Vol. 72: 247-254, 1991 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published June 4

Foot-raising behaviour and active participation during the initial phase of post-metamorphic drifting in the gastropod *Lacuna* spp.

André Martel*, Fu-Shiang Chia

Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9
and
Bamfield Marine Station, Bamfield, British Columbia, Canada V0R 1B0

ABSTRACT: Macrocinematographic video recordings showed that *Lacuna* spp. can produce a mucous thread and initiate drifting when exposed to water flows (particularly oscillating currents). The gastropods can play an active role in their dispersal by raising the metapodium – regardless of their orientation to water flow direction – until most of the sole's surface no longer contacts the substratum (only the most anterior [propodial] region remains fixed). The mucus produced and accumulated at the posterior of the sole of the foot is then taken away with the water current, and stretched up to 160 times the length of the gastropod. The mucous thread pulled by water currents then transports the gastropod, enabling it to drift in an almost neutrally buoyant fashion. In *Lacuna* spp., the production of a mucous thread also greatly reduces sinking rates (3- to 8-fold), while extension of the foot and antennae during the descent does not. Mucous threads also increase the drifting gastropod's ability to obtain rapid contact with, and attach to, nearby substrata.

INTRODUCTION

Post-metamorphic drifting is a widespread phenomenon in benthic marine molluscs. This mode of dispersal is achieved by juveniles – and even adults in the case of small-sized species – drifting in the water column using specialized byssal or mucous threads. It commonly occurs in numerous species of marine bivalves with a planktonic larval stage (Bayne 1964, Sigurdsson et al. 1976, Blok & Tan-Maas 1977, Lane et al. 1985, Martel 1988, 1990, Beukema & Vlas 1989) as well as in several species without a planktonic larval stage (brooders) (Martel 1988, 1990, Martel & Chia in press [a]). Post-metamorphic drifting also occurs in gastropods (Sigurdsson 1980, Vahl 1983, Johnson & Mann 1986, Martel 1988, 1990). In some mollusc species, post-metamorphic drifting plays a determinant role in recruitment (Bayne 1964, Beukema & Vlas 1989, Martel 1990). In these molluscs, microscopically thin mucous threads many times the length of the animal are secreted by specialized glands situated in the foot. These long invisible mucous threads increase the hydrodynamic drag on juveniles and allow drifting in the water column as juveniles are transported by water currents (Sigurdsson et al. 1976, Lane et al. 1982, 1985, Martel 1988, 1990).

Prezant & Chalermwat (1984) reported active participation in transport (drifting) by small adults of the freshwater clam *Corbicula fluminae*; standing on its foot, the bivalve secretes a copious amount of mucus which becomes a long thread that can lift the clam in water currents. In laboratory study on the floating behaviour of the tellinid bivalve *Macoma balthica*, Sorlin (1988) observed that the clam protrudes its foot prior to leaving the substratum and drifting in the water column. Although post-metamorphic drifting occurs in numerous species of marine bivalves and gastropods, whether or not it is an active, voluntary behavioural response by the mollusc is unknown (but see Sorlin 1988). Moreover, to our knowledge, the specific behavioural patterns involved during the initial phase of post-metamorphic drifting, together with the secretion and release of the drifting mucous thread in water currents, have never been shown for any marine species.

The first objective of the present study was to demon-

* Present address: Canadian Museum of Nature, Malacology Section, Zoology Division, PO Box 3443, Stn D, Ottawa, Ontario, Canada K1P 6P4

0171-8630/91/0072/0247/$ 03.00

strate that 2 congeneric species of marine gastropods can actively initiate post-metamorphic drifting, and that in such species drifting is not just a consequence of accidental dislodgement. The second objective was to examine several properties of mucous threads produced by drifting *Lacuna* spp.

MATERIALS AND METHODS

The study was carried out at the Bamfield Marine Station (48° 50′ N, 125° 08′ W), on the west coast of Vancouver Island, British Columbia, Canada. The gastropods (*Lacuna variegata* and *L. vincta*) used for the study of behaviour and drifting were collected in Barkley Sound, in the vicinity of Bamfield.

Behaviour and initiation of drifting. The behaviour of *Lacuna variegata* and *L. vincta* producing mucous threads and initiating drifting was studied in a low-velocity surge tank (90 cm long × 90 cm wide × 35 cm deep). The oscillating flow was adjusted to between 7 and 10 s cycle^{-1}, with corresponding peak velocities of 15 to 25 cm s^{-1}. A juvenile *Lacuna* (either *L. variegata* or *L. vincta*) (1.5 to 3 mm shell length) was placed on a 2 cm long piece of the eelgrass *Zostera marina*, which was glued in a horizontal position on top of a Plexiglas™ podium. The podium with the gastropod on top was placed in the middle of the water column of the flow chamber. An RCA-BW video camera equipped with a 55 mm macro Nikkor lens (35 mm format) was set up against the Plexiglass™ window of the tank. Three incandescent 100 W lamps with reflectors were distributed both beside and behind the tank to help illuminate the mucus by refraction.

Length of mucous threads. To estimate the length of the mucous thread of drifting *Lacuna vincta*, gastropods were placed on a small piece of turf algae *Gracilaria pacifica*, which was then immersed and attached in the flow tank. With the water flow adjusted at 2 to 2.5 cm s^{-1}, the gastropod was gently dislodged from the alga with a pair of forceps. It remained linked to the alga by its mucous thread, preventing it from being transported by the water current. The gastropod, with its stretching thread, was left in this position until the mucous thread ruptured, and the gastropod was immediately transported by the water flow The distance between the gastropod and the alga just before the mucous thread broke was used as the maximum length at which the mucous thread was capable of holding the gastropod in the water flow. Gastropods of shell length ranging from 1.3 to 5.6 mm were used to test for effects of size on the length of mucous thread produced.

Effects of mucous thread on sinking rates. The effect of mucus on gastropod sinking rates was studied using a transparent Plexiglass cylinder (height: 120 cm, diam.: 10 cm) to which we attached a 1 m ruler. The cylinder was filled with seawater (temp. = 10 °C). Adult and juvenile *Lacuna variegata* were placed individually in a finger bowl and gently spun for a few seconds. This method effectively induced the formation of the mucous thread. The gastropod was then dropped into the middle of the cylinder with minimal water disturbance. The time required by the sinking gastropod to cross the bottom 50 to 80 cm of the cylinder was recorded. This allowed enough time for the dropped gastropod to reach its terminal velocity (usually within the first 10 to 20 cm of the water column).

To compare sinking rates of individual *Lacuna variegata* without mucous threads, gastropods were blotted with a paper towel, held by the sides of the shell with forceps and dropped directly in the middle of the cylinder. Although the gastropod rapidly extended its foot and antennae during the first few cm of the descent, in most cases no mucous thread was produced. Controls were individuals that had been placed in a dilute formalin-seawater solution for several minutes. These gastropods remained withdrawn into their shell during the course of the experiment.

Attachment to substratum while drifting. The ability of gastropods to attach to the substratum while drifting was tested by placing a plastic screen (9 × 15 cm; thickness: 1 mm) with 9 mm square holes vertically across the flow chamber of a flow tank (velocity adjusted to 15 cm s^{-1}). *Lacuna vincta* between 2.5 and 6 mm shell length were put individually into a finger bowl filled with seawater and gently spun with a pair of forceps for a few seconds. The water containing the gastropod was then poured out of the bowl into the flow tank (15 to 20 cm ahead of the plastic screen). The gastropod was allowed to drift downstream using its mucous thread. As the gastropod passed through the screen the thread was usually caught. The ability of the thread to retain the gastropod once passing through the screen was recorded. A negative result occurred when the drifting gastropod passed directly through the screen without becoming attached. In a second treatment, gastropods were dropped into the tank by holding the sides of the shell with forceps without allowing the foot to contact anything. With this technique, most gastropods could not rapidly produce a mucous thread but were usually capable of protruding their foot while being carried by the currents. The ability of these gastropods to become attached to the screen with their extended foot was determined. Finally, gastropods that had been out of the water for 10 to 15 min and had withdrawn into their shells were used as controls.

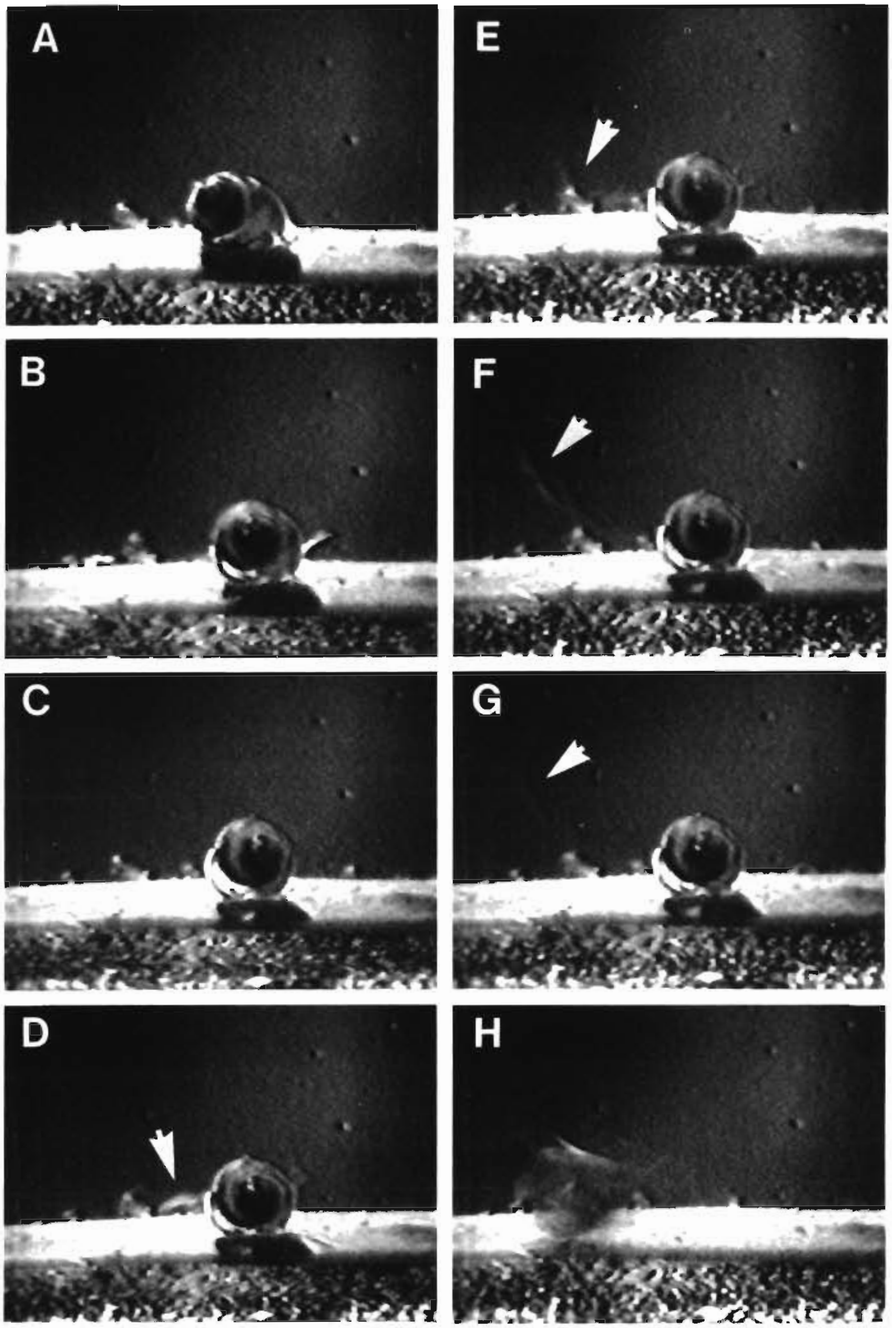

Fig. 1 *Lacuna variegata*. Photographs from a video sequence showing a juvenile (2 mm shell length) producing a mucous thread and initiating drifting in a surge tank. Water flow originated from the right at 15 to 25 cm s^{-1} (A) Prior to raising the foot. (B, C) Raising of the posterior part of the foot. (D to G) Release and stretching of the mucus from under the posterior part of the foot (see arrows); note that the mucous thread becomes less visible as the stretching process takes place. (H) Gastropod pulled by its mucous thread initiates drifting. The duration of the sequence is 1.6 s

RESULTS

Behaviour and initiation of drifting in *Lacuna* spp.

Macrocinematographic recordings of juvenile *Lacuna* spp. exposed to an oscillating flow similar to the surge observed in the intertidal zone demonstrated that the gastropod can control mucous thread production and the initiation of drifting. Fig. 1 shows a typical behavioural sequence during which a 2 mm juvenile *L. variegata* produced a long mucous thread before initiating drifting. The gastropod crawled and explored the seaweed for a few minutes; then it stopped and remained stationary for a few seconds. Facing the water flow (anterior region toward current) (15 to 25 cm s^{-1}), the gastropod suddenly lifted the posterior part of its foot (metapodium) until it reached ⅓ to ½ the height of the shell (Fig. 1 A, B, C). At this point, mucus produced and accumulated under the foot was carried by vortices downstream from the shell (Fig. 1 D, E, F) and rapidly stretched until it was no longer visible (Fig. 1 G). The juvenile lifted off quickly and initiated drift-

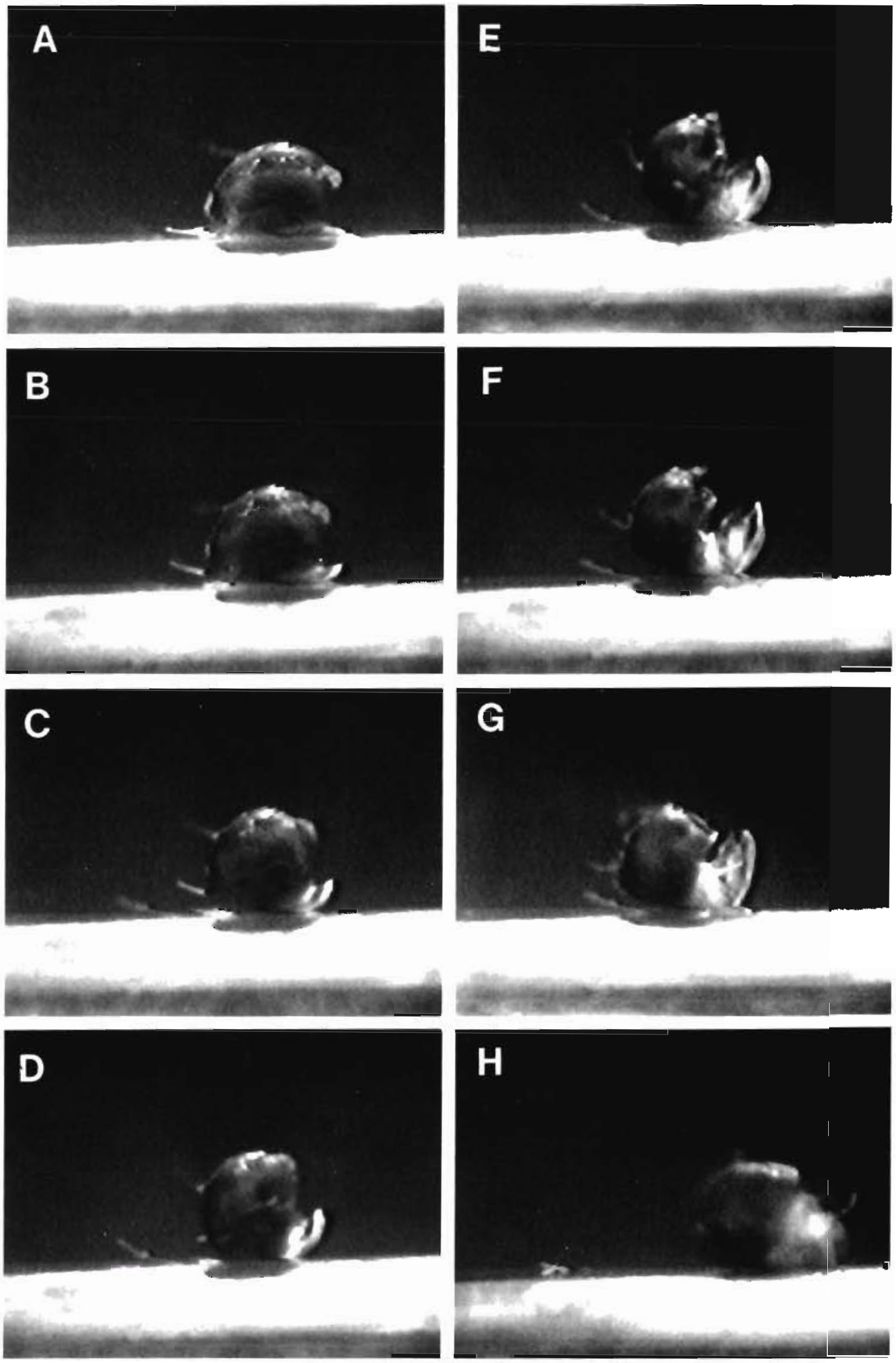

Fig. 2. *Lacuna variegata*. Photographs from a video sequence showing a juvenile (2.5 mm shell length) raising the posterior part of its foot prior to initiating drifting. A mucous thread, not visible in the pictures, was produced. Flow originated from the right at 15 to 25 cm s^{-1} Note the height reached and the concave shape of the foot sole which reduces the surface contact between the foot and the substratum. The gastropod initiated drifting and moved towards the left, carried by the water flow, even though (H) gives the contrary impression (picture framing problem). The duration of the sequence is 3.5 s

ing (Fig. 1 H). This sequence lasted less than 1.6 s. Upon leaving the substratum, the gastropod drifted in the water column of the wave tank and was transported by the water turbulence for many minutes, until it came into contact with the side of the tank, at which time the foot became attached and the gastropod started crawling. This behaviour was repeatedly recorded for both *L. variegata* and *L. vincta*.

Fig. 2 represents a video sequence that shows how gastropods raise the rear part of the foot to initiate drifting. Contrary to the first sequence, the gastropod in Fig. 2 initiated drifting while the posterior region

(metapodium) was facing the water flow. The behavioural pattern remained the same – the posterior part of its foot was lifted – even though the individual was oriented in the opposite direction. In this behavioural sequence, it is clear that the concave shape of the sole at the time the foot is raised contributed to reducing the surface contact between the gastropod and the substratum.

Gastropods exposed to even lower velocity oscillating flows (5 to 10 cm s^{-1}) usually displayed the same behavioural pattern but often did not initiate drifting; they remained in a 'somersault' position, raising the posterior region of the foot with only the anterior region (propodium) contacting the substratum. Following failure to initiate drifting, *Lacuna* spp. usually lowered their foot back onto the substratum and started crawling. These observations, coupled with laboratory experiments that gastropods exposed to water flow as high as 70 cm s^{-1} were not dislodged, confirm that in *Lacuna* spp. foot-raising behaviour and drifting are initiated by the individual: the gastropod actively participates in releasing itself from the substratum.

Length of mucous threads

The mucous thread produced by *Lacuna vincta* during drifting can be surprisingly long (Fig. 3). In small juveniles, the length of the mucous thread before rupturing can be 50 to 160 times the length of the shell. For example, one juvenile *L. vincta* of 2 mm shell length had a thread 320 mm long, 160 times the length of the shell (Fig. 3). Large juveniles and adults, which produced the greatest amount of mucus, produced longer threads than did small individuals (Fig. 3). Although there was much variability, the thread length and the size of the gastropod were significantly correlated ($r = 0.52$, $n = 26$, $p < 0.05$).

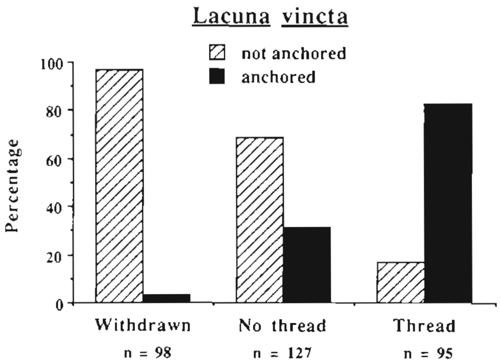

Fig. 3. *Lacuna vincta*. Relationship between shell length and the length of the mucous thread produced. Experiments were conducted in a flow tank (2.5 cm s^{-1}). Each point represents length of mucous thread measured at the point of rupture; $r = 0.52$, $n = 26$, $p < 0.05$

Effects of mucous threads on sinking rates

The presence of a mucous thread greatly reduced sinking rates of gastropods (Fig. 4). Sinking rates of juvenile *Lacuna variegata* of 1.25 to 2.25 mm shell length averaged 3.63 times lower when gastropods produced a mucous thread compared with those that did not (with thread: mean = 1.889 cm s^{-1}, SD = 1.898, n = 41; without thread: mean = 6.861 cm s^{-1}, SD = 1.588, n = 27) (one-way ANOVA, $F = 90.69$, $p < 0.001$) (Fig. 4). Similar observations were made with *L. vincta*. The extension of the foot and antennae during descent did not significantly reduce sinking rates of gastropods; the method employed to measure sinking rates did not allow the detection of a difference in sinking rates between gastropods displaying either behaviour (foot and antennae protruded versus withdrawn) (ANCOVA, differences among slopes and among means: $p > 0.05$) (Fig. 4).

Large juvenile and adult *Lacuna* spp. could significantly reduce their sinking rates using mucus (Fig. 4). Given sufficient water current and turbulences, adults in aquaria could drift and remain in the water column for extended periods of time (Fig. 4). They required greater upward flows to remain in suspension and were not as efficient at drifting as juveniles ≤ 2 mm shell length.

Attachment to substratum while drifting

Mucous threads enabled drifting *Lacuna* spp. to attach to a substratum (Fig. 5). As many as 83.2 % of the *L. vincta* with mucous threads attached to the screen using their thread as they passed though the holes, compared to only 31.5 % of gastropods without threads (*G*-test, $G(W) = 153.12$, $p < 0.001$) (Fig. 5). This ratio is conservative since it was not always possible to elimi-

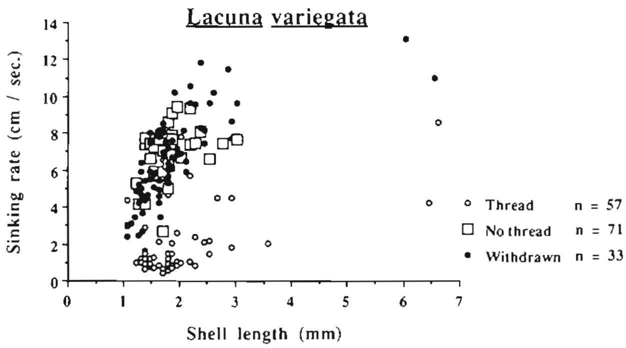

Fig. 4. *Lacuna variegata*. Sinking rates in 3 behavioural situations: (1) gastropod with mucous thread, (2) gastropod without mucous thread, and (3) gastropod withdrawn into shell

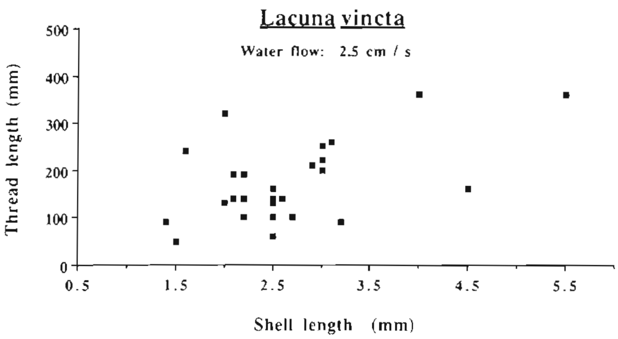

Fig. 5. *Lacuna vincta.* Percentage of adults capable of attaching to a substratum while drifting in the water column during 3 behavioural situations: (1) gastropod with mucous thread, (2) gastropod without mucous thread, and (3) gastropod withdrawn into shell

nate the production of mucous threads by gastropods dropped when holding the sides of the shell with forceps. The value of 3.1 % attachment by control (withdrawn) gastropods is explained by a few individuals that rapidly came out of their shells during their descent and successfully attached to the screen with their sticky foot as they passed through. The difference in the proportion of gastropods that were successful in attaching to the substratum is significant between all subsets (R × C, *G*-test, $p < 0.001$; Sokal & Rohlf 1981).

DISCUSSION

Properties of drifting mucous threads

Lacuna vincta produced mucous threads 50 to 160 times the length of the gastropod, with a 2 mm juvenile producing a 320 mm long thread. Lane et al. (1985) studied the drifting byssal threads of juvenile mussels (*Mytilus edulis*, shell lengths of ca 0.5 to 1.1 mm) and reported similar thread length/shell length ratios. Their values were not from direct measurements but from calculations relating sinking rates and drag. In our study, the maximal length of the mucous thread of *L. vincta* was determined by allowing it to stretch with water current until its rupture (see a similar method in Beukema & Vlas 1989). This method probably underestimates the total length of threads produced in natural conditions, since threads of gastropods that drift freely in the water column may experience significantly weaker pulling forces than those involved when the end of the thread is caught on a fixed object. In situations where the mucous thread is attached and the gastropod at the other end is being carried away with water currents, the thread is likely to stretch faster and to rupture at a shorter length. This supposition is supported by laboratory observations of free-drifting large juvenile *L. vincta* where the mucous thread was made visible by detritus and estimated to be at least 500 to 600 mm in length, thus longer than any measurements of thread length made using the flow tank method.

The production of mucous threads by *Lacuna* spp. reduced sinking rates 3- to 8-fold. Moreover, contrary to Johnson & Mann's (1986) conclusion for the same species, the extension of the foot and antennae did not significantly reduce sinking rates (difference not measurable with the method employed). Only the production of a mucous thread, which increases the surface area and thus the viscous drag (Vogel 1981, Lane et al. 1985, Denny 1988) effectively modified the sinking rate. Upward flows of 0.4 to 1.0 cm s^{-1} were sufficient for juveniles $\leq$ 2 mm to remain suspended in the water column. These sinking velocities are similar to those obtained by Johnson & Mann (1986) for *L. vincta* and by Lane et al. (1985) and Beukema & Vlas (1989) for juvenile *Mytilus edulis* and *Macoma balthica* respectively.

Our results also showed the superior ability of juvenile *Lacuna* spp. $\leq$ 2.5 mm to drift in the water column compared with large individuals (Fig. 4). On the other hand, even large juvenile and adult *Lacuna* spp. are capable of water column drifting if upward water velocities are 3 to 8 cm s^{-1}. In semi-exposed rocky intertidal areas, even during calm days, water currents created by ground swell and surge are usually much greater than a few centimeters per second. Such conditions, therefore, likely provide sufficient water velocities to keep both small and large *Lacuna* spp. in the water column.

The attachment of larvae and post-larval stages to substrate by byssal threads occurs in the mussel *Mytilus edulis* (Blok & Tan-Maas 1977, Eyster & Pechenik 1987). An important function of mucous threads produced by *Lacuna* spp. is enhancing the gastropod's ability to attach to a substratum (e.g. algae) while drifting in the water column. This was observed in flow tanks as well as in the field during SCUBA where drifting *Lacuna* spp. became entangled and attached to algal blades by their mucous thread as they were carried by water currents (Martel pers. obs.). Vahl (1983) proposed a similar function for mucus produced by the limpet *Helcion pellucida* living on the kelp *Laminaria hyperborea*. In semi-exposed intertidal seaweed communities, where prevailing water turbulences likely maintain gastropods in suspension, the ability of the mucous thread to enable drifting gastropods to attach themselves effectively to algae may be one of its most important functions.

Behaviour and active role in drifting

Gastropods of the genus *Lacuna* can initiate drifting. Video recordings indicate that the gastropod can, via

the foot raising behaviour, play an active role in its dispersal. Although individual *Lacuna* spp. that were manually or accidentally dislodged were capable of producing enough mucus to drift in the water column (Martel pers. obs.), evidence of an active role played by the gastropod during the initial phase of drifting reinforces the view that post-metamorphic drifting is adaptive and is part of the behavioural repertoire of these molluscs (Martel 1990).

The phenomenon of post-metamorphic drifting in *Lacuna* spp. and in other molluscs may have several adaptive benefits. In addition to constituting a dispersal mechanism capable of affecting population dynamics as well as the area of distribution in some molluscs (Martel 1988, Beukema & Vlas 1989, Martel 1990, Martel & Chia in press [a, b]), post-metamorphic drifting may represent an adaptive behaviour enabling individuals to escape unfavorable conditions (see Sorlin 1988, Beukema & Vlas 1989). Juvenile and adult *Lacuna* spp. placed in a wave tank and put on algal blades that offer no shelter or folds (present study), where the gastropod can graze while remaining cryptic, initiate drifting more readily than individuals put on blades with deep folds or blades kept stable and where gastropods can crawl underneath and remain cryptic (Martel pers. obs.). This ability to escape in the absence of shelter may constitute an adaptation that reduces risks of predation by fishes such as seaperch (Embiotocidae), which prey on *Lacuna* spp. (Martel 1990). Studies on larval settlement and recruitment of *Lacuna* spp. also indicated that this behaviour enables juveniles to relocate and migrate to adult habitats following initial settlement episodes on seaweeds heavily used by veligers but not by adults (Martel 1990, Martel & Chia in press [b]). Similar migrations of juveniles to adult habitats play an important role in the recruitment of the mussel *Mytilus edulis* and the clam *Macoma balthica* (Bayne 1964, Beukema & Vlas 1989).

Finally, results from the present study corroborate with reports in which *Lacuna* spp. were found to show high post-metamorphic dispersal capabilities (Johnson & Mann 1986, Martel 1990, Martel & Chia in press [a]). Studies on drifting marine benthic invertebrates conducted in Barkley Sound and involving the use of off-bottom intertidal and subtidal algal collectors indicated the presence of up to 17 molluscan taxa, of which *Lacuna* spp. and mussels *Mytilus* spp. were among the most abundant drifters (up to 30 juveniles caught per collector per day) (Martel 1988, 1990, Martel & Chia in press [a]). Considering the widespread occurrence of post-metamorphic drifting and its likely important role in the dispersal and recruitment of many marine gastropods and bivalves, it is probable that active participation in drifting and foot behaviours similar to those reported in *Lacuna* spp. occur in the behavioural repertoire of juvenile stages of other molluscs.

Acknowledgements. We are grateful to D. Boag, D. Craig, K. Durante, G. Gibson, R. Koss, J. Lawrence, P. Qian, A. Spencer, R. Zimmer and 2 anonymous reviewers for critical reading and suggestions on earlier drafts of the ms. Special thanks to K. Klein for her support and assistance with laboratory work throughout the study, as well as for her valuable comments and suggestions on the ms. We thank the graduate students at the Bamfield Marine Station, especially G. Jensen, for their ideas and lively discussions on animal behaviour We are also grateful to the Director and staff of the Bamfield Marine Station for their assistance and help during this study. This research was supported by NSERC and Province of Alberta scholarships to A.M. and NSERC grants to F.S.C.

LITERATURE CITED

Bayne, B. L. (1964). Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J. Anim. Ecol. 33: 513–523

Beukema, J. J., 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

Blok, J. W. de, Tan-Maas, M. (1977). Function of byssus threads in young postlarval *Mytilus*. Nature, Lond. 267: 386–387

Denny, M. W (1988). Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, New Jersey

Eyster, L. S., Pechenik, J. A. (1987). Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. J. exp. mar Biol. Ecol. 114: 99–110

Johnson, C. R., Mann, K. H. (1986). The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. J. exp. mar. Biol. Ecol. 97: 231–267

Lane, D. J. W., Nott, J. A., Crisp, D. J. (1982). Enlarged stem glands in the foot of the post-larval mussel, *Mytilus edulis*: adaptation for bysso-pelagic migration. J. mar. biol. Ass. U.K. 62: 809–818

Lane, D. J. W., Beaumont, A. R., Hunter, J. R. (1985). Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. Mar. Biol. 84: 301–308

Martel, A. (1988). Drifting as an important dispersal and recruitment mechanism in small intertidal invertebrates. Am. Zool. 28: 139A

Martel, A. (1990). Recruitment, post-metamorphic drifting and reproductive ecology in the herbivorous gastropod *Lacuna* spp. within kelp canopies and intertidal seaweed communities. Ph.D. dissertation, University of Alberta

Martel, A., Chia, F. S. (in press [a]). Drifting and dispersal of small bivalves and gastropods with direct development. J. exp. mar. Biol. Ecol.

Martel, A., Chia, F. S. (in press [b]). Oviposition, larval abundance, in situ larval growth and recruitment of the herbivorous gastropod *Lacuna vincta* in kelp canopies in Barkley Sound, Vancouver Island, British Columbia. Mar. Biol.

Prezant, R. S., Charlermwat, K. (1984). Floatation of the bivalve *Corbicula fluminea* as a means of dispersal. Science 225: 1491–1493

Sigurdsson, J. B. (1980). Byssus-drifting, a dispersal mechanism in post-larval bivalve molluscs, with notes on

gastropods. Ph.D. thesis, University of Newcastle-upon-Tyne

Sigurdsson, J. B., Titman, C. W., Davies, P. A. (1976). The dispersal of young post-larval bivalve molluscs by byssus threads. Nature, Lond. 262: 386–387

Sokal, R. R., Rohlf, F. J. (1981). Biometry, 2nd edn. W. H. Freeman and Co., San Francisco

This article was presented by J. M. Lawrence, Tampa, Florida, USA

Sorlin, T. (1988). Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). Oecologia 77: 273–277

Vahl, O. (1983). Mucus drifting in the limpet *Helcion* (= Patina) *pellucidus* (Prosobranchia, Patellidae). Sarsia 68: 209–211

Vogel, S. (1981). Life in moving fluids: the physical biology of flow. Willard Grant Press, Boston

Manuscript first received: December 4, 1990
Revised version accepted: March 8, 1991