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Effects of flow velocity on fitness-related behaviours of the sea urchin *Mesocentrotus nudus*: new information on stock enhancement

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Abstract

The effects of flow velocity on the fitness-related behaviours of *Mesocentrotus nudus* remain largely unknown, greatly hampering the efficiency of stock enhancement. To explore the appropriate velocities for stock enhancement, we investigated dislodgement and immobilization velocities up to 90 cm s^{-1}. The experimental results showed that *M. nudus* (test diameter of ~30 mm) were dislodged at 73.50 ± 7.7 cm s^{-1} and that *M. nudus* movement occurred only when the flow velocity was less than 33.40 ± 2.7 cm s^{-1}. Three flow velocities less than 33.40 ± 2.7 cm s^{-1} (2, 10 and 20 cm s^{-1}) were subsequently used to study the effects of flow velocities on covering behaviour and the righting response time of *M. nudus*. The downstream movement velocity of *M. nudus* was significantly larger than that upstream at 2 cm s^{-1} ($P = 0.016$) and 10 cm s^{-1} ($P = 0.008$), but not at 20 cm s^{-1} ($P = 0.222$). The righting response time of *M. nudus* was significantly longer at 20 cm s^{-1} than that at 2 cm s^{-1} ($P = 0.015$). The present study indicates that a flow velocity less than 20 cm s^{-1}, preferably 2–10 cm s^{-1}, is probably appropriate for the stock enhancement of *M. nudus*. Notably, the current study is a laboratory investigation without considering the hydrographic complexity in the field. Further studies should be carried out to investigate the long-term effects of water flow on feeding and growth of *M. nudus* both in the laboratory and the field.

Introduction

Besides their ecological importance (Willoughby, 2018; Ling *et al.*, 2019), sea urchins are of commercial importance (Lauzon-Guay & Scheibling, 2007; Rahman *et al.*, 2014). Sea urchins have been overfished around the world because of the increasing market requirements (Cirino *et al.*, 2017), leading to a reduction in supply. Stock enhancement, which introduces small sea urchins into the field, is an important approach to meeting the increasing market requirements of sea urchins. Water flow greatly affects a series of fitness-related behaviours, including movement (Morse & Hunt, 2013), grazing (Kawamata, 1998; Tamaki *et al.*, 2009) righting (Challener & McClintock, 2017) and covering (James, 2000; Dumont *et al.*, 2007). Because these behaviours link to survival and growth, water flow is important for stock enhancement of sea urchins. Nevertheless, information is still limited on appropriate flow velocities for stock enhancement of sea urchins, although the effects of high water velocity were documented in the field (Lawrence, 1996).

Sea urchins use their tube feet to attach to the sea bottom, effectively resisting the dislodgement risk in water flow (Morse & Hunt, 2013). The adhesion of tube feet regulates the movement of sea urchins and thus plays an important role in their foraging and risk avoidance (Cohen-Rengifo *et al.*, 2017; Tamaki *et al.*, 2018). Further, righting behaviour is essential to maintain activity in water flow (Lawrence, 1975; Hagen, 1994). Besides, covering behaviour plays a role in the response to waves, by increasing their weight (Crook, 2003; Dumont *et al.*, 2007). However, quantitative studies of these fitness-related behaviours are still insufficient at certain flow velocities, despite their important implications for stock enhancement.

The sea urchin *Mesocentrotus nudus* is a commercially important species appropriate for stock enhancement, but not for long-line culture. In Japan, stock enhancement of *M. nudus* provides high-quality gonads and thus great commercial benefits (Agatsuma, 2020). Stock enhancement of *M. nudus* has also been important in China to meet the increasing market demands (~US$ 20 kg^{-1} in Chinese markets) (Wang *et al.*, 2006; Ding *et al.*, 2020). Releasing size is an important concern in the stock enhancement of *M. nudus* (Agatsuma & Kawai, 1997). For example, *M. nudus* (test diameter >20 mm) were reseeded in April and harvested when the test diameter reached ~70 mm in Dalian, China. For the purposes of studying stock enhancement, we thus used *M. nudus* of test diameter of ~30 mm for the present study in April. The maximum flow velocity was ~90 cm s^{-1} in the Changshan Islands, which is the major field for the stock enhancement of *M. nudus* in China (Zhang, 2019). Therefore, the maximum flow velocity was set as 90 cm s^{-1} for the adhesive ability experiments. High flow velocity (>20 cm s^{-1}) significantly inhibits the feeding and foraging of *M. nudus* (Agatsuma, 2013), seriously affecting their survival and growth. Thus, we set 20 cm s^{-1} as the maximum flow velocity, 10 cm s^{-1} as the medium flow velocity and 2 cm s^{-1} was set as the control flow velocity for the experiments of movement, righting and covering behaviours.

The main purposes of the present study were to investigate (1) the mean flow velocities to trigger dislodgement and to stop the movement of *M. nudus* and (2) the effects of velocities (2, 10 and 20 cm s^{-1}) on movement, righting and covering behaviours of *M. nudus*. A better understanding of behavioural responses to water flow can provide valuable information on stock enhancement of *M. nudus*.

Materials and methods

Sea urchins

Mesocentrotus nudus were collected locally in the intertidal of Heishijiao in August 2017 and were cultured in the Key Laboratory of Mariculture & Stock Enhancement in North China's Sea, Ministry of Agriculture and Rural Affairs, China, until the experiments started in April 2018. One-third of the seawater in the tanks was changed every 3 days. The sea urchins were fed fresh kelp (*Saccharina japonica*) and wakame (*Undaria pinnatifida*). We used different sea urchins for each behavioural experiment. Before the experiment, test diameter and height were measured by a digital Vernier calliper (16EWR, Mahr Co., Germany). They were weighed using an electronic balance (JJ1000Y, G&G Co., USA). A total of 45 sea urchins were involved in the righting, covering and movement experiments. There was no significant difference in test diameter (29.97 ± 0.30 mm), test height (14.52 ± 0.24 mm) and body weight (10.69 ± 0.35 g) ($P = 0.221$ for test diameter, $P = 0.771$ for test height, $P = 0.556$ for body weight).

Experimental facility

The experimental facility was a one-level tank made by acrylic material with eight separate runways (length × width × height = 420 × 60 × 80 mm) to exclude potential interference between individuals (Figure 1). Water flow regulators were independent to ensure the consistency of water flow in each of the eight separated runways. The experimental area was limited between the two nets in the runway (length × width × height = 240 × 60 × 80 mm) to ensure flow stability (Figure 1). Flow velocity was controlled by a ball valve and measured using a flow meter (JDC Electronic SA Co., Switzerland). Water flow was unidirectional. Water circulation was supported by a water pump (200 W, 20,000 l h^{-1}, Jebao, China). We investigated the dislodgement and immobilization velocities within the maximum flow velocity (90 cm s^{-1}) in a single runway. Further, three flow velocities (2 cm s^{-1}, 10 cm s^{-1} and 20 cm s^{-1}) were used for the experiments of movement, righting and covering behaviours.

Dislodgement and immobilization velocity

We individually assessed the velocity that dislodged *M. nudus* from the bottom (Tuya *et al.*, 2007). After sea urchins adhered to the bottom and moved normally, we increased the flow velocity from 0 cm s^{-1} to that which detached sea urchins (the maximum was 90 cm s^{-1}) within 3 min. The flow velocity was constantly accelerated for each trial. The flow velocity that detached sea urchins was recorded as the dislodgement velocity (N = 10). If the maximum flow did not dislodge the sea urchin, we recorded the dislodgement velocity as 90 cm s^{-1}.

To measure the flow velocity that prevents the movement of *M. nudus*, we recorded the flow velocity that caused the sea urchin to stop moving. After the individual adhered to the bottom and moved normally, flow velocity was gradually increased until the sea urchin stopped moving. The immobilization velocity was that at which the sea urchin did not move within 15 s (N = 5).

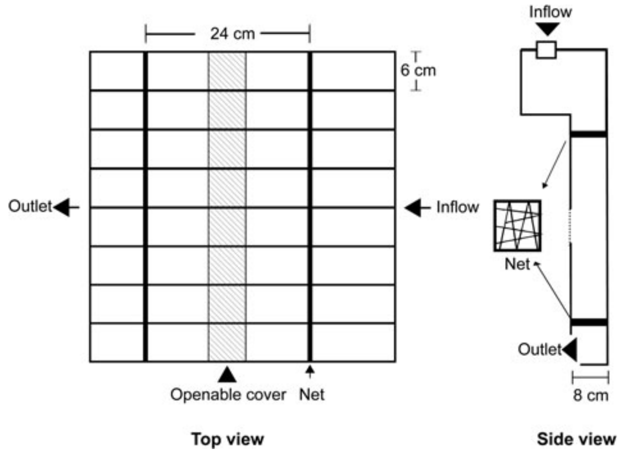

Fig. 1. Diagram of the facility used for measuring behaviours of *Mesocentrotus nudus*. The area of a runway is 24 × 6 × 8 cm (length × width × height), with two nets to limit the experimental area. The lid can be opened to put sea urchins into the facility. It was closed during the experiment.

Movement

We individually recorded the movement direction and distance and subsequently calculated the movement velocity of sea urchins at 2, 10 and 20 cm s^{-1} using a camera (FDR-AXP55, SONY Co., Japan). The experimental duration was 15 min. Since the water flow was unidirectional, we recorded the movement of sea urchins along with the water flow as downstream movement and against the water flow as upstream movement, respectively. Total movement distance, movement time, the distance of downstream and upstream movement were recorded using a video in the movement experiment. Movement velocity, upstream and downstream movement velocity were subsequently calculated (N = 5).

Covering behaviour

Covering is the behaviour in which sea urchins hold material (for example, particles and debris) on their aboral surface with their tube feet (Lawrence, 1976). Twenty clear, white, round polished shells of small scallops (*Mizuhopecten yessoensis*, 20 ± 0.22 mm in diameter) were randomly placed in the experimental area for each experiment. The number of shells used for covering was measured for each sea urchin 15 min after the beginning of the experiment at each flow velocity (N = 5).

Righting response time

Righting response time refers to the time needed for a sea urchin to resume its normal posture with the aboral side up after being inverted to the aboral side down (Lawrence, 1976). We measured the righting response time of *M. nudus* exposed to the three flow velocities within 5 min. When the individual did not right, we recorded the righting response time as 300 s (N = 5).

Statistical analysis

Normal distribution and homogeneity of variance were analysed using Kolmogorov–Smirnov test and Levene's test, respectively. One-way ANOVA was used to compare the movement velocity between the three flow velocities. Least-Significant Difference

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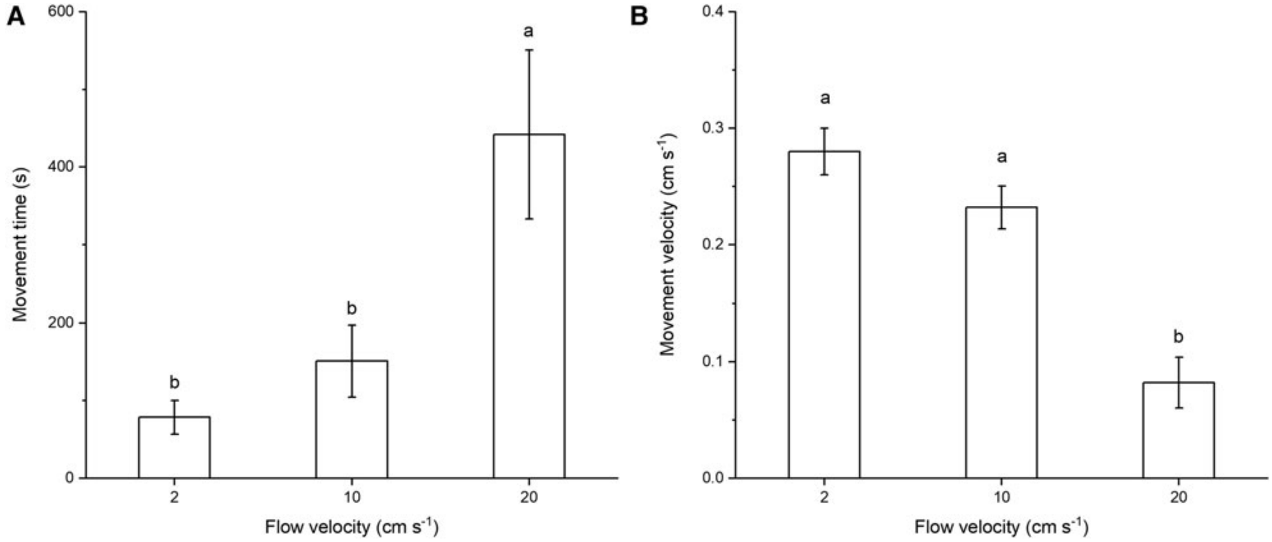

Fig. 2. Total movement time (A) and movement velocity (B) of *Mesocentrotus nudus* at 2, 10 and 20 cm s^{-1} flow velocity (N = 5, mean ± SE). Different letters above the bars refer to the significant difference among experimental groups.

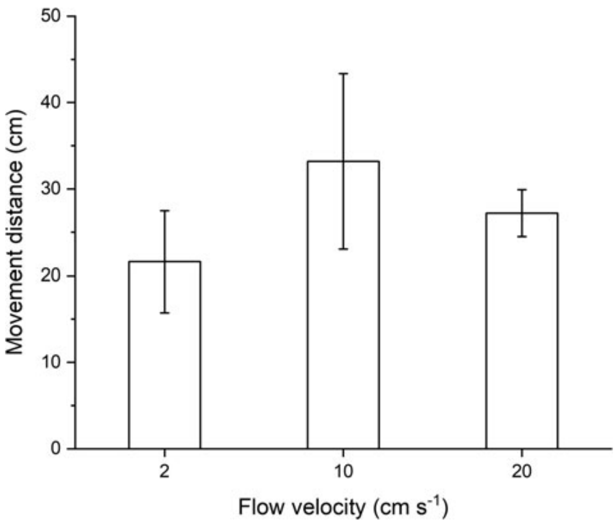

Fig. 3. Movement distance of *Mesocentrotus nudus* during 15 min at 2, 10 and 20 cm s^{-1} flow velocity (N = 5, mean ± SE).

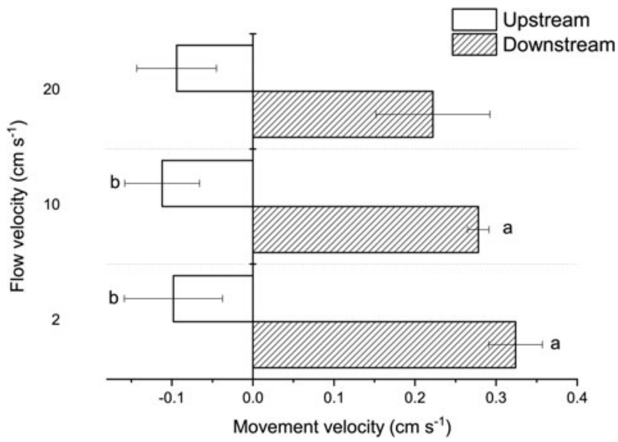

Fig. 4. Movement velocity of *Mesocentrotus nudus* upstream and downstream at 2, 10 and 20 cm s^{-1} flow velocity (N = 5, mean ± SE). Different letters beside the bars refer to the significant difference among experimental groups.

(LSD) test was used for *post hoc* comparisons when significant differences were found in the ANOVA. We analysed righting response time, covering and movement using the Kruskal–Wallis test and movement direction in a flow velocity using the Mann–Whitney *U* test, because of the heterogeneity of variance and/or abnormal distribution of the data. Statistical analyses were performed using SPSS (Version 22.0). A probability level of $P < 0.05$ was considered significant.

Results

Dislodgement and immobility velocities

The mean dislodgement velocity of *M. nudus* was 73.50 ± 7.7 cm s^{-1} (N = 10). The mean flow velocity that inhibited *M. nudus* movement was 33.40 ± 2.7 cm s^{-1} (N = 5).

Movement

Flow velocity significantly affected movement time ($P = 0.041$, Figure 2A) and movement velocity ($P < 0.001$, Figure 2B), but not movement distance ($P = 0.842$, Figure 3). The movement time of *M. nudus* exposed to 20 cm s^{-1} was significantly longer than that at 2 cm s^{-1} ($P = 0.036$), while there was no significant difference between 2 cm s^{-1} and 10 cm s^{-1} ($P = 0.965$). Movement velocity of *M. nudus* exposed to 2 cm s^{-1} ($P < 0.001$) and 10 cm s^{-1} ($P < 0.001$) was significantly higher than that at 20 cm s^{-1}. However, there was no significant difference of movement velocity between 2 cm s^{-1} and 10 cm s^{-1} ($P = 0.117$).

Neither movement distance ($P = 0.405$ and 0.482), movement velocity ($P = 0.400$ and 0.803), nor movement time ($P = 0.664$ and 0.082) varied significantly at 2 cm s^{-1}, 10 cm s^{-1} and 20 cm s^{-1} in downstream and upstream movement. However, the velocity in the downstream movement was significantly higher than that in the upstream at 2 cm s^{-1} ($P = 0.016$) and 10 cm s^{-1} ($P = 0.008$) (Figure 4). There was no significant difference in movement velocity between downstream and upstream at 20 cm s^{-1} ($P = 0.222$).

Covering behaviour

There was no significant difference in the number of shells used for covering among 2 cm s^{-1}, 10 cm s^{-1} and 20 cm s^{-1} ($P = 0.073$, Figure 5A).

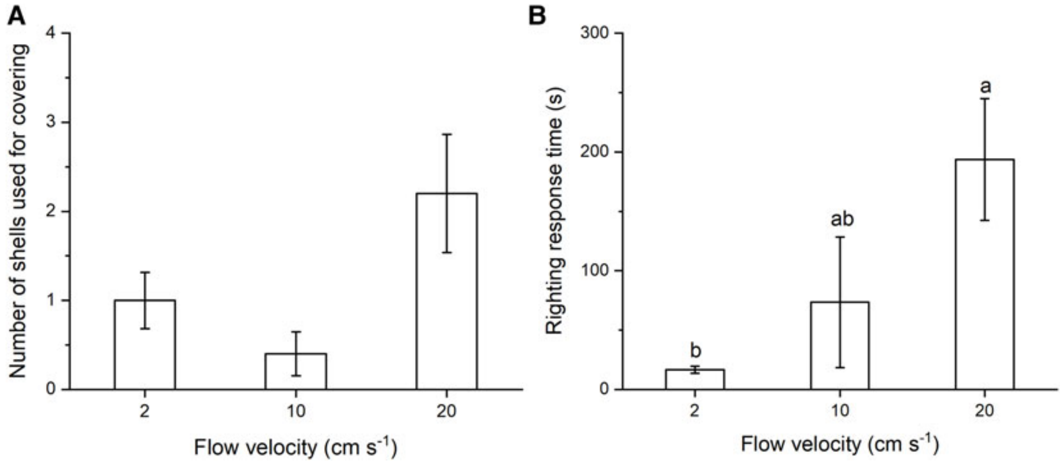

Fig. 5. Number of shells used for covering (A) and righting response time (B) of *Mesocentrotus nudus* at 2, 10 and 20 cm s^{-1} flow velocity (N = 5, mean ± SE). Different letters above the bars refer to the significant difference among experimental groups.

Righting response time

Righting response time of *M. nudus* exposed to 20 cm s^{-1} was significantly longer than that at 2 cm s^{-1} ($P = 0.015$). However, there was no significant difference of righting response time among *M. nudus* at 2 cm s^{-1} and 10 cm s^{-1} ($P = 1.000$, Figure 5B).

Discussion

Sea urchins use tube feet to attach to the sea bottom to prevent dislodgement at high water flow velocities (Santos & Flammang, 2008). This is essential for the survival and consequently for stock enhancement of *M. nudus*. In the present study, we found that the dislodgement velocity was 73.50 ± 7.7 cm s^{-1} for *M. nudus* (~30 mm test diameter). The dislodgement velocity of *M. nudus* was greater than that of the sea urchin *Diadema antillarum* (test diameter of 22–27 mm), but less than that in the sea urchin *Arbacia lixula* (test diameter of 23–29 mm) (Tuya *et al.*, 2007). This suggests that differences of adhesion ability exist among sea urchin species with different spine size, orientation and the number of tube feet available for attachment (Sharp & Gray, 1962; Tuya *et al.*, 2007). Alternatively, the disparity may be partially due to the test diameter which is slightly larger in the present study, considering adherence is size-independent according to the safety factor evaluated by the attachment ability of the sea urchin *A. lixula* (Santos & Flammang, 2007). The current result indicates that tube feet of *M. nudus* could not adhere at a flow velocity of ~70 cm s^{-1} and is thus easily dislodged (Agatsuma, 2013). Therefore, the reseeding of *M. nudus* is probably not appropriate in the areas with a flow velocity of more than ~70 cm s^{-1}.

Movement occurs when the flow velocity is in the safe range (Santos & Flammang, 2008). In the present study, 33.40 ± 2.7 cm s^{-1} was the flow velocity that inhibited the movement of *M. nudus*. This result generally agrees with the finding of Kawamata (1998) that *M. nudus* ceased movement at >40 cm s^{-1}. The partial disagreement between the two studies is probably because of the difference of test diameter, which is ~30 mm in the present study and 55–86 mm in Kawamata (1998). These results indicate that small *M. nudus* could be reseeded in areas with a flow velocity below 30 cm s^{-1}. This is because movement is the basis for the other fitness-related behaviours such as foraging (Agatsuma, 2013) and sheltering (Tamaki *et al.*, 2018) of sea urchins (Santos & Flammang, 2008; Morse & Hunt, 2013).

To better understand the behavioural responses of *M. nudus* to water flow, we investigated their movement, displacement direction, covering and righting behaviours at flow velocities below 33.40 ± 2.7 cm s^{-1} (2, 10 and 20 cm s^{-1}). In the present study, movement velocity was reduced by more than half at 20 cm s^{-1}, compared with that at 2 cm s^{-1}. This result is consistent with the report that movement velocity significantly decreased under high-velocity water currents in *M. nudus* (Kawamata, 1998; Agatsuma, 2013) and *Strongylocentrotus droebachiensis* (Morse & Hunt, 2013). A reasonable explanation is that sea urchins probably use more energy to maintain body stability at high water velocity (Morse & Hunt, 2013). There was no significant difference in movement distance among the three flow velocities. However, movement time was longer at 20 cm s^{-1} than those at 2 cm s^{-1} and 10 cm s^{-1}. Shorter movement time probably impacts the capacity to find shelter and consequently increases the risk of predation in the field, although *M. nudus* can retain movement and other behaviours, including sheltering (Tamaki *et al.*, 2018) and grazing (Kawamata, 1998) at 20 cm s^{-1}. Further, flow velocity affected the movement velocity of the sea urchins in the two directions. Downstream movement velocity of *M. nudus* was significantly higher than upstream movement velocity at 2 cm s^{-1} and 10 cm s^{-1} ($P = 0.016$ and $P = 0.008$), but not at 20 cm s^{-1} ($P = 0.222$). This result indicates that *M. nudus* tends to move downstream at low flow velocities, while this trend decreases at high flow velocities. This result is consistent with the finding of Morse & Hunt (2013) that sea urchins tended to move downstream and upstream at low and high flow velocities, respectively. Twenty cm s^{-1} significantly limits the movement direction of *M. nudus* and is probably detrimental to its escape from adverse environments. This suggests that flow velocity above 20 cm s^{-1} markedly affects the movement of *M. nudus* and thus probably is not appropriate for reseeding.

Covering behaviour supports the sea urchin *Lytechinus anamesus* to stabilize under wave exposure (Lees & Carter, 1972). Sea urchins cover themselves with objects to increase their weight, partly because light individuals are susceptible to strong water flow (Crook, 2003). In the present study, however, no significant difference in covering behaviour was found between 2, 10 and 20 cm s^{-1}. This suggests that 20 cm s^{-1} may not affect the stability of *M. nudus*. Righting response time of *M. nudus* is significantly longer at 20 cm s^{-1} (16.60 ± 3.11 s) than at 2 cm s^{-1} (193.80 ± 51.26 s, $P = 0.015$). This indicates that righting behaviour is weakened at high flow velocities. However, this result is not consistent with the finding of Challener & McClintock (2017) that *L. variegatus* improved righting behaviour at high flow velocity. This disagreement is probably because of the difference of the sediment and flow type, which was a smooth surface and unidirectional water flow (2–20 cm s^{-1}) in the present study but sand surface and in waves (60 cm s^{-1}) in Challener & McClintock (2017). Notably, the present study is a laboratory investigation and probably different from the hygrographic conditions in the field.

Conclusions

In conclusion, a velocity below 30 cm s^{-1} would be indicated to be appropriate for reseeding of *M. nudus* (test diameter of ~30 mm) to avoid dislodgement and to ensure their movement. Flow velocity of 20 cm s^{-1} significantly affected the righting ($P = 0.015$) and movement behaviours ($P < 0.001$) of *M. nudus*. Sea areas with a flow velocity less than 20 cm s^{-1}, preferably 2–10 cm s^{-1}, would be expected to be appropriate for stock enhancement of *M. nudus*. The present study provides valuable information for stock enhancement of *M. nudus*. Future investigations, however, should be carried out on the effects of long-term water flow on feeding and growth of *M. nudus* both in the laboratory and the field.

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