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Influence of turbidity on group level responses to feeding in the Pacific white shrimp (*Litopenaeus vannamei*)

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ABSTRACT

The use of behaviour as a tool to improve welfare conditions within aquaculture is increasing, and our understanding of individual and group behaviour of commercially important penaeid shrimp has grown in recent years. However, the majority of studies investigating shrimp behaviour have used clear water conditions allowing for easier observation. Little is known about the influence of water turbidity on the feeding behaviour and social interactions of penaeid shrimp even though they are commonly reared for aquaculture in highly turbid ponds. Here, the behaviour of groups of four *Litopenaeus vannamei* juveniles (n = 144; 6.42 ± 0.28 g, mean ± S.E., body mass) was observed at three different turbidities; clear water (approximately 2 NTU, Nephelometric Turbidity Unit), medium turbidity (approximately 14.5 NTU) or high turbidity (approximately 30 NTU). Groups of shrimp were observed for 20 min within an experimental arena provided with feed, and video footage analyzed using an automated tracking software (EthoVision XT V14). Feed intake was greater in the high turbidity treatment compared to clear water, although no differences in behaviours related to the feeding area (e.g. time spent feeding, latency to feed) were found between treatments. Turbidity influenced exploratory behaviours, where shrimp held at the medium turbidity were more active than in the other treatments. Shrimp held in high turbidity also moved much more closely to each other than in the other treatments. These results highlight the importance of accounting for turbid water conditions when studying shrimp behaviour.

1. Introduction

It is acknowledged that a better understanding of shrimp behaviour could guide farmers towards improved feeding efficiency and profitability of shrimp aquaculture (Saberioon et al., 2017; Bardera et al., 2018). Recent work focusing on the feeding behaviour of farmed species of shrimp has provided valuable insights into the effects of stocking density (Costa et al., 2016), light conditions (Santos et al., 2016), moult status (Bardera et al., 2019) and sex (Bardera et al., 2020). The majority of this published research on *L. vannamei* behaviour has been conducted in optimal water quality under laboratory conditions (e.g. Pontes et al., 2006, 2008; Costa et al., 2016; Bardera et al., 2019, 2020). However, such conditions are far removed from those found in the majority of aquaculture ponds, where close control over water quality is more difficult to ensure and where there are often challenges that relate to water turbidity. Turbidity is an optical property of water causing light scattering and absorption (Ranåker et al., 2012; Borner et al., 2015), resulting in a diminution of visual cues for animals and changes to behaviours (Utne-Palm, 2002; Kimbell and Morrell, 2015). For behavioural experiments under laboratory conditions, turbidity is usually kept to a minimum through the application of recirculating technologies with mechanical filters. In ponds, however, fluctuating turbid conditions are present and originate from the suspension of sediments such as soil particles (Lin et al., 1992; Boyd and Tucker, 1998) and phytoplankton (Boyd and Tucker, 1998), but also from humic substances resulting from the degradation of plants (Boyd and Tucker, 1998). Farming protocols themselves can also heavily influence pond turbidity through water exchange rates, water decantation times and shrimp stocking densities.

In penaeid shrimp, previous studies have focused on the influence of water turbidity and light intensity on physiology (Lin et al., 1992; You

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et al., 2006; Guo et al., 2012; Kathyayani et al., 2019); to our knowledge no research has been published on the influence of turbidity on the behaviour of penaeid shrimp, including *L. vannamei*. In fishes, the influence of turbidity on behaviour has been studied extensively and shown to affect both predator-prey and social interactions (e.g. Benfield and Minello, 1996; Abrahams and Kattenfeld, 1997; Ranåker et al., 2012; Borner et al., 2015; Kimbell and Morrell, 2015; Zanghi and Ioannou, 2025). In turbid environments, prey species may be better able to hide from visual predators, with the foraging success of predatory species negatively impacted (Zanghi and Ioannou, 2025). For example, Benfield and Minello (1996) found fewer daggerblade grass shrimp (*Palaemonetes pugio*) were consumed by Gulf killifish (*Fundulus grandis*) in turbid conditions. However, effects of turbidity on predator-prey interactions become more complex when combined with other environmental stressors such as increased temperature (Zanghi et al., 2023).

Turbidity can also alter a variety of social interactions through interference with visual signals (Borner et al., 2015; Zanghi and Ioannou, 2025). Fish shoals often become less cohesive in turbid conditions (Chamberlain and Ioannou, 2019), the cohesion of the group may become less stable (MacGregor and Ioannou, 2023), and groups can become less aggregated (Allibhai et al., 2023). Another aspect of social behaviour potentially influenced by turbidity is the level of inter-individual variation. Within a social group, individuals may alter their behaviour to be more similar (conformity) or different (differentiation) to their conspecifics (Ioannou and Laskowski, 2023), likely as a result of visual cues. Conformity may enhance group cohesion in social species, but may also be driven by antagonism in cannibalistic species such as crickets (Bazazi et al., 2010). Research into the behavioural effects of turbidity in aquatic animals has focused primarily on fishes, and the impacts of turbidity on penaeid shrimp behaviour, both in relation to feeding and social interactions remain unexplored.

The aim of this study was to provide a better understanding of the influence of turbidity on *L. vannamei* behaviour. The impact of three water turbidity treatments (2.4 ± 0.4, 13.6 ± 0.4 and 30.4 ± 0.7 NTU, Nephelometric Turbidity Unit, mean ± S.E.) on juvenile shrimp group behaviour was investigated, exploring changes in key behaviours related to shrimp interaction with feed, use of the tank environment and inter-individual variation in behaviour.

2. Materials and methods

2.1. Animal husbandry

Two batches of 72 *L. vannamei* shrimp (6.42 ± 0.28 g; mean ± S.E., body mass) were purchased 1 month apart from Great British Prawns Ltd (Balfron, United Kingdom) which used indoor facilities with a recirculating aquaculture system (brown water). Shrimp were then held inside two 300 L recirculation systems in a laboratory at the University of the West of Scotland, each system comprising three holding tanks (60 × 37 × 40 cm, length × width × depth) and a sump tank (65 × 50 × 39 cm) with aeration provided within all the tanks. Water temperature was kept at 27°C (± 1°C), salinity at 20 $g.L^{-1}$ through the use of artificial sea salt (Seamix, Peacock salt), pH at 7.8 and dissolved oxygen > 5 $mg.L^{-1}$. Water was exchanged at a rate of 20 % per day. Photoperiod was set at 12 h:12 h (light:dark) and nitrogenous compounds were kept below the safety limits of 2.44 $mg.L^{-1}$ for ammonia-N and 6.1 $mg.L^{-1}$ for nitrite-N for juvenile *L. vannamei* (as per (Lin and Chen, 2001), (Lin and Chen, 2003) through biological filtration and water exchanges. For the first week, shrimp were fed *ad libitum* with a 57 % crude protein diet (Gemma Diamond 1.0, Skretting France) equally divided across four meals per day (08.30, 13.00, 16:00 and 19.00). Excess food and faeces were removed after each meal.

2.2. Experimental design

Following a week within the stock tanks, shrimp were selected from the recirculation systems to form 36 groups of four individuals, where each group was given an ID. Prior to placing into their groups, shrimp were held in small individual cages (diameter 18 cm) within three acclimation tanks with the same water quality parameters as the holding tank. Shrimp were held in individual cages to avoid aggression during acclimation. Acclimation tanks were either supplied with clear (2.4 ± 0.4 NTU, mean ± S.E.) or turbid water (13.6 ± 0.4 or 30.4 ± 0.7 NTU) through the addition of kaolin clay (AkuaPro, Imerys Kaolin) suspended in the water column with airstones and a pump to generate a water current. Turbidity was manipulated either by turning the pump off and allowing the clay to settle, thus decreasing turbidity, or by adding clay to the sump. Turbidity was monitored by twice daily measurements in the acclimation tanks (08.00 and 19.30) using a Hach 2100 A turbidimeter. Although both TSS (Total Suspended Solids) and nephelometric measurements are commonly reported in aquaculture studies (e.g. Ferreira et al., 2011, Ma et al., 2013, Mohanty et al., 2018), the latter was chosen to measure turbidity in the experiment as advised by APHA (1999). Strong relationships between NTU and TSS values have been found in the existing literature (e.g. Hannouche et al., 2011; Xu and Boyd, 2016), where it has been suggested that one measurement can be used as a proxy for the other (Nasrabadi et al., 2016).

The main experimental design involved exposing groups of shrimp to three different turbidity treatments sequentially. To ensure that there were no confounding effects of repeated behavioural observations on the same group of shrimp over time, we firstly exposed four groups of shrimp to three consecutive treatments of the same turbidity (three turbidity treatments = 12 groups in total). The three turbidities were: clear water (CW, 2.4 ± 0.4 NTU, mean ± S.E.), medium turbidity (MT, 13.6 ± 0.4 NTU) and high turbidity (HT, 30.4 ± 0.7 NTU). Each shrimp spent an initial 24 h acclimating to its treatment turbidity within its individual cage and was then placed in its group into the experimental arena (see below) containing water of the same turbidity for behavioural observation (respectively 1.8 ± 0.1, 15.8 ± 0.2 and 29.2 ± 0.4 for CW, MT and HT treatments, mean ± S.E.). Once this was complete, shrimp were returned to their individual cages within the acclimation tanks at the same turbidity level for 24 h before this process was repeated twice more. Returning shrimp to their individual cages in between behavioural observations avoided high levels of conspecific aggression. Each group of shrimp was therefore recorded three times (n = 4 groups per treatment). Shrimp were only fed during observation sessions in the experimental arena.

As no significant effects of repeated behavioural observations on the same group of shrimp over time were found (see Results), for the main experiment, each group of four shrimp was exposed sequentially to the three different turbidity treatments in a randomized sequence (n = 4 groups per sequence, 24 groups in total) as shown in Table 1. Each shrimp spent an initial 24 h acclimating to its first turbidity treatment within its individual cage and was then placed in its group into the experimental arena with water of similar turbidity. Once this was complete, shrimp were returned to their individual cages within the acclimation tanks at the turbidity level corresponding to their next treatment in the sequence for 24 h before this process was repeated for the remaining turbidities. Each group of shrimp went through one

Table 1
Randomized orders of turbidity treatments that groups of shrimp (n = 4 groups per sequence, 24 groups in total) were exposed to during the main experiment. CW=clear water, MT=medium turbidity, HT=high turbidity.

Sequence number	Treatments
1	CW – MT – HT
2	HT – MT – CW
3	MT – CW – HT
4	CW – HT – MT
5	MT – HT – CW
6	HT – CW – MT

sequence of turbidity treatments and was therefore recorded three times. As before, shrimp were only fed during observation sessions in the experimental arena.

2.3. Experimental arena

A circular experimental arena was used to observe the behaviour of the groups of shrimp (69 cm×36 cm; diameter × depth), filled with 50 L of artificial sea water. Following preliminary experiments, the tank bottom was covered with white plastic to increase contrast between shrimp and the background and contrast settings on the camera software were optimized for the room conditions (see Fig. 1a,b). Light conditions above the experimental arena were the same between trials (measured at 271 ± 10 Lux, mean ± S.E.) with a light source directed away from the surface of the tank to avoid light reflection and loss of shrimp tracking. For each recording, shrimp were placed into the experimental arena within their individual cages and allowed to acclimate for 10 min. After the acclimation period, individual cages were removed and 20 min of footage was recorded using a camera (acA1300–30gm, Basler AG, Germany) positioned 110 cm above the water surface, providing a top-bottom view of the tank. A known amount of feed (36.6 % protein and 7.9 % fat content; 2 g; Skretting ARC, Stavanger) was added into a central feeding area (i.e. in the center of the tank) before shrimp were initially introduced.

Footage was recorded on a laptop using the Basler pylon Viewer software with high contrast settings (Fig. 1a,b). It was then analysed automatically using EthoVision XT version 14 (Noldus Information Technology, the Netherlands) with EthoVision Social Interaction Module at 5 frames per second, which allowed for tracking of the shrimp and the acquisition of their coordinates. Manual corrections to tracking results were applied when necessary, particularly when occlusions occurred as individuals crossed paths or remained on the feed.

Turbidity was checked twice during the 20 min recording period, a minute before shrimp were introduced to each other and 1 min after the last shrimp was removed from the tank at the end of the experiment. For this, a 25 mL water sample was taken from the water column in the middle of the tank and measured using a Hach 2100 A turbidimeter. A generalized linear model (GLM, Gaussian family) using the R package 'lme4' (Bates et al., 2021) with treatment and time of water sampling as fixed factors confirmed an effect of treatment (χ^2 (2) $= 6764.4$, $p < 0.001$) but not time of sampling (χ^2 (1) $= 1$, $p = 0.31$) or their interaction (χ^2 (2) $= 1.9$, $p = 0.39$) on turbidity values.

Water was changed between each observation and new feed was provided. While moulting phase was monitored continuously throughout the trials (according to Bardera et al., 2019), shrimp were selected from across the whole moult cycle as it was not logistically possible to select individuals at certain moult stages.

Feed leftovers were siphoned after each recording to allow for the calculation of feed intake which was calculated by dividing the amount of feed recovered (g, dried at 60°C for 12 h) from the tank after the observation session by the initial amount of feed provided in the tank (g, on a dry matter basis). To account for feed dry matter losses in water, three control feed samples were previously immersed in water for 30 min without any shrimp and then dried in the oven (at 60 °C for 12 h).

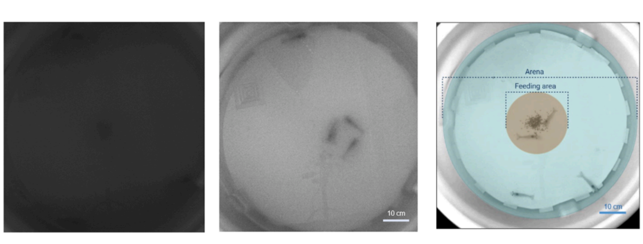

Fig. 1. (a, b) Two frames of the same four shrimp at a similar water turbidity level (28 NTU) before (a) and after (b) reflective background material and high contrast settings were applied. (c) Top view of the test arena in control (CW) conditions with the feeding area at the center. Created with BioRender.com.

2.4. Behavioural units and summary metrics

A 24 cm diameter feeding area was defined around the feed on EthoVision (Fig. 1c) and behaviours displayed by each individual within a group during each video were determined. To process video footage, an ethogram was developed based on known feeding responses, interactions with the test arena and social interactions (Table 2). The behaviours tracked and calculated by EthoVision were time spent feeding on the central feeding area, latency to first feeding, number of transitions to the feeding area, mean distance to feed, time spent moving, total distance moved, mean velocity, and mean distance between subjects.

2.5. Statistical analysis

To determine whether repeated observations of the same group of shrimp on consecutive days affected behaviour, the effect of turbidity was first analysed for each behaviour in groups of shrimp that were consecutively exposed to the same turbidity using generalized linear mixed models (GLMM) in the R package 'lme4' (Bates et al., 2021). Turbidity and time were included as fixed factors and group ID as a random factor ($n = 4$ groups for each turbidity level with three repeated observations for each group over time) (Zuur et al., 2009). To assess whether residuals followed the assumed distribution, q-q plots were visually assessed (functions 'qqnorm' and 'residuals' from the package 'stats'). Data followed Gamma distributions except for 'Number of transitions' which followed a Poisson distribution.

Based on these initial analyses, time was not found to have a significant effect on repeated group observations (see Results), therefore for the main experiment univariate models were built for each behaviour with turbidity as a fixed factor and group ID as a random factor using the R package 'lme4' for trials where shrimp were randomly exposed to different turbidities ($n = 4$ groups for each turbidity sequence, six sequences; as in Table 1) (Zuur et al., 2009; Bates et al., 2021). Where significant effects of turbidity were found, post-hoc comparisons between treatments were conducted using the R package 'multcomp' (Hothorn et al., 2021). Sequence was not included as a factor in statistical analysis as no effects of time were found in the preliminary trials and the number of groups per sequence was low.

As shrimp were at varying stages of the moult cycle, individual

Table 2
Metrics measured using EthoVision XT V14 tracking software (adapted from Costa *et al.,* 2016 and Bardera et al., 2021).

Behaviours	Metric	Description
Behaviours in relation to feeding area	Time spent feeding	Time (s) spent on the feeding area, eating food.
	Latency to first feeding	Time (s) taken by shrimp to first arrive at the feeding area.
	Number of transitions	Number of times the shrimp entered the feeding area.
	Mean distance to feed	Mean distance (cm) between shrimp and feeding area during the recording.
Behaviours in relation to test arena	Time spent moving	Total time spent moving (s) during the recording.
	Total distance moved	Distance (cm) travelled by shrimp during the recording.
	Mean velocity	Mean velocity (cm.s^{-1}) of the shrimp during the recording.
Social behaviour	Mean distance between subjects	Mean distance (cm) between shrimp of the same group during the recording.

shrimp were not marked in this study and so could not be tracked across different observation sessions. However, as the behaviour of each individual shrimp was observed within each group, the levels of within-group variation could be considered for each separate time point. To compare the levels of intra-group variation in shrimp behaviours and assess whether it differed between turbidity treatments, coefficients of variations were calculated for each group and observation session for the six sequences where turbidity was consecutively changed (see Table 1), resulting in 24 measurements of variation per treatment. Coefficient of variation is a measure of dispersion, calculated by dividing the standard deviation of the dataset by its mean. Therefore, for each group and observation session, the standard deviation for each behavioural metric among all four shrimp was calculated and divided by its mean. Differences in coefficients of variation between treatments were investigated using the previously described method, i.e. generalized linear mixed models (GLMM, Gamma family) in the R package 'lme4' (Bates et al., 2021) with turbidity as a fixed factor and group ID as a random factor (n = 4 groups for each turbidity sequence, six sequences) (Zuur et al., 2009). Where significant effects of turbidity were found, post-hoc comparisons between treatments were conducted using the R package 'multcomp' (Hothorn et al., 2021).

Differences in the percentages of feed consumed by shrimp between treatments were investigated using a Friedman test from the R package 'rstatix' (Kassambara, 2021) followed by post-hoc pairwise Wilcoxon signed-rank tests from the same package. A Bonferroni correction was applied to account for multiple comparisons.

3. Results

Where groups of shrimp were consecutively exposed to the same turbidity, there was no effect of time (i.e. repeated observations) on any of the behaviours (time spent on feeding area: χ^2 (2) = 1.61, p = 0.45; latency to first feeding: χ^2 (2) = 1.69, p = 0.43; number of transitions: χ^2 (2) = 4.02, p = 0.13; mean distance to feed: χ^2 (2) = 1.06, p = 0.59; time spent moving: χ^2 (2) = 0.27, p = 0.88; total distance moved: χ^2 (2) = 0.48, p = 0.79; mean velocity: χ^2 (2) = 0.21, p = 0.90; mean distance between subjects: χ^2 (2) = 2.29, p = 0.32).

3.1. Influence of turbidity on behaviour

No significant effect of turbidity was found on behaviours related to the feeding area which included the amount of time spent feeding (χ^2 (2) = 2.24, p = 0.32), latency to first feeding (χ^2 (2) = 2.66, p = 0.27), number of transitions (χ^2 (2) = 5.43, p = 0.07) and mean distance to feed (χ^2 (2) = 2.64, p = 0.27). A significant effect of turbidity was found on group-level variability for the mean distance to feed metric (χ^2 (2) = 8.61, p = 0.01) with groups observed at high turbidity showing more variability than in clear water (Z = 2.89, p = 0.01). However, no treatment effects on group-level variability were found for the other feeding behaviours (time spent feeding: χ^2 (2) = 1.67, p = 0.43; latency to first feeding: χ^2 (2) = 1.08, p = 0.58; number of transitions: χ^2 (2) = 1.81, p = 0.40).

For behaviours related to use of the test arena, a significant effect of turbidity was found on the amount of time shrimp spent moving (χ^2 (2) = 8.94, p = 0.01), with individuals exposed to high turbidity spending less time moving compared to medium turbidity (Z = -2.99, p = 0.01, Fig. 2a). A significant effect of turbidity was also observed on the total distance moved (χ^2 (2) = 25.68, p < 0.001) with shrimp exposed to medium turbidity travelling more compared to those in clear water (Z = 4.99, p < 0.001) or high turbidity (Z = -3.99, p < 0.001) (Fig. 2b). A significant effect of turbidity was also found on the mean velocity (χ^2 (2) = 9.00, p = 0.01) with shrimp at medium turbidity moving faster than at higher turbidity (Z = -2.83, p = 0.01, Fig. 2c). No significant differences in the level of variation were found for all behaviours related to use of the test arena (total time spent moving: χ^2 (2) = 3.70, p = 0.16; total distance moved: χ^2 (2) = 1.42, p = 0.49; mean velocity: χ^2 (2) = 1.42, p = 0.49).

Regarding social behaviours, a significant effect of water turbidity was observed on the mean distance between subjects (χ^2 (2) = 19.56, p < 0.001) with shrimp held at high turbidity being closer to each other than in clear water (Z = -4.22, p < 0.001, Fig. 3) and medium turbidity (Z = -3.15, p = 0.047). No significant effect of turbidity was found on group-level variability for the mean distance between subjects (χ^2 (2) = 2.46, p = 0.29).

3.2. Influence of turbidity on feed intake

There was a significant effect of turbidity on the feed intake (χ^2 (2) = 16, p < 0.001) with shrimp held at the highest turbidity ingesting more feed than those observed in clear water (Wilcoxon signed rank test: v = 11, p < 0.001) (Fig. 4). No significant differences were observed between the medium turbidity treatment and the clear water (Wilcoxon signed rank test: v = 138, p = 1.0) or high turbidity treatment (Wilcoxon signed rank test: v = 230, p = 0.06).

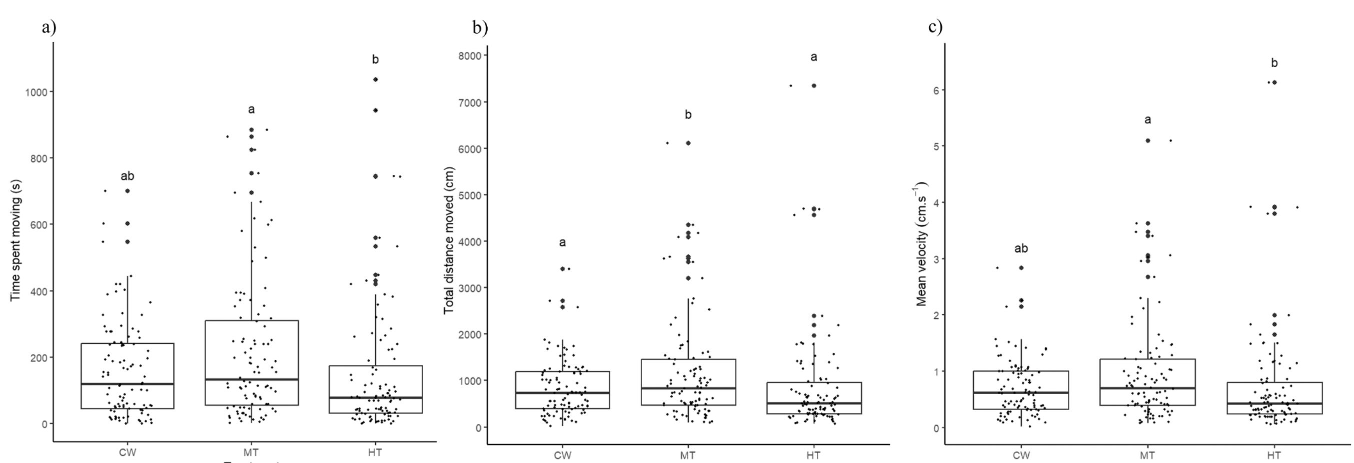

Fig. 2. Behaviours related to use of the test arena according to turbidity with (a) time spent moving, (b) total distance moved, (c) mean velocity (clear water CW, medium turbidity MT and high turbidity HT) (n = 4 groups for each turbidity sequence, six sequences). Results are presented as box plots with superimposed points that are individual shrimp (n = 96), median and interquartile ranges. Significant differences (p < 0.05) are indicated by different letters where boxes sharing a letter are not significantly different.

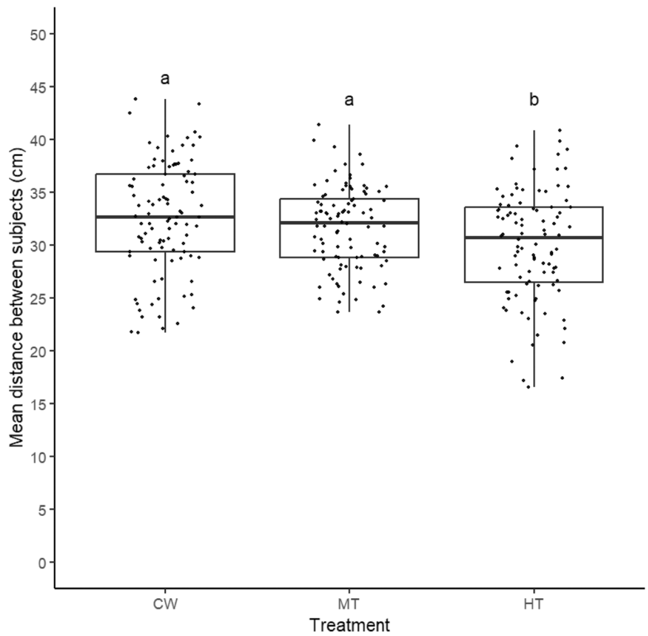

Fig. 3. Mean distance between subjects according to turbidity (clear water CW, medium turbidity MT and high turbidity HT) (n = 4 groups for each turbidity sequence, six sequences). Results are presented as box plots with superimposed points that are individual shrimp (n = 96), median and interquartile ranges. Significant differences ($p < 0.05$) are indicated by different letters where boxes sharing a letter are not significantly different.

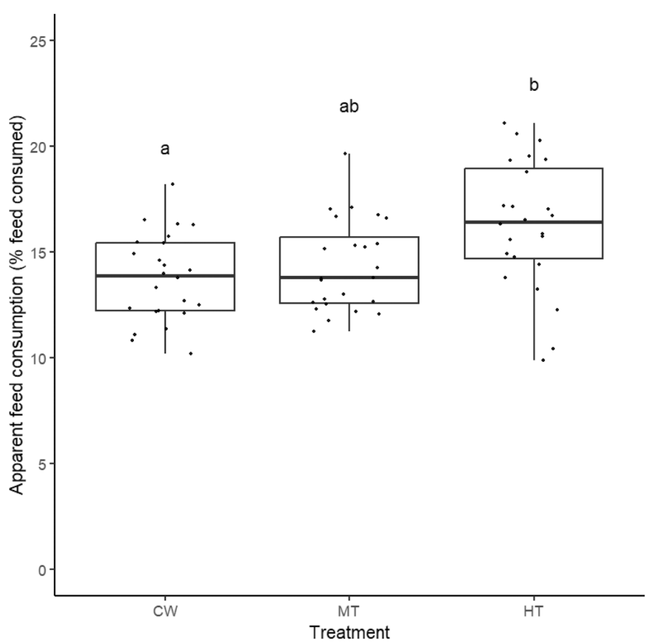

Fig. 4. Feed consumption according to turbidity (clear water CW, medium turbidity MT and high turbidity HT) (n = 4 groups for each turbidity sequence, six sequences). Results are presented as box plots with superimposed points representing the value for each group (n = 24), median and interquartile ranges. Significant differences ($p < 0.05$) are indicated by different letters where boxes sharing a letter are not significantly different.

4. Discussion

Although general understanding of the behaviours of cultured penaeid shrimp species is growing (e.g. Pontes et al., 2006; Costa et al., 2016; Bardera et al., 2019, 2020), little is still known about the role of water turbidity in influencing feeding behaviour and the construction of social interactions. Therefore in this study, an automatic tracking software (EthoVision XT V14) was used to assess the effect of turbidity on the behaviour of *L. vannaemei,* a commercially important species of penaeid shrimp. Through exposure to clear water, medium and high turbidity conditions, differences were found in exploratory behaviours, with shrimp held at high turbidity less active than those held at medium turbidity. Shrimp observed at high turbidity also moved closer to each other. While no significant differences were observed on metrics related to feeding behaviour among treatments, shrimp held at high turbidity consumed more feed than in clear water. We therefore highlight the important influence that turbid conditions can have on group-level shrimp behaviour and feed intake.

Turbidity had a significant effect on exploratory behaviours, with shrimp held in medium turbidity being more active than shrimp held in high turbidity, moving faster, spending more time moving and travelling greater distances. Additionally, shrimp held in medium turbidity travelled greater distances on average than shrimp held in clear water. No differences were observed in exploratory behaviours between shrimp held in the high turbidity and clear water treatments. This finding aligns with several fish species where an increase in turbidity decreases activity and swimming speeds (e.g. Gray et al., 2012, Borner et al., 2015, MacGregor and Ioannou, 2023). However, Wing et al. (2021) suggested that those findings could be highly dependent on the surrounding environment, and especially on the presence or absence of food within the observation tank. In line with this, Leahy et al. (2011) reported a significant decrease in exploration among juveniles of the spiny damselfish (*Acanthochromis polyacanthus*) from medium to high turbidity, but did not find any differences between clear water and medium or high turbidity treatments. A similar pattern was found here for most metrics related to exploration.

It is possible that shrimp perceived the medium turbidity water as less risky than the highly turbid and clear water environments. This is similar to findings of Chamberlain and Ioannou (2019), who demonstrated that increased water turbidity resulted in a higher perception of predation risk in groups of sticklebacks (*Gasterosteus aculeatus*) compared to clear water. However, this does not explain why no differences were found between the clear water and high turbidity treatments in any of the exploratory behaviours. It is also possible that individuals took longer to assess their environment in the high turbidity treatment through vision (Chamberlain and Ioannou, 2019), which could have resulted in this reduction of activity from the medium to the high turbidity treatments.

This study found that the highest turbidity led to closer distances between individual shrimp. One explanation is that shrimp avoid each other when kept in clear water, and that reduced water clarity lowers stress induced by the presence of conspecifics and aggression is reduced, as seen in brown trout, *Salmo trutta* (Eaton and Sloman, 2011). Although penaeid shrimp are known to be less cannibalistic than other cultured groups of crustaceans such as crabs and lobsters (Romano and Zeng, 2017), aggressive behaviours between conspecifics have been documented (Moss and Moss, 2006; Bardera et al., 2021). Newly moulted individuals are also more likely to be attacked and eaten (Bolingbroke and Kass-Simon, 2001; Marshall et al., 2005; Romano and Zeng, 2017), and an explanation for the apparent high moulting intensity in shrimp ponds after sunset during the new moon, is that shrimp can better hide and avoid cannibalism (Lemos and Weissman, 2021). Turbidity could therefore influence responses induced by the presence of conspecifics, and may partially explain the reduced distance between subjects in the high turbidity treatment. Cannibalistic species may also show conformity in social behaviours to avoid conspecific aggression (Bazazi et al., 2010) however, little evidence for influences of turbidity on inter-individual behavioural variation was seen in the present study. Nevertheless, such explanations should be considered in future trials, especially in ponds where social behaviours might be different from laboratory conditions.

The behavioural differences observed in shrimp may be a result of stress responses in reaction to turbidity and light intensity. Previous studies in penaeid shrimp suggest that an increase in fleeing behaviour and eye beat frequency are indicators of an increase in stress levels (Bardera et al., 2019, 2020). Those events were not recorded in this trial but could be investigated in future work in combination with stress-related physiological parameters. Very high turbidity (120 NTU) led to four times higher mortality of *L. vannamei* (Kathyayani et al., 2019) compared to shrimp held in clear water after 21 days of exposure. Physiological parameters (i.e. osmolality, glucose and lactate) were also higher at 120 NTU than in clear water (Kathyayani et al., 2019). Reduction in light intensity induced by an increase in turbidity in ponds, where depth can sometimes reach 3 m, is another factor that may influence stress levels and growth of the animals since there is evidence that moulting is particularly intense during the new moon when light is minimal as previously mentioned (Lemos and Weissman, 2021).

There were no significant differences in shrimp feeding behaviours between turbidity treatments, although an upward trend for the amount of time spent on the feeding area with increased turbidity was observed. However, a significant increase in feed intake at high turbidity compared to the clear water treatment was found. Previous work on the behaviour of *L. vannamei* held at similar shrimp densities did not find significant relationships between the amount of feed consumed and behaviours related to the test arena (Table 2, Bardera et al., 2021), in agreement with findings in the present study. This observed increase in feed intake with turbidity aligns with previous observations that penaeid shrimp rely mostly on olfaction to detect feed and not vision, with *L. vannamei* individuals reared in the dark for 50 days showing similar levels of feed intake to shrimp exposed to an incandescent light source during the day but also both during the day and night (You et al., 2006). In contrast, Kawamura et al. (2017) found sight to play a significant role in feeding, since blinded *L. vannamei* juveniles (with painted eyestalks) detected feed pellets only after accidentally touching them with their walking legs, compared to untreated individuals who approached the feed faster. However, the authors observed plasticity in the feeding behaviour of blinded shrimp, with individuals modifying their food search posture after first contact with a pellet (Kawamura et al., 2017).

In the trials reported here turbidity was artificially induced through the addition of kaolin clay in both the water used for the conditioning of the shrimp and for behavioural observations. However in shrimp industrial ponds and tanks, turbidity may result from other factors such as the presence of earth materials, phytoplankton blooms and suspended organic matter such as bacterial flocs. Furthermore, it is known that shrimp production systems can result in turbidity values far greater than the maximum tried in this study, which was set at 30 NTU to still be able to automatically track the shrimp. Further studies should therefore focus on assessing the impact of water sampled from different types of production systems on shrimp behaviour, which would widen our understanding. Shrimp production systems or protocols such as bioflocs for example are known to result in high turbidity values (Krummenauer et al., 2014). However, water from facilities using these kinds of techniques also might have different impacts on shrimp behaviour when compared to water from other production systems at the same turbidity values because of the differences in the nature of suspended materials and water chemistry.

It should also be noted that in turbid aquaculture ponds, an additional novel alternative to visual assessment of feeding activity is the use of passive acoustic monitoring based on the clatter of penaeid shrimp's mandibulae, which can be used as a proxy of feeding activity (Smith and Tabrett, 2013). Feeders based on the pond acoustics are currently in use in most shrimp producing regions, such as South-East Asia and Latin America (Reis et al., 2022). Although passive acoustic systems could be used to study shrimp behaviour in relation to time, space and water parameters (including turbidity) at a large scale in ponds (Smith and Tabrett, 2013), such studies have yet to be published (Darodes de Tailly et al., 2021, Reis et al., 2022).

5. Conclusion

The present study demonstrated the influence of water turbidity on the behaviours of *L. vannamei*. Shrimp were more active in the medium turbidity treatment, moving 1.4 times the mean distance explored in clear water or high turbidity. Although no significant differences in the display of feeding behaviours were observed between groups, shrimp held at the highest turbidity were found to feed 22 % more than in the clear water treatment, which highlights the importance of water turbidity in the feed intake of penaeid shrimps. Distances between shrimp were also influenced by water turbidity, with shrimp kept at the highest turbidity moving closer to each other during observation sessions. Further studies will need to focus on the effect of water turbidity on stress in shrimp, through a combination of behavioural and physiological approaches and the use of other agents to artificially increase turbidity.

CRediT authorship contribution statement

Jean-Benoit Darodes de Tailly: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Guillermo Bardera:** Writing – review & editing, Conceptualization. **Matthew Owen:** Writing – review & editing, Conceptualization. **Jonas Keitel:** Writing – review & editing, Conceptualization. **Jose Alcaraz-Calero:** Writing – review & editing, Conceptualization. **Katherine Sloman:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Mhairi Alexander:** Writing – review & editing, Supervision, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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