (i.e. fresh sea water constantly flowed through the apparatus); thus, odour cues were not likely to be used by fish to find the tide pools. Furthermore, the entire rock platform

(including pools) was scrubbed clean before running a new fish to eliminate concern of confounding effects of odour cues.

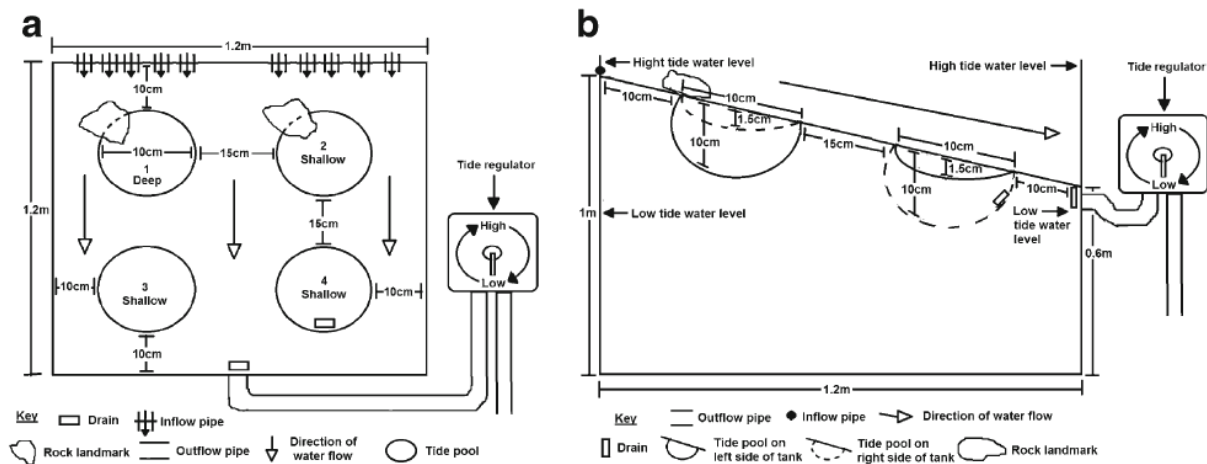


Fig. 1 Schematic of the test tank. a Top view and b left side view of the experimental tank. Tide pool 1 consists of a deep depression (10 cm) that will retain water to a depth of 10 cm at simulated low tide. Tide pools 2 and 3 consist of a shallow depression (1.5 cm) that will retain water to a depth of 1.5 cm at simulated low tide. Lastly, tide pool 4 consists of a deep depression (10 cm) with a drain that will retain water to a depth of 1.5 cm at simulated low tide. The two highest pools (tide pools 1 and 2) have a rock landmark positioned over their top left corner prior to probe trials; these rock landmarks are later positioned over the top left corner of the two lowest pools (tide pools 3 and 4) during probe trials

The gobies were tested individually and were determined to have a capacity for learning/memory if they were able to consistently locate the pool that retains the most water (tide pool 1) to wait out the simulated low tide for five consecutive trials. It has been shown that shallower tide pools make stranded fish feel uncomfortable (i.e. behaviours such as erratic swimming and digging in the sand to create deeper pockets within the pool in which fish could sit were observed); thus, it is expected that fish should avoid the shallower pools in future trials.

Experimental procedure

Tests for orientation and learning were performed as follows: on day 0, pre-training began and a fish was placed in pool 1 at low tide. In most cases, the fish immediately swam under the rocks or buried itself under the sand. After allowing one artificial high tide to occur (i.e. 12 h acclimation time) during which the fish could explore the spatial relationships of the four tide pools and their topographical features (video recordings show that all species were equally curious in exploration of all tide pools during high tides), experimental procedures began. The first training trial began immediately thereafter as the water drained to low tide height and the fish sought refuge in one of the four available tide pools for its duration. Fish were subjected to a total of ten consecutive tide cycles (i.e. trial 1–10) over the next 5 days before a probe trial was conducted.

Probe trials were used to determine if the fish were employing rock landmark cues in order to locate tide pool 1. During a probe trial (i.e. trial 11), the rock landmarks over the two highest pools (tide pool 1 and 2) were moved down to the two lowest pools (tide pools 3 and 4). After the probe trial, fish were subjected to

re-learning trials for a further five consecutive tide cycles (i.e. trials 12–16) during which rock landmarks remained positioned over tide pools 3 and 4.

All fish were held for a total of 8 days and subjected to 16 tide cycles before being released back into the wild at sites of capture.

Scoring learning and cue use

A camera (Swann Security) positioned 1m above the centre of each tank allowed us to view the fish on a remote laptop computer. Footage of each day was recorded directly to an external hard drive. We scored each fish's learning ability from video recordings of the 8-day study period, a score of 1 was recorded if the fish waited out the simulated low tide in pool 1 (retains the most water and has rocks to hide under) and a score of 0 was recorded if the fish was found in any of the other pools (retains least amount of water and limited shelter). A secondary score was recorded for the probe trial (i.e. trial 11): if fish that had previously selected pool 1 now selected the lower pools over which rock landmarks were now positioned, we recorded the cue choice "landmark" or if they continued to return to the same pool as previous trials, then "other spatial strategy" was recorded.

Statistical analysis

Learning scores were averaged for prior rock movement (training trials 1–10) and post rock movement (re-learning trials 12–16) producing two separate values for each fish for analysis. The design of this experiment was such that we expected rock pool dwelling species would choose tide pool 1 to wait out the low tide, while sand-dwelling species would end up in pool 4. This means there would be no variance in some individuals as well as heterogeneity of within-group variance among the various fishes (i.e. the data is not normally distributed). Thus, nonparametric statistics were used in all analyses. We also used a Bonferroni multiple comparisons correction (i.e. P values must be <0.008 to be significant).

A Kruskal-Wallis test was used to determine if there were differences in learning performance (mean of training trials 1–10) between the four goby species, followed by pairwise species contrasts using Mann-Whitney U tests. Lastly, a paired sign test was used to compare differences in pool choice during training trial 10 and during the probe trial (trial 11) to determine which fish used the rock landmark for orientation. Size was not included in any of the above comparative analyses because it is confounded by species differences (i.e. mean total length \pm SD: Cocos frillgoby 4.88 ± 0.60 cm; Krefft's goby 4.12 ± 1.01 cm; eastern longfin goby 4.92 ± 0.27 cm; Hoese's sandgoby 4.73 ± 0.76 cm). Thus, we analysed size intraspecificly using regressions. All analyses were performed using StatView Version 5.0.1 (SAS Institute Inc.).

Here, we present data for tide pool 1 only. However, fish were also commonly found in tide pool 4 and never found in pools 2 and 3. Thus, data for tide pool 4 is simply the reciprocal of that for tide pool 1 (see supplementary information S2).

Results

Learning

All four goby species obtained significantly different learning performance scores prior rock movement (Kruskal-Wallis: $H=41.64$, $df=3$, $P<0.0001$). Pairwise species contrasts using Mann-Whitney U tests revealed all species were significantly different from one another in their learning performances ($P\leq 0.001$ in all cases). After Bonferroni correction, sand-dwelling species did not differ significantly from one another in learning performance ($Z=-0.253$, $P=0.01$) and the difference between rock pool dwelling species was

borderline significant ($Z=-0.264$, $P=0.0083$) (Table 1). Both rock pool-dwelling species learnt very quickly; most individuals immediately found the deepest pool and 100 % of individuals were able to locate pool 1 by the tenth trial. The sand species, Hoese's sandgoby, showed some improvements by the end of the tenth trial but eastern longfin goby were not observed in tide pool 1 at all by the tenth trial (Fig. 2). Sand species were more likely to end up stranded in tide pool 4, no fish utilised tide pools 2 or 3 (see supplementary material 2 for analysis of tide pool 4)

Re-learning

Furthermore, all four species obtained significantly different learning performance scores post rock movement during relearning trials (Kruskal-Wallis: $H=40.99$, $df=3$, $P<0.0001$) (Fig. 2). Pairwise species contrasts of re-learning scores revealed all species were significantly different from one another in their re-learning performances (Mann-Whitney U: $P\leq 0.001$ in all cases), except for eastern longfin goby and Hoese's sandgoby which did not differ from one another in learning performance ($Z=-0.217$, $P=0.83$) (Table 1). Cocos frill gobies re-learnt the location of tide pool 1 very quickly after the rock landmark was moved (probe trial), with 100 % of fish found in tide pool 1 by the final trial (Fig. 2). Krefft's gobies on the other hand took much longer to re-learn the location of rock pool 1 after the probe trial, with only 76 % of fish found in tide pool 1 by the final trial. Rock movement had little influence on sand species, they continued to use tide pool 4 (see Supplementary material).

Table 1 Mann-Whitney U pairwise species contrast results for prior rock movement (before probe trials) and post rock movement (during probe trials)

Species	Prior rock movement					Post rock movement (probe trials)				
	No.	Mean	U value	z value	P value	No.	Mean	U value	z value	P value
Cocos frillgoby (R)	13	99	39.5	-2.641	0.0083	13	91	29.0	-2.984	0.003
Krefft's goby (R)	13	88				13	62			
Cocos frillgoby (R)	13	99	0.0	-4.598	<i><0.0001</i>	13	91	0.0	-4.501	<i><0.0001</i>
Eastern longfin goby (S)	12	2				12	3.33			
Cocos frillgoby (R)	13	99	0.0	-4.662	<i><0.0001</i>	13	91	0.00	-4.77	<i><0.0001</i>
Hoese's sandgoby (S)	15	13.33				15	4			
Krefft's goby (R)	13	88	0.0	-4.404	<i><0.0001</i>	13	62	0.0	-4.397	<i><0.0001</i>
Eastern longfin goby (S)	12	2				12	3.33			
Krefft's goby (R)	13	88	0.0	-4.531	<i><0.0001</i>	13	62	0.0	-4.69	<i><0.0001</i>
Hoese's sandgoby (S)	15	13.33				15	4			
Eastern longfin goby (S)	12	2	44.0	-2.525	0.0116	12	33.3	87.0	-0.217	0.83
Hoese's sandgoby (S)	15	13.33				15	4			

Bonferroni corrected for multiple comparisons (i.e. to be significant $P<0.008$). Significant result is shown in ital

Mean mean percentage of trials fish waited out the low tide in pool 1 (deepest pool),

R rock pool-dwelling species, S sand-dwelling species

Spatial cue use

Paired sign tests for training trial 10 vs probe trial revealed that there was no significant difference in the number of fish choosing the deepest pool (tide pool 1) during training trial 10 and during the probe trial for any species (paired sign test: $P>0.05$ in all cases), except for one rock pool species. Krefft's goby was more likely to return to the deepest pool (tide pool 1) during training trial 10 (prior to rock landmark

movement) than during probe trials (paired sign test: $P=0.03$) suggesting reliance on the rock landmark for orientation. Krefft's goby was also the only species to show significant effects between training (prior rock movement) vs re-learning (post rock movement) scores. Which indicates that this species was more likely to return to the deepest pool (tide pool 1) prior to rock landmark movement than post rock landmark movement (paired sign test: $P=0.012$) suggesting that rock landmark movement had significantly confused these fish and impacted on their re-learning skills (Fig 3).

Regression analyses only revealed a correlation between body size and percentage of fish choosing tide pool 1 prior (training) or post (re-learning) rock movement for the sand species, Hoese's sandgoby. Larger fish waited out the low tide in the deepest pool (tide pool 1) more often than smaller fish prior to rock landmark movement for probe trials ($R^2=0.279$, $F_{1,14}=5.03$, $P<0.05$).

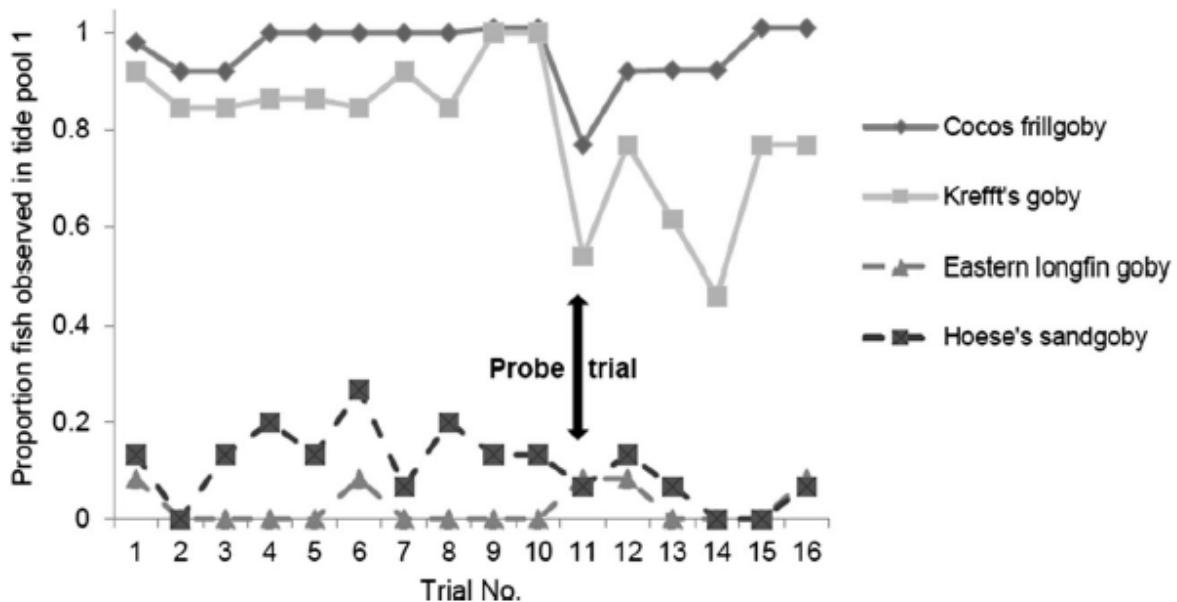


Fig. 2 Proportion of fish observed in tide pool 1 prior to rock movement (trials 1–10) and post rock movement (probe trial 11 and re-learning trials 12–16) in the four species. Rock pool-dwelling species (Cocos frillgoby and Krefft's goby) are represented with *solid lines* and sand-dwelling species (eastern longfin goby and Hoese's sandgoby) are represented with *dashed lines*. The *arrow* indicates the probe trial

Discussion

The primary aim of this study was to test whether gobies from different habitats vary in their ability to store information about a familiar environment in their memory and use this information to return to a particular tide pool refuge at low tide. Most sand-dwelling fish were repeatedly found in rock pool 4, having followed the tide out. As expected, gobies from sandy beaches were unable to retain a spatial memory of the location of tide pool 1 (deepest pool); less than 20 % of individuals were returning to pool 1 by the tenth trial. Whereas gobies that inhabit intertidal rocky platforms learnt the location of the tide pool 1 very quickly, 100 % of individuals returned to pool 1 by the tenth trial. Many of the rock pool fish identified the safe pool from the very first trial. This result lends support to the ecological cognition hypothesis (Healy and Braithwaite 2000) by demonstrating that fish from rock pools require much better learning skills in order to revisit safe rock pools to avoid being stranded in bad locations at low tide. The results are also

consistent with our previous field experiments that showed that rock pool residents are regularly found in the same pool and can relocate that pool if displaced elsewhere on the rock platform (White and Brown 2013).

Fish living in the intertidal zone, particularly in rock pools, are expected to have a highly accurate awareness of geographic location (Aronson 1951; Gibson 1968; Jorge et al. 2012). For example, numerous intertidal fish species are capable of successfully homing to their original pool after displacement (Blennidae: Santos et al. 1989; Cottidae: Williams 1957; Gibson 1967; Green 1971; Gobiidae and Tripterygidae: Griffiths 2003; White and Brown 2013; Sebastidae: Mitamura et al. 2005). Furthermore, it is likely that high tide exploration and feeding expeditions are responsible for their ability to learn and memorise the topographical characteristics of the areas surrounding their home rock pool so that it may be relocated if they should become displaced (Jorge et al. 2012). Thus, we suggest that rock pool species memorise the location of tide pool 1 during simulated high tide so that they can be relocated as a safe haven to wait out simulated low tide.

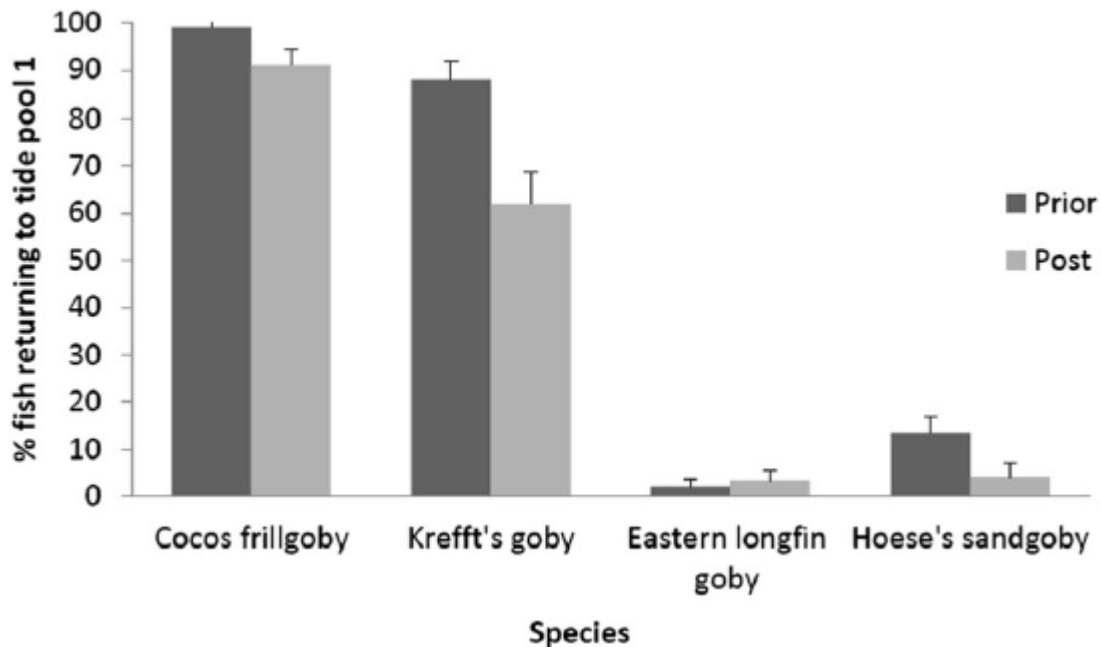


Fig. 3 The percentage (\pm SE) of rock pool- and sand-dwelling fish choosing tide pool 1 (deepest pool) prior to rock movement and post rock movement (during probe trials)

Sandy shores, in stark contrast, are structurally dynamic and relatively homogeneous in nature, meaning that few refuges are available for fishes to remain intertidally over periods of low tides. Thus, these species tend to follow the tide back and forth. In this context, it makes sense that sand-dwelling species do not remember the location of the tide pool 1 because in the wild these, fish simply enter and leave the intertidal zone with each tide (Gibson 1999). It is interesting to note just how unchanging this behaviour is. The sand species show almost no flexibility in their strategy even though they are repeatedly stranded in our tide pool simulator. There are multiple reasons why these fish do not seek shelter in the deepest pool even after multiple exposures. Firstly, shelter seeking is not a natural behaviour for these fish in the real world and they likely rely on a simple set of rules learned through experience to move in their environment (e.g. maintain 1-m depth). Secondly, they may not have the cognitive abilities to retain

spatial information for extended periods of time. According to Braithwaite et al. (1996), memory duration may depend on environmental predictability. For example, in an environment that is constantly changing, long-term memories may be of low adaptive value because within a short period of time, the information that has been memorised will lose its relevancy. Therefore, on highly homogenous and mobile sandy shores, a fish's memory should not last very long and should thus be continually updated through new learning experiences. This may in turn explain why sand species were unable to learn the location of tide pool 1. In contrast, fish living in stable and spatially complex environments, such as rock pools, would be expected to have longer-lasting memories and be more reliant on visual cues for orientation. Mackney and Hughes (1995) provide further support for these predictions in their study on memory retention of prey handling skills in closely related stickleback (*Gasterosteus*) species from differing habitats. Fish gathered from more changeable habitats (i.e. estuarine and marine) presented a shorter memory for foraging skills related to certain types of prey than freshwater species. The freshwater population was gathered from a landlocked pond containing a less diverse population of prey items; thus, the ability to recall particular prey-handling skills for longer would be a highly advantageous adaptation. It is unclear if the differences in learning and memory between species from contrasting habitats is domain general (general intelligence) or specific (e.g. spatial). To adequately address this question, one would have to test gobies in other learning and memory domains, such as search image retention.

The differences in learning ability observed between the species could have been generated by early experience of differing spatial problems (Seymour et al. 1996; Odling-Smee and Braithwaite 2003a). For example, post-fledging mountain chickadees (*Poecile gambeli*) that have not received caching and retrieval experience display limited spatial memory capacities and reduced neural development (Clayton 2001). Experience in rocky intertidal areas during early ontogeny may aid in the learning of new unfamiliar rock pools later in life. Thus, sand species are unable to learn the location of tide pool 1 because they have never experienced rocky shore habitats before. When fish recruit to their perspective habitats, they may develop spatial learning abilities that are appropriate to that particular location. Although unlikely in the present context, this hypothesis could be tested in future experiments by rearing fish in contrasting environments and observing the development of their learning abilities.

Although there are obvious genetic differences between all four species examined here, rock pool species are more closely related to one another than they are to sand species and vice versa (Thacker and Roje 2011; GEW and CB unpublished). It might be suggested, therefore, that differences observed in learning and memory abilities between these two species from these contrasting habitats may have evolved once deep in goby phylogeny. Examination of the goby phylogeny suggest that the split between sand- and rock pool-dwelling species happened once deep within the goby phylogeny (Thacker and Roje 2011). This implies that the spatial memory and habitat preference of the species studied here may have evolved in parallel with the early colonization of these habitats and were likely refined further during the diversification that followed thereafter. Future studies could examine the development of newly recruited juveniles to determine the extent of heritability in these traits.

The second half of this experiment aimed to determine the effects of ecology on visual landmark use, with the expectation that gobies from rock pool habitats would rely on visual landmark cues for orientation to a greater extent than sand-dwelling species. As expected, differences in ability to locate the tide pool 1 prior (training trials) and post rock movement (probe trial) were noted only in rock pool-dwelling species, indicating that some individuals were using landmarks to orientate, especially in the case of Krefft's goby. Fish of this species were more likely to return to tide pool 1 prior to rock movement than post rock movement (during the probe trial). Field observations on butterfly fish species (family *Chaetodontidae*) have likewise demonstrated that the displacement of visual landmarks can deflect fish from their path (Reese 1989). Furthermore, previous work on other fish species has revealed that fish collected from

spatially complex and simple habitats or stable and unstable environments rely on different types of spatial information to navigate (Girvan and Braithwaite 1998; Braithwaite and Girvan 2003; Odling-Smee and Braithwaite 2003a; Brown and Braithwaite 2005). The results shown here lend support to these findings by showing that gobies from stable complex rock pool habitats use visual landmarks cues to orientate towards tide pool 1 to a greater extent than sand species. However, it was noted that some individuals did not change their tide pool choice during the probe trials, indicating that they were not using rock landmark cues to orient but instead may have been relying on other cues (e.g. perhaps the geometric relationship between pools, topography of the rock platform, water depth, flow direction, extra apparatus cues etc.). Future studies in this area should focus on determining what types of spatial or non-spatial cues sand species use to orientate and to confirm the role that visual landmarks play in the orientation strategy of rock pool species.

To conclude, this experiment provides further evidence that an animal's behaviour and cognition is shaped by the habitat in which it lives. There is a large amount of current interest focusing on comprehending the links existing between ecology and cognition (reviewed in Healy and Braithwaite 2000). Studies that offer insight into the role of environmental experience on the development of spatial learning abilities are highly valued as they help demonstrate more clearly how natural selection can shape spatial learning and memory.

Ethical standards

Experimental methods in this study conformed to the standards set by Macquarie University Animal Ethics committee (ARA# 2009/021-4). Fish collections were conducted under NSW fisheries Scientific Collection Permit number P08/0010-3.0.

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