Mucous-cord secretion for drifting by the clam *Meretrix lusoria* (Veneridae) under varying light/dark and submergence/exposure conditions

YASUO NAKAMURA*

National Institute for Environmental Studies, Tsukuba, Ibaraki 305–8506, Japan

Received 24 April 2014; Accepted 25 November 2014

Abstract: Both juveniles and adults of the venerid clam *Meretrix lusoria* secrete a transparent mucous cord and drift over tidal flats, using the mucous cord as a “sail.” To clarify the ecological roles of mucous-cord secretion, the conditions affecting secretion were examined in the laboratory using clams burrowing in sand. Darkness and sand exposure played important roles in mucous-cord secretion: Under a 12-h : 12-h Light/Dark cycle with continuous sand submergence, 84% of mucous-cord secretions occurred in the dark. Under a 6-h : 6-h Submergence/Exposure cycle in continuous darkness, 79% of mucous-cord secretions occurred within 2 h of the submergence. Since clams secreted mucous cords without being exposed to adverse conditions such as hypoxic waters, it appears that mucous-cord drifting in the field does not necessarily serve as an escape mechanism when the clam encounters unfavorable conditions. On the contrary, it is suggested that drifting is a risk-dispersion (bet-hedging) strategy to sustain the population under the varying and unpredictable conditions of tidal flats.

Key words: light/dark, *Meretrix lusoria*, mucous-cord secretion, submergence/exposure

Introduction

Some bivalve species drift in the water column and expand their distribution during post-metamorphic stages (e.g., Bayne 1964, Prezant & Chalermwat 1984, Beukema & Vlas 1989, Hiddink & Wolff 2002). In many cases, such drifting is facilitated by mucous materials such as a long byssus threads secreted from the foot (Sigurdsson et al. 1976, Lane et al. 1985, Beukema & Vlas 1989) or mucous cords released through the exhalant siphon (Prezant & Chalermwat 1984). These materials act like a sail by increasing hydrodynamic drag. One suggested ecological role for such drifting is escape from unfavorable environments (Beukema & Vlas 1989, Hiddink & Wolff 2002).

The present study focused on the venerid clam *Meretrix lusoria*, which lives in sandy sediments of shallow coastal waters of Japan and the southern part of the Korean Peninsula (Torii et al. 2010). This clam and a congener *M. petechialis* secrete from their posterior region a transparent mucous cord used to enable them to drift (Kishinouye 1913, Fig. 1 in Nakamura 2013). This phenomenon has been known for over 230 years in Japan: on the basis of a

description of a mirage in an ancient Chinese historical record (Shih-chi BC 90), a Japanese woodblock printmaker (Sekien Toriyama) in 1776 drew “The Specter Mirage,” wherein *M. lusoria* on the seafloor is pictured secreting a mucous cord from which a wavering castle (i.e., mirage) emerges.

In a scientific setting, Uchida (1941) observed that *Meretrix meretrix* (probably *M. lusoria*, according to Torii et al. 2010) trailed a mucous cord into the tidal current and drifted on a flat in the southern part of the Korean peninsula. He also placed rectangular-mouthed “clam traps” with collecting nets above the surface of a tidal flat in the north-western part of the Korean Peninsula and found that *M. meretrix* (probably *M. petechialis*) drifts mainly in the water layer close to the sediment on ebbing spring tides during the warm season.

Based on histological analysis, Hamada & Ino (1954) suggested that the mucous cord of *M. lusoria* is secreted from tissue in the inner wall of the mantle surrounding the siphons. Takahi & Henmi (2011) suggested that the drifting of *M. lusoria* occurs mainly from January to July on Shirakawa tidal flat in Kyushu, Japan, based on the monthly counts of *M. lusoria* stranded on obstacles on the tidal flat.

For species that show post-metamorphic drifting, clarifi-

*Corresponding author: Y. Nakamura; E-mail, yasuo@nies.go.jp

cation of the conditions that facilitate drifting is essential to understand their population dynamics (e.g., Sorlin 1988, Martel & Diefenbach 1993, Hiddink & Wolff 2002, Beukema & Dekker 2003) and thus helps to find ways to restore diminished populations such as those of *M. lusoria* (Higano 2004). In this context a previous laboratory study examined the conditions affecting cord secretion by *M. lusoria* (Nakamura 2013) and the results were summarized as follows: in small beakers (200 mL) with seawater and without sand, 1) clams over a wide size range (shell length 11–45 mm) secreted mucous cords over a wide range of temperatures (10–30°C) with stimulation by bubbling air through the water and 2) cord-secretion activity depended on the season in which they were examined, with maximum activity in spring and minimum in summer. In addition, in 4 L plastic containers with sand, 3) lighting induced some burrowing clams to secrete mucous cord following exposure of the sand to air for 13 h and submergence for 1 h in the dark.

These experiments, however, were only preliminary: the absence of sand in the beaker experiments could have caused some stress to the clams and biased the results toward mucous-cord secretion, and the experiments with sand were not conducted systematically. In the present study, attempts were made to induce mucous-cord secretion in clams burrowing in sand by changing Light/Dark (LD) and Submergence/Exposure (SE) conditions systematically, to clarify the conditions favorable for mucous-cord secretion. The possible ecological roles of mucous-cord secretion by these clams are then discussed.

Materials and Methods

Clams and sampling sites

There were two sources of *Meretrix lusoria* clams: 1) from the natural population on the upper part of Shirakawa tidal flat (~1.5 m above mean low water level at spring tide; Kyushu, Japan; 32°47'N, 130°36'E; Takeuchi et al. 2013); or 2) introduced from Shirakawa flat to cages on Oi tidal flat (~1 m above the mean low water level at spring tide; Tokyo Bay, Japan; 35°35'N, 139°45'E; Nakamura et al. 2010) in October 2012 and reared there. The clams in cages on Oi flat were labelled with an identification number (ID) at the start of rearing. Although there was no natural population of *M. lusoria* on Oi flat, the clams there grew rapidly with high survival and their reproductive cycle was the same as that on Shirakawa flat (Nakamura et al. 2010). The seasonal change of water temperature over both flats follows almost the same pattern: a maximum (30°C) in August and minimum (12°C) in February; the salinities on Shirakawa and Oi flats were generally 25–30 and 15–25, respectively (Nakamura et al. 2010).

Experimental procedures

General experimental conditions

The seawater used throughout this study was from the Kuroshio, filtered through Whatman GF/C filters and diluted to a salinity of 25. Pretreatments and experiments were conducted at 20°C under cool-white fluorescent lights at an irradiance of approximately 40 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (except for the dark period; see below). Because *M. lusoria* grows rapidly at 20°C and a salinity of 25 (Nakamura et al. 2005, 2010), the above conditions were not considered stressful for the clams. Plastic containers (3 L; 10 cm in height) with sand (4 cm deep) and seawater (1 L when provided) were used throughout the study. For periodic exposure and submergence of the sand, seawater was removed from the containers by decantation or poured gently into the container, respectively, to minimize disturbance of the sand.

Clam pretreatment

Clams collected were placed in a 3 L plastic container without sand, maintained at 10–15°C, and brought to the laboratory within 24 h (from Shirakawa flat) or 3 h (Oi flat) of collection. During transport, no seawater was added to the containers so that the clams would not secrete a mucous cord. For clams from Oi flat, shell lengths were recorded with ID before placing them into a plastic container.

Just after the clams arrived at the laboratory (at around 1500 local time), they were placed in experimental containers with oxygen-saturated seawater (without bubbling air) to select clams for subsequent experiments: clams that burrowed into the sand within 30 min were used. The clams chosen were retrieved from the sand; the minimum and maximum shell lengths were measured for clams from Shirakawa flat. They were then redistributed into four experimental containers (20–25 clams in each container) with oxygen-saturated seawater (without bubbling). When redistributing the clams, care was taken to lessen bias in shell size distribution among the containers. After all clams had burrowed into the sand in the experimental containers, air-stones were introduced (20 mm in diameter; flow rate = ~200 mL min⁻¹). Although the speed of the water current induced by bubbling was not homogeneous in the containers, it was in the order of 1–10 cm s⁻¹ by inspection. Then the clams were acclimated for 6–8 h until 0000 local time, when the cord secretion experiments started.

Mucous-cord secretion experiments

Following the pretreatment, the clams were monitored for mucous-cord secretion for 48 h on five occasions from January to May 2013 (Runs 1–5). In each run, two containers were used as experimental treatments and another two served as controls.

The controls in Runs 1–5 were placed under 12-h : 12-h

LD and 6-h : 6-h SE cycles. Light was provided between 0700 and 1900; the sand was exposed to air from 0000 to 0600 and from 1200 to 1800; and the seawater was aerated through an air-stone (as above). In a previous study (Nakamura 2013), lighting induced some clams to secrete a mucous cord following exposure of the sand and 1 h submergence in the dark. Thus, the lights were set to turn on or off 1 h after the start of the submergence period in the controls. Conditions for experimental treatments are characterized as follows: in the experimental treatments of Run 1 (Experiment A), air bubbling was stopped for the first 2 h of the submergence periods (0600–0800 and 1800–2000), as mucous-cord secretion by sand-burrowing clams were induced without bubbling in a previous study (Nakamura 2013). In this experiment, dissolved oxygen in the seawater was measured with an electrode (model 5739, YSI Co) at the end of the no-bubbling period. Light was not provided in the experimental treatments of Runs 2 and 3 (Experiment B), and the sand was continuously submerged in seawater in the experimental treatments of Runs 4 and 5 (Experiment C). The other conditions in the experimental treatments were the same as in the controls.

The clams were checked for mucous-cord secretion at 20-min intervals (15, 35, and 55 min after the start of each hour: e.g. 1715, 1735, 1755 local time) during the period of submergence. When clams were lying flat on the surface of the sand, they were checked for mucous-cord secretion by pipetting about 2 mL of water from around the siphons of the clam (Nakamura 2013). For clams that had secreted a cord, their ID (Runs 1, 2) or shell length (Runs 3–5) were recorded, and then they were removed from the container. During the dark period, the surface of the sand was checked under a flashlight reflected against the wall ($<1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). In cases where the sand was continuously submerged (experimental treatments of Runs 4 and 5), seawater was replaced twice a day at 0000 and 1200. In other cases, fresh and oxygen-saturated seawater was supplied at the start of each submergence period. For data analysis, the number of clams that had secreted cords at the three observation times in each hour, in both experimental or both control containers, were combined and the sum (n_s) was used as an index of cord secretion in each hour.

Observation of clams during and following cord secretion

In the control containers, some clams started to secrete a cord just after the lights came on at 0700 (see Results). In these cases the clam was monitored continuously to estimate the time required to dig back into the sand; once the clam started to dig, it was removed from the container.

Results

Mucous-cord secretion in controls

Among a total of 221 clams, cord secretion was ob-

served for 125 clams during the experimental period of 48 h. The ratio of cord secretion was 57% (Table 1; data from Runs 1 to 5 were combined). The shell lengths of the clams that secreted mucous cords ranged from 19.2 mm (Run 3) to 35.2 mm (Run 1), while those used in controls were in the range 17.9–35.8 mm. When the data from Runs 1 and 2 were combined, 19, 23 and 20 clams secreted mucous cords among 25, 32 and 32 clams examined in the size categories of 20–27, 27–31 and 31–36 mm, respectively. Mucous cord secretion was not significantly affected by shell length (Chi-square test, $\chi^2_2 = 0.40$, $0.8 < P < 0.9$).

Mucous-cord secretion showed a conspicuous temporal pattern (Table 1, Figs 1–3). During the light period, except for 0700–0800, most clams burrowed in the sand and mucous-cord secretion occurred only occasionally. Within the first hour of submergence in the dark (0600–0700) or 2 h after extinguishing the lights (1900–2100), many clams (about 50%, but not counted) emerged from the sand and “stood up” on the sand surface. During these same periods, clams actively secreted mucous cords. Among 125 clams that secreted mucous cord, 60% and 13% of mucous-cord secretion occurred during 1900–2100 and 0600–0700, respectively (Table 1). In addition, there was active mucous-cord secretion (17% of cord secretion events) in the first hour of the light period (0700–0800). Following the surge in cord secretion during 1900–2100, the number of upright clams decreased gradually and cord secretion occurred only rarely from 2100 to 0000. The frequency of cord-secretion during dark periods was significantly higher than in light periods (Chi-square test, $\chi^2_1 = 35.9$, $P < 0.001$; com-

Table 1. *Meretrix lusoria*. Diurnal pattern of mucous-cord secretion events in the controls (data from Runs 1–5 were combined).

Local time	Light/dark (L/D) condition	Relative frequency of cord secretions (f , %)*
0600–0700	D	13
0700–0800	L	17
0800–0900	L	3
0900–1200	L	2
1800–1900	L	2
1900–2000	D	43
2000–2100	D	17
2100–2400	D	4
Total number of clams secreting a mucous-cord within 48 h of experimental periods (N_s)		125
Total number of clams examined (N_T)		221
The ratio of cord secretion [$100 \times (N_s/N_T)$]		57%

*The clams that secreted the cords were removed from containers immediately and the frequency of cord secretions in each time period is given by $N_s \times f/100$.

Fig. 1. *Meretrix lusoria* (Experiment A). Temporal pattern of mucous-cord secretion under (a) alternation of bubbling and no bubbling (experimental treatments), and (b) continuous bubbling (control). n_s : the number of clams per hour secreting a mucous-cord.

binned data from Run 1–5), and the frequency of mucous-cord secretion in the first half of the submergence period (0600–0900, 1800–2100) was significantly higher than that in the second half (0900–1200, 2100–2400) (Chi-square test, $X^2_1=98.5$, $P<0.001$; combined data from Run 1–5; Table 1).

The activities of clams secreting mucous cords were sometimes monitored. Immediately after the start of the light period at 0700, most of the standing clams burrowed back into the sand, but some started to crawl on the surface, greatly extending their foot and siphons for 1–2 min as observed in a previous study (Nakamura 2013). They then stopped crawling, lay flat on the sand with extended siphons and gaping valves, and secreted the mucous cord. The time required to burrow back into the sand after the start of crawling was recorded for five clams and averaged 23.4 min (SD 6.9 min). When the clams started to dig again, their mucous cords were still attached.

Effects of cessation of air bubbling, continuous darkness, and continuous submergence on cord secretion

Under conditions alternating between bubbling and no bubbling (experimental treatments in Run 1; Experiment

Fig. 2. *Meretrix lusoria* (Experiment B). Temporal pattern of mucous-cord secretion under (a) continuous darkness (experimental treatments), and (b) 12-h : 12-h light/dark cycle (control). Dark and light parts of vertical bars indicate n_s in Runs 2 and 3, respectively.

A), cord secretion occurred mainly during the dark period (81% of cord-secretion events) as in the control (Table 2; Fig. 1). The ratio of cord secretion was not significantly different from that in the control (Chi-square test, $X^2_1=0.02$, $0.8<P<0.9$). However, only two clams (8% of mucous-cord secretion events) secreted a mucous cord in the first hour of the dark period (1900–2000; no air bubbling), while mucous-cord secretion in the control occurred actively during the same period (56% of mucous-cord secretion events); mucous-cord secretion occurred mainly within 1 h after the resumption of air bubbling at 2000 (18 clams; 69% of cord-secretion events). The frequency of cord secretions during 1900–2000 was significantly lower than that during 2000–2100 in the experimental treatments (Chi-square test, $X^2_1=12.8$, $P<0.001$). The dissolved oxygen level at the end of the no-bubbling period (0800 and 2000) was $>48\%$ saturation.

Under continuous darkness (experimental treatments of Runs 2 and 3, Experiment B), the ratio of cord secretion was not significantly different from that in the control (Chi-square test, $X^2_1=0.86$, $0.3<P<0.5$ for Run 2; $X^2_1=0.05$, $0.8<P<0.9$ for Run 3; Table 3). The temporal pattern of cord secretion in the experimental treatments was

Fig. 3. *Meretrix lusoria* (Experiment C). Temporal pattern of mucous-cord secretion under (a) continuous submergence (experimental treatments), and (b) 6-h : 6-h submergence/exposure cycle (control). Dark and light parts of vertical bars indicate n_s in Runs 4 and 5, respectively.

similar to that in the control (Fig. 2); the frequency of cord-secretion events in the first half of the submergence periods (0600–0900 and 1800–2100) was significantly higher than in the second half (0900–1200 and 2100–2400; Chi-square test, $X^2_1=27.0$, $P<0.001$ for Run 2 and $X^2_1=12.3$, $P<0.001$ for Run 3) as in the control.

Under continuous submergence (experimental treatments in Runs 4 and 5, Experiment C), the ratio of cord secretion was not significantly different from that in the control (Table 4; Chi-square test, $X^2_1=0.64$, $0.3<P<0.5$ for Run 4; $X^2_1=0.77$, $0.3<P<0.5$ for Run 5); cord secretion occurred more frequently in the dark (0000–0700, 1900–2400) than in the light (0700–1900) (Chi-square test, $X^2_1=7.1$, $P<0.01$ for Run 4 and $X^2_1=9.8$, $P<0.01$ for Run 5). However, in contrast to the controls, there were no specific temporal trends in mucous-cord secretion during the dark period under continuous submergence (Fig. 3): when the data from Runs 4 and 5 were combined, the frequency of mucous-cord secretions in the four 3 h periods of the dark period (1900–2200, 2200–0100, 0100–0400, 0400–0700) were 8, 8, 10 and 5, respectively, and did not differ significantly among these periods (Chi-square test, $X^2_3=1.65$, $0.5<P<0.7$; Table 4).

Discussion

About 50% of the *M. lusoria* clams secreted a mucous cord under ‘mild’ experimental stimulations such as water bubbling and alternation of light/dark and submergence/exposure. It took 23 min on average for the cord-secreting clams to dig into the sand again, and thus the 20-min interval for observations in the present study was appropriate for quantitative monitoring of the temporal pattern of cord

Table 2. *Meretrix lusoria*. Effects of cessation of bubbling on diurnal pattern of mucous-cord secretion events (Experiment A).

Local time	Light/dark (L/D) condition	(A) Alternation of bubbling and no bubbling (experimental treatment)		(B) Bubbling (control)
		Bubbling condition	Relative frequency of mucous-cord secretion (f , %)	Relative frequency of mucous-cord secretion (f , %)
0600–0700	D	No bubbling	0	4
0700–0800	L	No bubbling	8	7
0800–0900	L	Bubbling	4	0
0900–1200	L	Bubbling	8	7
1800–1900	L	No bubbling	0	4
1900–2000	D	No bubbling	8	56
2000–2100	D	Bubbling	69	15
2100–2400	D	Bubbling	4	7
Total number of clams secreting a mucous-cord within 48 h of experimental period (N_s)			26	27
Total number of clams examined (N_T)			44	44
The ratio of cord secretion [$100 \times (N_s/N_T)$]			59%	61%

Clams (22–36 mm SL) were sampled from Oi tidal flat in January 2013. Further details as in legend to Table 1.

Table 3. *Meretrix lusoria*. Effects of continuous darkness on diurnal pattern of mucous-cord secretion events (Experiment B).

Local time	(A) Continuous darkness (treatment)		(B) 12-h : 12-h L/D cycle (control)		
	Relative frequency of mucous-cord secretion (f , %)		Light/Dark (L/D) condition	Relative frequency of mucous-cord secretion (f , %)	
	Run 2	Run 3		Run 2	Run 3
0600–0700	0	0	D	9	14
0700–0800	30	38	L	6	43
0800–0900	0	13	L	6	0
0900–1200	0	6	L	0	0
1800–1900	0	38	L	0	0
1900–2000	52	0	D	51	21
2000–2100	19	6	D	23	21
2100–2400	0	0	D	6	0
Total number of clams secreting a cord within 48 h of experimental period (N_S)	27	16		35	14
Total number of clams examined (N_T)	44	42		45	40
The ratio of cord secretion [$100 \times (N_S/N_T)$]	61%	38%		78%	35%

Clams were sampled from Oi flat in February for Run 2 and from Shirakawa flat in March 2013 for Run 3. Size of the clams were 20–34 and 18–32 mm for Run 2 and 3, respectively. Further details as in legend to Table 1.

Table 4. *Meretrix lusoria*. Effects of continuous submergence on diurnal pattern of mucous-cord secretion events (Experiment C).

Local time and light/dark (L/D) condition	(A) Continuous submergence (treatment)		(B) 6-h : 6-h submergence/exposure cycle (control)	
	Relative frequency of mucous-cord secretion (f , %)		Relative frequency of mucous-cord secretion (f , %)	
	Run 4	Run 5	Run 4	Run 5
0100–0400 D	29	15	—	—
0400–0600 D	6	15	—	—
0600–0700 D	0	20	18	22
0700–0800 L	0	5	18	26
0800–1200 L	0	5	0	7
1200–1800 L	18	5	—	—
1800–1900 L	0	0	5	0
1900–2000 D	6	0	45	30
2000–2200 D	18	30	14	15
2200–0100 D	23	5	0	0
Total number of clams secreting a cord within 48 h of experimental period (N_S)	17	20	22	27
Total number of clams examined (N_T)	45	46	45	48
The ratio of cord secretion [$100 \times (N_S/N_T)$]	38%	43%	49%	56%

Clams were sampled from Shirakawa flat in April and May 2013 for Run 4 and 5, respectively. Size of the clams were 22–35 and 22–33 mm in Run 4 and 5, respectively. Further details as in legend to Table 1.

secretion.

Transporting clams without seawater from the field to the laboratory could have caused some stress and biased the results of the cord secretion experiments. However, as the time required for transport from Oi flat (3 h; Runs 1 and 2) was less than the exposure period of the clams on the flat, the stress caused by the transportation from Oi flat was considered minimal. In addition, the temporal secretion pattern in the controls of Runs 3–5, in which clams were used after 24 h transport from Shirakawa flat, was similar to that in the controls from Oi flat (Figs. 1, 3). Thus, the transportation of clams did not seem to affect mucous-cord secretion in the present study.

There are some cases in which temporal patterns of mucous-cord secretion differed between two runs of the same experiment: for example, in treatment of Run 2 (Experiment B), mucous-cord secretion did not occur at all during 1800–1900 and occurred frequently in 1900–2000, while the opposite was true for Run 3 (Table 3). Such differences could be due to the difference in sampling locations and/or date, or some experimental artifact, but the exact cause requires further investigation.

Conditions affecting mucous-cord secretion

Cessation of air bubbling

Mucous-cord secretion rarely occurred during no-bubbling periods including the first hour of the dark period (1900–2000) in Experiment A, and clams actively secreted mucous cords just after the resumption of air bubbling in the dark at 2000 (Fig. 1; Table 2). However, in control containers, mucous-cord secretion during the first hour of the dark period (1900–2000; bubbling) was very active. These findings strongly suggest that air bubbling plays an important role in eliciting mucous-cord secretion.

During the period of no bubbling or sand exposure, clams could have experienced oxygen stress due to oxygen depletion in seawater or tight closing of the valves, respectively. Thus, one might think that the release from oxygen stress by air bubbling is responsible for the induction of cord secretion. However, this scenario is unlikely because 1) the dissolved oxygen concentration was >48% saturation throughout the no-bubbling period, and 2) mucous-cord secretions under continuous sand submergence with air bubbling (no oxygen stress; experimental treatment in Experiment C) occurred actively as in the control (6-h : 6-h SE cycle).

The stimulating effects of water currents on the secretion of mucous material for drift have been observed in other bivalve and gastropod species (e.g., Prezant & Chalmers 1984, Sorlin 1988, Martel & Diefenbach 1993), and the drifting of *Meretrix* clams on tidal flats is enhanced during spring ebb tides or on windy days when strong water currents are expected (Uchida 1941). Thus it is tentatively concluded that cord secretion by *M. lusoria* in the present study was stimulated by the water current induced by air bubbling.

Light conditions

Under a 12-h : 12-h LD cycle with continuous submergence (Experiment C, treatments), just over 80% of mucous-cord secretions occurred in the dark in Run 4 and 5 (Table 4). In addition, in the controls of Experiments A–C, cord secretion during the dark period occurred more frequently than during light (Table 1). These findings indicate that darkness plays an important role in cord secretion. The importance of darkness for the drifting of bivalves was observed in the previous studies where drift-related behavior (burrowing displacement) of the bivalve *Macoma balthica* was more common at night (Sorlin 1988) and the abundance of bivalves drifting in the water column was higher at night than in daytime (Armonies 1992, Hiddink et al. 2002).

In controls, some clams that were upright on the sand started to crawl on the sand and secreted a cord immediately after illumination began, and cord secretions during the light period were concentrated within the first 1 h of the light period (0700–0800; Table 1). These observations indicate that lighting also acts as a trigger for cord secretion, as observed previously (Nakamura 2013).

Sand exposure/submergence

Under continuous darkness with a 6-h : 6-h SE cycle (Experiment B), the mucous-cord secretion was concentrated within 2 h after the start of submergence (Table 3; Fig. 2). However, under continuous submergence with a 12-h : 12-h LD cycle (Experiment C), cord secretion during the dark period was not concentrated within a specific period (Table 4, Fig. 3). These observations indicate that the conspicuous temporal pattern of cord secretion was not triggered by the change in light conditions, but by the alternation of submergence and exposure.

Ecological considerations

One suggested ecological role of byssus-thread secretion for drifting by *Macoma balthica* during post-metamorphic stages is escape from unfavorable conditions (Beukema & Vlas 1989, Hiddink & Wolff 2002), and it is natural to speculate that mucous-cord secretion by *M. lusoria* has the same ecological role. However, cord secretion during the present study was induced by mild stimulation of water bubbling in the dark, and this suggests that mucous-cord secretion in the field does not necessarily serve as an escape mechanism from unfavorable conditions. If this is true, it is necessary to search for another reason to explain why the mucous cord is secreted.

Monitoring of benthic species at 99 stations on Shirakawa tidal flat during 2004–2008 (Takeuchi et al. 2013) indicated that juvenile *M. lusoria* (less than 10 mm in shell length) were abundant at stations close to the main stream of the Shirakawa River. Larger clams (higher than 10 mm in shell length) were distributed widely on the tidal flat, probably facilitated by drifting through the use of mucous cords. If the dense distribution of juveniles close to a river

and subsequent expanded distribution on a tidal flat is a general pattern for *Meretrix* clams, then the following is presented as a possible ecological role of drifting by mucous cords.

An aggregated juvenile population of *M. lusoria* close to a river is probably established in response to some still unidentified favorable conditions there for recruitment (e.g. preferable salinity for settlement, low abundance of predators or abundant food). At the same time, however, such clams have the potential risk of large-scale mortality of the population through a thick accumulation of muddy sediments close to a river, resulting from heavy precipitation (once every several years in the Shirakawa River). Based on these points and observations that cord-secretion is active from late winter through late spring (=preceding the season of heavy rain; Takahi & Henmi 2012, Nakamura 2013), an ecological role of drifting by *M. lusoria* over a wider area of a flat seems to be a strategy that protects the clam population from mass mortality through sporadic but disastrous mud accumulation. In other words, since the drifting takes the risk of straying into an unfavorable area (Takahi & Henmi 2012) or predation (Hiddink et al. 2002), mucous-cord drifting serves as a risk-dispersion (bet-hedging) strategy (Nakaoka 2003) to sustain the clam population under the varying and unpredictable conditions on tidal flats.

Acknowledgements

The author thanks G. Kanaya, K. Muto, and S. Shibuya for their technical assistance during the overnight experiments.

References

- Armonies W (1992) Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Mar Ecol Prog Ser* 83: 197–206.
- Bayne BL (1964) Primary and secondary settlement in *Mytilus edulis* L (Mollusca). *J Anim Ecol* 33: 513–523.
- Beukema JJ, Dekker R (2003) Redistribution of spat-sized *Macoma balthica* in the Wadden Sea in cold and mild winters. *Mar Ecol Prog Ser* 265: 117–122.
- Beukema JJ, Vlas J de (1989) Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Mar Ecol Prog Ser* 52: 193–200.
- Hamada S, Ino T (1954) Studies on the movement of the Japanese hard clam, *Meretrix meretrix lusoria* (Roeding) I. Histological studies on the mucous gland in relation to locomotion. *Bull Jap Soc Sci Fish* 20: 1–8. (in Japanese with English abstract)
- Hiddink JG, Wolff WJ (2002) Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. *Mar Ecol Prog Ser* 233: 117–130.
- Hiddink JG, Kock RP, Wolff WJ (2002) Active pelagic migrations of the bivalve *Macoma balthica* are dangerous. *Mar Biol* 140: 1149–1156.
- Higano J (2004) Influence of environmental changes in tidal flats on the filtration and respiration of bivalve mollusks. *Bull Fish Res Agency Suppl* 1: 33–40.
- Kishinouye K (1913) On a peculiar mode of locomotion of a clam *Meretrix meretrix* L. *Zoologischer Anzeiger* bd 41: 445–446
- Lane DJW, Beaumont AR, Hunter JR (1985) Byssus drifting and the drifting of the young post-larval mussel *Mytilus edulis*. *Mar Biol* 84: 301–308.
- Martel A, Diefenbach T (1993) Effects of body size, water current and microhabitat on mucous-thread drifting in post-metamorphic gastropods *Lacuna* spp. *Mar Ecol Prog Ser* 99: 215–220.
- Nakamura Y (2013) Secretion of a mucous cord for drifting by the clam *Meretrix lusoria* (Veneridae). *Plankton Benthos Res* 8: 31–37.
- Nakamura Y, Hashizume K, Koyama K, Tamaki A (2005) Effects of salinity on sand burrowing activity, feeding and growth of the clams *Macra veneriformis*, *Ruditapes philippinarum* and *Meretrix lusoria*. *J Shellfish Res* 24: 1053–1059.
- Nakamura Y, Takano T, Yurimoto T, Maeno Y, Koizumi T, Tamaki A (2010) Reproductive cycle of the venerid clam *Meretrix lusoria* in Ariake Sound and Tokyo Bay, Japan. *Fish Sci* 76: 931–941.
- Nakaoka M (2003) *Kotai-gun doutai to seikatsushi* [Population dynamics and life history of marine benthos]. In: Ecology of marine benthos (ed Wada K). Tokai University Press, Hadano, pp. 33–115. (in Japanese)
- Prezant RS, Chalermwat K (1984) Floatation of the bivalve *Corbicula fluminea* as a means of dispersal. *Science* 225: 1491–1493.
- Sigurdsson JB, Titman CW, Davies PA (1976) The dispersal of young post-larval bivalve mollusc by byssus threads. *Nature* 262: 386–387.
- Sorlin T (1988) Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). *Oecologia* 77: 273–277.
- Takahi S, Henmi Y (2011) Migration by mucous cord in the hard clam *Meretrix lusoria*. *Jpn J Benthology* 65: 76–81. (in Japanese with English abstract)
- Takeuchi S, Takahara Y, Agata Y, Nasuda J, Yamada F, Tamaki A (2013) Response of suspension-feeding clams to natural removal of bioturbating shrimp on a large estuarine intertidal sandflat in western Kyushu, Japan. *J Exp Mar Biol Ecol* 448: 308–320.
- Torii H, Sato S, Hamaguchi M, Henmi Y, Yamashita H (2010) The comparison of shell morphology and genetic relationship between *Meretrix lusoria* and *M. petechialis* in Japan and Korea. *Plankton & Benthos Res* 5: 231–241.
- Uchida K (1941) *Hamaguri no idou-shuusei ni tsuite*. [Migration of *Meretrix meretrix* on Korean tidal flat]. *Suisangakkaihou* 8: 218–230. (in Japanese)