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Friends without benefits: familiarity does not improve fitness-related behaviours in larvae of a marine shoaling fish

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It has long been recognized that associating with familiar individuals may confer fitness benefits. However, gaps in our knowledge remain about how behaviours critical for fish survival are affected by social experience in early stages. In this study, we tested the hypothesis that familiarity acquired during early life stages improves larval performance. Using sand smelt, *Atherina presbyter*, we examined the effect of familiarity on foraging efficiency, swimming behaviour and escape response. In view of the benefits of familiarity, we predicted that sand smelt larvae are more responsive and perform more successful escape responses and prey strikes when in groups of familiar conspecifics. The results indicate that sand smelt are indeed more prone to associate with conspecifics based on familiarity; however, contrary to our expectations, familiarity, at this life stage, did not improve behaviours closely related to survival. This may be related to the highly dynamic nature of shoaling, characterized by frequent exchange of individuals among groups, meaning that individuals must constantly adjust their behaviour to that of new members, limits the relevance of familiarity during this life stage. This research underscores the importance of evaluating the ecological and developmental context when investigating social behaviours in early life stages.

Familiarity plays a crucial role in the social dynamics and behaviour of many animal species, including fish (Ward & Hart, 2003). The concept of familiarity refers to the ability to discriminate between individuals based on prior contact (Griffiths, 2003) and implies that conspecifics can discriminate between individuals based on visual, auditory and olfactory cues (Coffin et al., 2011; Fitch & Reby, 2001; Zajitschek & Brooks, 2008). The importance of familiarity is particularly evident in species that form social groups or shoals (Barber & Wright, 2001; Griffiths & Magurran, 1997), where the presence of familiar individuals can offer several fitness benefits. Familiarity improves foraging success in fish (Clark & Mangel, 1984; Krause & Godin, 1994; Pitcher et al., 1982), as prior social interactions could facilitate social learning, allowing fish to follow more experienced individuals when locating food sources, ultimately optimizing resource use (Swaney et al., 2001). Similarly, familiarity influences predator avoidance strategies. In antipredator scenarios, familiar groups may exhibit stronger cohesion (Chivers et al., 1995; Griffiths et al., 2004), reduced aggressive interactions (Griffiths et al., 2004; Johnsson, 1997; Tanner & Keller, 2012), fast-start escape responses (Nadler et al., 2021) and more synchronized escape responses, as individuals are more likely to trust each other's alarm signals (Bairos-Novak et al., 2019). Such coordinated reactions can improve predator avoidance and reduce individual predation risk. However, while these benefits are well-documented in adult fish, their role in early life stages remains less well understood. In particular, social learning during vulnerable stages such as larval and juvenile development plays a critical role in survival, as it allows individuals to learn from conspecifics and improve their chances of survival (Brown & Laland, 2003; Manassa & McCormick, 2013). Previous studies have shown that fish larvae and juveniles exhibit a preference for associating with familiar individuals, whether from their own brood (Gerlach et al., 2007; Rajakaruna & Brown, 2006) or those with whom they have previously interacted (Griffiths et al., 2003). Such preferences could have important consequences for their ability to form stable shoals, which, in turn, may enhance protection from predators and improve foraging efficiency (Griffiths et al., 2003, 2004). A better

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understanding of how familiarity influences these interactions can offer important insights into social and survival strategies of fish, as strong social bonds could enhance both cooperative foraging and collective defence against predators.

The current study aimed to explore the role of familiarity in the behaviour of fish larvae, focusing on how fish associate with familiar versus unfamiliar shoals and the potential impacts on foraging, routine swimming and escape responses, using wild sand smelt, *Atherina presbyter*, as a model species. Sand smelt is a marine shoal fish that lives in coastal and estuarine areas (Bamber et al., 1985; Pajuelo & Lorenzo, 2000). Adults spawn in coastal waters, laying large benthic eggs attached to vegetation that hatch into well developed (6.5–7.5 mm standard length) larvae (Bamber et al., 1985). Field and behavioural observations indicate strong group cohesion soon after hatching (A.M.Faria, personal observation), and ability to discriminate among habitats and conspecifics based on chemical cues (Vicente et al., 2020). We therefore hypothesize that sand smelt can show strong association with familiar individuals and expect that familiarity will enhance fitness related behaviours, namely foraging, routine swimming and escape response.

To test this hypothesis, we created two groups of sand smelt larvae: familiar groups, consisting of individuals that had been housed together for 2 weeks, and unfamiliar groups, composed of individuals from multiple tanks. By examining these behaviours in controlled laboratory settings, this study seeks to deepen our understanding of how familiarity influences the development of social and survival strategies in early life stages and how these behaviours may ultimately contribute to ecological success in the wild.

METHODS

Ethical Note

Sand smelt larvae were collected in the wild under the approval of Institute for Nature Conservation and Forests (ICNF; permit S-040651/2021). The study was conducted according to ISPA's animal ethics guidelines and under approval of General Directorate of Food and Veterinary Affairs (DGAV; permit 0421/000/000/2020). The behavioural observations were designed to avoid stress and discomfort to the subjects and followed the ASAB/ABS Guidelines for the Use of Animals in Research (https://doi.org/10.1016/j.anbehav.2019.11.002). The subjects were monitored throughout the experiment to ensure that they did not show signs of distress. All fish used in the experiment were naïve to the experimental protocol. After completion of the experiment, fish were placed back in maintenance tanks and later returned to the original collection site. Exception applies to fish used in the escape response trial, which were euthanized using an excessive dose of MS222 (400 mg/litre) for measurements purposes. Fish were left in the MS222 solution following cessation of opercular movement for 15 min.

Experimental Set-up and Design

Sand smelt larvae, of 21.48 ± 4.57 mm standard length (SL) (average ± SE), were collected at Portinho da Arrábida, Portugal (38°28′57.13″ N, 8°58′35.68″ W) on 9 July 2021, using 1 mm mesh dip nets. Larvae were immediately transported to the fish facilities of ISPA–Instituto Universitário, in 30-litre containers filled with sea water and gentle aeration. Upon arrival, larvae were randomly assigned to a total of six 30-litre tanks, at a density of 40 larvae per tank. Each tank was filled with artificial sea water, equipped with biological and chemical filtration, and maintained at a constant temperature of 16 °C and salinity of 35, mirroring conditions from the collection site. The photoperiod was set to 14:10 h light: dark to replicate the natural summer light cycle in Portugal. Opaque white sheets separated the tanks to prevent visual contact between the larvae. Larvae were fed ad libitum with recently hatched *Artemia* nauplii twice a day and left in the rearing tanks for a 2-week period, to familiarize prior to testing (Griffiths & Magurran, 1997).

Of the six rearing tanks, three were used as the source of fish to create familiar groups in the experimental arena, and three were used as the source of unfamiliar groups. The unfamiliar groups were formed by randomly taking one fish from each of the three source tanks and placing them together in the experimental arenas. Familiar groups were created by sourcing fish from the same tank. To minimize additional manipulation that could lead to mortality and because we meant to return larvae to the sea after the trials, individuals were not measured. However, the average fish size in the familiar and unfamiliar groups closely matched both within and between the groups, as shoals in the wild are often size-assorted (A.M.Faria, personal observation).

Larvae were initially tested for their preference to associate with familiar versus unfamiliar shoals. A total of 26 trials (i.e. 26 focal fish, 26 familiar shoals and 26 unfamiliar shoals) were conducted over days 1 and 2, between 0930 and 1830 hours. Each focal individual ($N = 26$) was tested once in their preference on either day 1 or 2. After these trials, fish were returned to their original tanks for further testing. From days 3–6, additional trials were conducted between 0930 and 1330 hours to evaluate foraging behaviour, routine swimming and escape responses. Different shoals were used for the different trials and test days.

Foraging behaviour was assessed once for shoal, in a total of 38 trials (19 familiar shoals and 19 unfamiliar shoals), after which the fish were transferred to different tanks, left undisturbed and were not further tested. Routine swimming and escape response trials were conducted sequentially, also once for shoal, in a total of 42 trials (21 familiar shoals and 21 unfamiliar shoals), where each shoal was first tested for routine speed and then immediately for escape response. Following these trials, fish were euthanized to obtain standard-length measurements for swimming speed analysis.

During experimental days, larvae were fed only after testing. At the study's conclusion, the remaining fish were returned to their original collection site. All experimental trials were conducted in a temperature-controlled room to minimize temperature fluctuations during testing, with set-ups enclosed by a black curtain to prevent external disturbances.

Familiarity

The response of larvae to familiar *vs.* unfamiliar shoals was tested in a choice arena (400 mm × 250 mm × 300 mm: length, width, depth), divided into three compartments, following a protocol adapted from Vicente and Faria (2021). The two outer compartments (each 70 mm wide) were separated from the central compartment (260 mm wide) by transparent, perforated Plexiglas barriers, with holes (1 mm in diameter, 5 ± 1 holes per cm^2) that allowed both visual and chemical cues to pass through. The choice arena was filled with artificial sea water at the same temperature and salinity as the rearing tanks.

Two stimulus shoals, each consisting of five fish (one familiar and one unfamiliar to the focal fish) following Ward et al. (2003), were placed in the two outer compartments. Familiar shoals comprised fish from the same tank as the focal fish, while unfamiliar shoals comprised fish from a different tank. After a 10 min habituation period, a focal fish was introduced to the central

compartment, inside a transparent, perforated cylinder (40 mm in diameter), positioned vertically at the centre. Following a 5 min habituation, the cylinder was removed, and the focal fish's behaviour was recorded for 10 min using a video camera (Sony Handycam DCR-SR58E). For the purpose of this experiment, a focal fish was defined as shoaling if it was within approximately two body lengths of the stimulus shoal.

After each trial, the focal fish and stimulus shoals were removed, and the test tank was washed with tap water before another trial. Each focal fish and stimulus shoal were used once to assess familiarity and subsequently returned to the original tanks. A total of 26 focal fish, 26 familiar shoals and 26 unfamiliar shoals were tested.

To account for possible side preference, the side of the tank occupied by familiar shoals was randomized between trials.

Video recordings were analysed blindly to treatment. The time spent by the focal fish in the central compartment and within the preference zone of each stimulus shoal was registered, as well as the number of visits to each zone.

Foraging

To investigate whether familiarity improved foraging, familiar and unfamiliar shoals composed of three individuals each were tested. Two 2-litre rectangular tanks were filled with artificial sea water at the same temperature and salinity of the rearing tanks. One familiar shoal and one shoal composed of unfamiliar fish were placed in each tank, and after 5 min of habituation, live *Artemia* (~300 individuals) were added to each tank. Behaviour was recorded from above (SONY handycam DCR-SR58E) for 2 min. After each trial, the shoals were transferred to different tanks, left undisturbed and were not further tested. Tanks were washed with tap water before another trial. A total of 19 familiar shoals and 19 unfamiliar shoals were tested.

Video recordings were analysed blindly to treatment. In each video, the number of strikes was determined. A strike was considered every time the fish opened the mouth and moved the head to attack the prey (Djurichkovic et al., 2019).

Routine Swimming and Escape Response

To investigate whether familiarity affected routine swimming and improved escape response, familiar and unfamiliar shoals composed of three individuals each were tested, following (Almeida et al., 2022; Warren et al., 2017) protocols. Briefly, one stimulus shoal was transferred to a circular test arena (190 mm in diameter, 80 mm depth), with temperature and salinity matching conditions from the rearing tanks. After a 5 min habituation period, routine swimming behaviour was recorded for 2 min. Subsequently, a startle response was elicited by dropping a weight attached to a wire (to touch the surface of the water and not collide with the fish), through a polyvinyl chloride (PVC) tube, placed above the arena. All fish responded to the first dropping of the weight and moved in the opposite direction. After the habituation period, when at least one of the three fish was facing the centre of the arena, the weight was dropped. Behaviour was recorded with a camera (Sony Cyber-Shot DSC-RX100M4) placed beneath the test arena. A mirror was positioned at a 45° angle from the horizontal so that the observed fish movement could be recorded, without external disturbances.

A total of 21 familiar shoals and 21 unfamiliar shoals were tested. Video recordings were analysed blindly to treatment. Minimum and maximum swimming speed (in body lengths per second, BL/s), and the total distance swam (cm) were determined to assess routine swimming behaviour. Escape response analysis included nonlocomotor [responsiveness, directionality, latency (ms)], and locomotor variables [distance (cm) and speed (BL/s)]. Videos were converted into frames (300 frames/s for latency analysis and 10 frames per second for speed and escape distance analysis) and analysed using ImageJ software (1.53v, https://imagej.net/ij/) with the manual tracking plugin. Latency was measured for the first individual to respond to the stimulus, as well as for the subsequent individuals, relative to the first responder.

After each trial, the shoals were removed, and the arenas were washed with tap water before another trial. Fish were euthanized with an excessive dose of MS222 and measured for SL.

Statistical Analysis

The time spent and the number of visits to each zone during the familiarity test was analysed using the generalized linear model (GLM) with tank zone as a fixed factor, following Tweedie distribution (link = 'log'). The Tukey post hoc test was used to examine the differences between zones. The number of strikes in the foraging test was analysed using the generalized linear mixed model (GLMM) with familiarity as a fixed factor and shoal as random factor, following a lognormal distribution. The minimum and maximum speed during routine swimming were analysed also with GLMM with familiarity as a fixed factor and shoal as random factor, following a Gamma (link = 'log') and lognormal distribution, respectively. However, the distance travelled was analysed with a linear effect model, according to a Gaussian distribution. For escape response, the latency of the response of the first individual and of the other fish to the response of the first were analysed using a GLMM with familiarity as a fixed factor and shoal as a random factor, according to a Gamma distribution (link = 'log'). While the escape distance and maximum speed were analysed using a GLMM with familiarity as a fixed factor shoal as random factor, following a lognormal and Gamma (link = 'inverse') distribution, respectively. Latency, escape distance and maximum speed during a response were measured for the three fish. All statistical analysis was developed in R statistics, RStudio (version 4.2.3, Posit Team, 2025). Values are reported as mean ± SE, and P values below 0.05 were considered significant.

RESULTS

Sand smelt larvae spent significantly more time close to familiar shoals (Table 1) and in the central area and visited familiar shoals more often compared with unfamiliar shoals (Fig. 1a and b).

Being in a familiar shoal did not prove to be advantageous in foraging activity, as the number of strikes to prey did not differ between familiar and unfamiliar shoals ($\chi^2 = 1.117$, $P = 0.291$), averaging 17.746 + 0.772 (Fig. 2).

Maximum and minimum speed ware not influenced by familiarity (max.speed $\chi^2 = 0.537$, $P = 0.464$; min.speed $\chi^2 = 0.694$,

Table 1
GLMM analysis of time spent and number of visits to each zone

	Estimate	SE	z	P
Time spent in each zone				
Familiar zone-central zone	1.22	0.238	1.041	0.551
Familiar zone-unfamiliar zone	22.60	8.665	8.131	**<0.001**
Central zone-unfamiliar zone	18.45	7.135	7.540	**<0.001**
No. of visits to each zone				
Familiar zone-central zone	0.927	0.22	−0.318	0.9456
Familiar zone-unfamiliar zone	8.476	3.37	5.370	**<0.001**
Central zone-unfamiliar zone	9.143	3.62	5.586	**<0.001**

P values in bold indicate statistical significance.

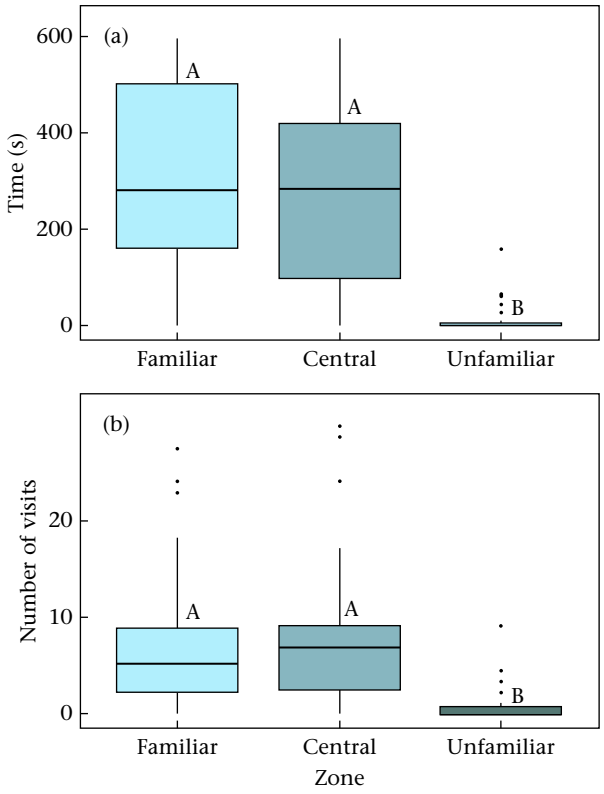

Figure 1. (a) Time spent and (b) number of visits to familiar shoal, central and unfamiliar shoal zones by sand smelt larvae. Different letters represent significant differences between zones. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

$P = 0.405$), ranging from 2.637+0.2 BL/s to 2.884 + 0.202 BL/s and from 0.169 + 0.014 BL/s to 0.151 + 0.014 BL/s, respectively (Fig. 3a and b). Similarly, the distance travelled was not influenced by familiarity either ($F = 0.0077$ and $P = 0.93$), varying between 447.117 + 28.208 cm and 450.761 + 25.924 cm (Fig. 3c).

Similarly, being in a familiar shoal did not improve escape performance of sand smelt larvae (response latency of first fish $\chi^2 = 0.44$ and $P = 0.51$; latency of the other individuals to the response of the first fish $\chi^2 = 0.15$ and $P = 0.7$; escape distance $\chi^2 = 0.055$, $P = 0.814$; maximum escape speed $\chi^2 = 2.2$, $P = 0.138$;

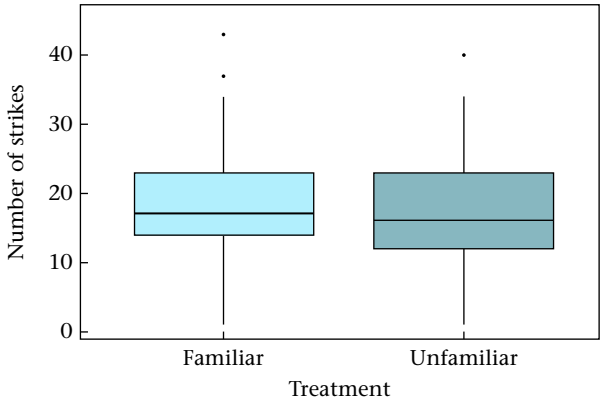

Figure 2. Number of prey strikes in familiar and unfamiliar shoals of sand smelt larvae. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

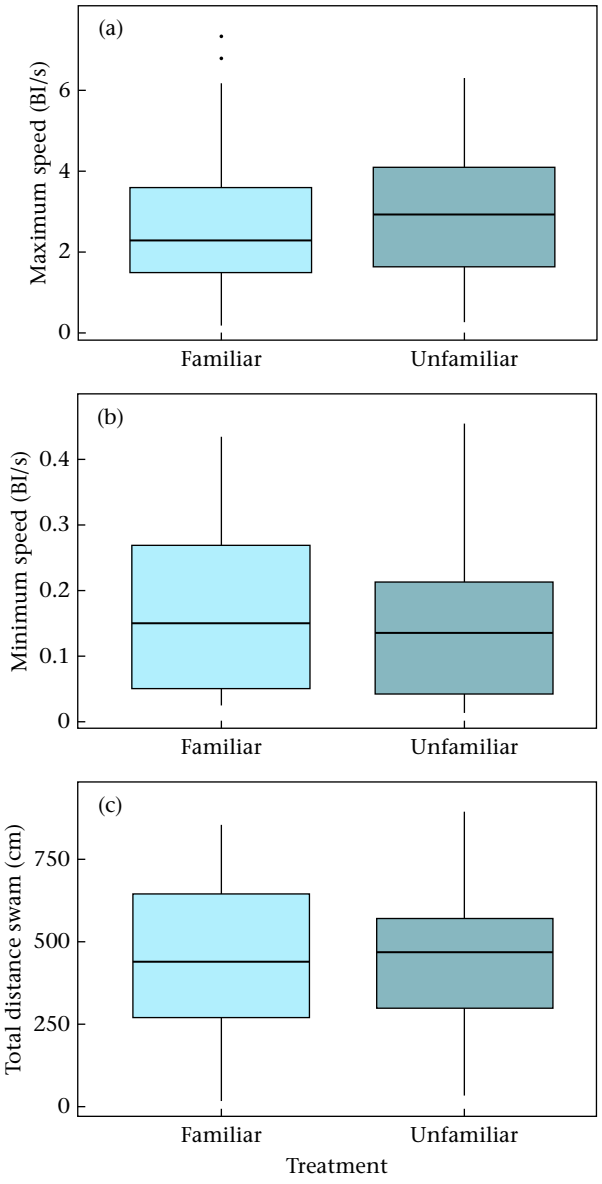

Figure 3. Routine swimming behaviour of familiar and unfamiliar shoals of sand smelt larvae. (a) Maximum speed (body lengths, BL/s), (b) minimum speed (BL/s) and (c) total distance swum (cm). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Fig. 4a–d). The percentage of fish that responded to the stimulus was 100%, with 100% turning away from the stimulus. The average latency of the first fish response was 28.545 ± 1.837 ms, and the latency to the first individual's response was 32.21 ± 3.363 ms, with larvae reaching a maximum speed of 3.921 + 0.193 BL/s and covering an average distance of 3.722 ± 0.183 cm.

DISCUSSION

Here, we provide evidence that shoals of sand smelt larvae may not be random assemblages of conspecifics, and that familiarity, based on past interactions, can influence the choice of shoaling partners. However, preference to associate with familiar conspecifics does not lead to fitness benefits, as familiarity did not translate into measurable improvements in behaviours critical to fitness, such as foraging, routine swimming or escape responses.

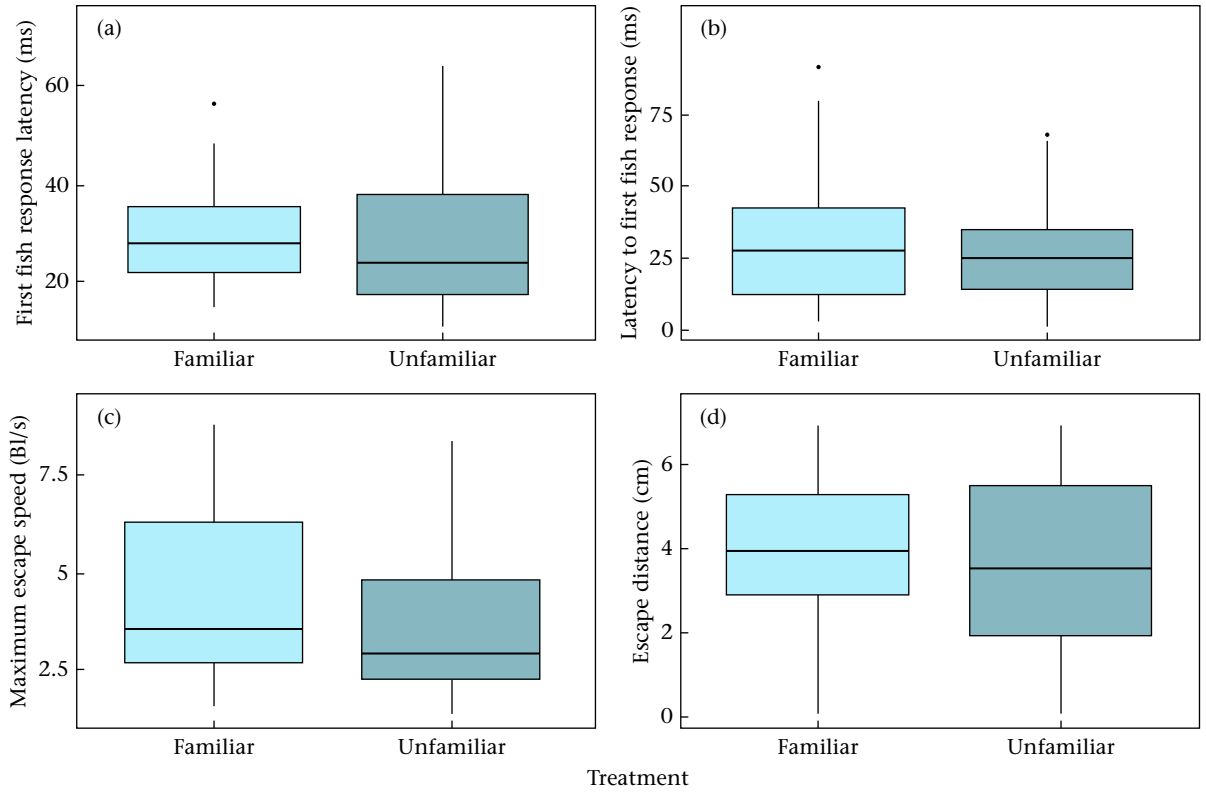

Figure 4. Escape response performance between familiar and unfamiliar shoals of sand smelt larvae. (a) Latency of response of first fish (ms), (b) latency to first fish response (ms), (c) maximum escape speed (body lengths, BL/s) and (d) escape distance (cm). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

To the best of our knowledge, this is the first study investigating familiarity benefits in larval stages.

Familiarity in fish, driven by prior social experiences, has been demonstrated across a wide range of species (Barber & Ruxton, 2000; Barber & Wright, 2001; Ward et al., 2003). This suggests that fish can recognize familiar conspecifics using group characteristics, such as chemosensory cues (Mehlis et al., 2008; Sisler & Sorensen, 2008) or visual traits like body size and coloration (Waas & Colgan, 1994; Ward & Krause, 2001). In this study, we provided sand smelt with access to both visual and chemical cues, following the findings of Vicente and Faria (2021), who proposed that visual cues and the combination of visual and chemical cues enhance association preferences more effectively than chemical cues alone. Interestingly, our results differ from Vicente and Faria (2021) who did not observe clear evidence of social preference for familiar individuals among sand smelt larvae. The authors hypothesized that the short period allowed for familiarity to be acquired (48 h) may have been insufficient for the larvae to develop a preference for conspecifics. Time is a known factor influencing schooling preferences (Griffiths & Magurran, 1997), and our findings appear to support this hypothesis: a 2-week period proved sufficient for the development of familiarity in sand smelt larvae.

The benefits of familiarity are well-documented across a variety of social species, where shoaling with familiar individuals can enhance survival through increased foraging efficiency (Ward & Hart, 2003), group cohesion (Chivers et al., 1995), body condition (Seppä et al., 2001) and improved predator escape response (Nadler et al., 2021). However, our findings tell a different story for sand smelt larvae: familiarity did not translate into fitness benefits when it came to foraging, swimming and escaping a threatening stimulus.

Several studies have provided evidence that familiar shoals convey significant foraging benefits. Shoals of familiar three-spined sticklebacks, *Gasterosteus aculeatus*, were faster to exploit food patches and obtained more prey items than shoals of unfamiliar fish (Ward & Hart, 2005) and were also more successful in finding food in a foraging task (Atton et al., 2014). Wild juvenile brown trout, *Salmo trutta*, foraged more than twice the rate of unfamiliar conspecifics (Griffiths et al., 2004). Morrell et al. (2008) similarly reported that natural shoals of the guppy, *Poecilia reticulata*, gain foraging benefits and that this may be facilitated by a reduced perception of risk among familiarized individuals and/or enhanced social learning mediated by following other individuals and small group sizes. Despite this evidence in the literature, sand smelt shoals of familiar fish did not show signs of higher foraging success compared with shoals of unfamiliar fish.

We anticipated that familiarity would induce changes in swimming patterns of shoals, predicting that shoals of unfamiliar fish would swim less and cover smaller distances, as a risk-averse strategy. However, we failed to detect an effect of familiarity on the swimming speed of sand smelt. Similarly, Ward and Hart (2005) reported no difference in the swimming behaviour of three-spined sticklebacks between familiar shoals and unfamiliar shoals, either in terms of position in the water column or distance swam.

We also investigated potential differences in the escape response between the familiar and unfamiliar shoals, predicting that familiar shoals would show an enhanced antipredator response. This was not the case, though. All fish, either from familiar or unfamiliar shoals, responded to the elicited stimulus, swimming in the opposite direction, and latency and kinematic components of the escape response (speed and distance) did not differ between treatment shoals. This result contradicts most of

the available literature on the topic. Familiar groups of juvenile brown trout responded faster than unfamiliar groups to a predator attack (Griffiths et al., 2004). In familiar schools of the tropical damselfish, *Chromis viridis*, first and subsequent responders exhibit shorter latency than unfamiliar individuals, and further, familiarity modulated kinematic performance in subsequent responders, demonstrated by increased agility and propulsion (Nadler et al., 2021). Preferential shoaling with familiar conspecifics of fathead minnows, *Pimephales promelas*, led to an increase in cooperative antipredator behaviour, attributed to increased group cohesion, a characteristic that might enhance predator confusion (Chivers et al., 1995). Despite this evidence, Wolcott et al. (2017) found that familiarity in guppies plays a less meaningful role in determining some behavioural components of the escape response, namely latency and magnitude of the response, which were correlated more with individual size than with level of familiarity within the group. They found support for their results in other studies (Gibb et al., 2006; Ojanguren & Braña, 2003) in which the magnitude of a fast-start response was largely determined by morphology, rather than by social conditions.

In summary, the overall results of our study suggest that familiarity does not enhance foraging, swimming speed or the response to a threatening stimulus in the early life stages of sand smelt. One hypothesis might in fact be related to the developmental stage. Larvae are still undergoing significant physiological and neurological development and may not yet possess the cognitive or motor abilities necessary to make the most of the advantages of familiarity. However, we are sceptical of this hypothesis, as prior studies have documented evidence of cognitive abilities even in larval stages (e.g. Roberts et al., 2013).

Alternatively, the conditions characteristic of larval life might explain the absence of fitness benefits associated with familiarity. Larvae inhabit environments where mortality risk is high, resources are abundant but patchy, and social groups exhibit a highly dynamic fission–fusion structure. Although grouping can confer several advantages, such as increased foraging and reduced risk of predation, it can also incur costs such as increased competition for resources, increased aggression and greater risk of parasitism (Kuruvilla et al., 2023). Therefore, groups might experience high turnover, meaning individuals must constantly adjust their behaviour to that of new members (Couzin, 2006). Such conditions may limit the evolutionary advantages of familiarity during the larval stage. Instead, being able to benefit from familiarity might only emerge later in life, when group cohesion and coordinated behaviours become more crucial for fitness and survival.

We cannot rule out the limitations of running this type of experiment in a controlled laboratory condition. The controlled environment, while essential for isolating the effects of familiarity, may not fully replicate the dynamic and complex environments larvae face in the wild. Factors such as varying predation pressures, habitat structures or competition could interact with familiarity in ways not captured here. Moreover, since we artificially established familiar groups rather than allowing them to form naturally, we might have influenced the outcomes of the study. Because wild-caught larvae were first pooled in the laboratory and then assigned to experimental groups, individuals with potentially different kinship ties, ecological backgrounds or prior social experiences were mixed and restructured into new groups. While this was necessary for maintaining experimental control, it likely disrupted any naturally occurring social bonds. As a result, the familiarity effects observed here may not fully capture those that would emerge in naturally assembled shoals. This disruption may also explain why familiarity did not lead to measurable behavioural benefits, as pre-existing social relationships, potentially shaped by shared experiences in the wild, might be essential for such advantages to arise. Future studies conducted in seminatural settings might reveal additional dimensions to these social interactions.

In summary, preference for associating with familiar conspecifics develops early in sand smelt; however, familiarity may offer little immediate advantage, underscoring that not all behaviours presumed to confer advantages do so at every stage of life. Future studies should investigate when (and if) sand smelt will benefit from familiarity later in life.

Author Contributions

Patrícia Nunes Vicente: Writing – original draft, Investigation, Writing – review & editing, Methodology, Formal analysis. **João Almeida:** Methodology, Formal analysis, Writing – review & editing, Investigation. **Ana Margarida Faria:** Writing – review & editing, Supervision, Project administration, Investigation, Formal analysis, Writing – original draft, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

The data set supporting this article is available in the Supplementary Material.

Declaration of Interest

We declare no conflicts of interest.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT to improve readability and language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123287.

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