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OBSERVATIONS ON BYSSUS SYSTEMS IN THE SPAT OF *CERASTODERMA GLAUCUM* AND *C. EDULE*

KOBINA YANKSON*
Department of Zoology, University College of Swansea, Singleton Park, Swansea SA2 8PP

(Figs. 1–8)

Observations made of the byssus apparatus of *Cerastoderma glaucum* and *C. edule* are reported and include an account of the mobility of the spat in the laboratory cultures. In their typical natural habitats both species are capable of an extended pelagic existence following initial settlement from the plankton. During this period *C. edule* alternates pedal crawling with byssal drifting to give horizontal dispersal; *C. glaucum* combines pedal crawling with byssal climbing of submerged vegetation resulting in vertical dispersal. It is suggested that the behaviour of young *C. glaucum* spat enables them to escape unfavourable conditions at the muddy bottom of their typical lagoon habitat, and to compete more favourably for food. The structural adaptations for these activities are in the byssus gland system which, in *C. edule* is relatively simple and secretes a thin unbranched thread; but in *C. glaucum* is more elaborate and secretes a stronger thread with anchoring side branches. These differences have incidental taxonomic value in separating these closely related species.

INTRODUCTION

Yonge (1962) suggests a possible universal occurrence of byssal apparatus in the post-larval spat of bivalves. Subsequent studies have revealed that the byssus thread secreted by the post-larval byssal apparatus of many bivalves is involved in settlement as well as migration by means of bysso-pelagic drifting (Sigurdsson, Titman & Davis, 1976; Blok & Tan-Maas, 1977; Board, 1983). Recent studies on the byssus and other foot glands in the early stages of bivalves have included *Ostrea edulis* (Cranfield, 1973*a*, *b*, *c*); *Pecten maximus* (Gruffydd, Lane & Beaumont, 1975); *Mytilus edulis* (Lane & Nott, 1975; Lane, Nott & Crisp, 1982); and *Chlamys varia* L. (Gruffydd, Budiman & Nott, 1979).

The byssus systems of juvenile Cardiacea have hardly been studied despite the frequent references to the use of a byssus thread in the climbing of submerged vegetation by *Cardium exiguum* Gmelin, *Cardium hauniense* Petersen & Russell, and *Cerastoderma glaucum* (Bruguière) (Peterson, 1958; Jelnes, Petersen & Russell, 1971; Petersen & Russell, 1971*a*, *b*; Boyden & Russell, 1972; Ivell, 1979; Brock, 1979; Barnes, 1980). *Cerastoderma edule* (L.) is generally regarded as a non-climber although Rygg (1970) reports that the spat of both *C. glaucum* and *C. edule* seem to climb vertical aquarium walls equally well. In the field the spat of the latter species are reported to anchor themselves to sand grains by means

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* Present address: Department of Zoology, University of Cape Coast, Cape Coast, Ghana.

of spines and threads (Franklin, 1972). They are also reported to be transported over the cockle bed till a size of about 2 mm is attained (Baggerman, 1953; Verwey, 1981).

This paper describes the structure of the byssus systems of the spat of the two closely related species of *Cerastoderma* (*C. glaucum* and *C. edule*). Observations on the mobility of the spat in laboratory cultures are reported and the results related to the behaviour and ecology of the two species.

MATERIALS AND METHODS

All the *C. glaucum* spat used in this study were obtained from artificial fertilization and rearing methods described by Yankson & Moyse (1983), the parents having originated from the Aberthaw Power Station Lagoon (S. Wales) (National Grid Reference ST 035 622). The *C. edule* spat were collected from the Burry Inlet (S. Wales) (SS 527962) by sieving (1 mm mesh) the sand.

Histology

Histological sections were prepared from spat fixed 'whole' in Bouin's fluid for 24 h for specimens dissected out of their shells and for 48 h for those processed within their shells. Standard procedures for dehydration, impregnation and embedding in paraffin wax were followed. Transverse and longitudinal sections (6–8 μm) were cut on a rotary microtome and stained in Gill's haematoxylin and eosin.

Observations on live specimens

Several batches of *C. glaucum* spat were observed from the day of settlement through periods of up to 20 weeks in the laboratory for the development and usage of the byssus thread. Two batches of *C. edule* spat in glass Petri dishes were observed under a dissecting microscope (up to × 60) while the floating and climbing activities in glass culture vessels were observed with the aid of a hand lens (× 5).

Free hand sketches were made of typical threads trailed by the climbing or floating spat of both species.

Experiments on the climbing activity

Successful laboratory production of *C. glaucum* spat enabled relatively more elaborate experiments to be conducted on the climbing activity of this species compared to *C. edule*.

The effect of age/size on the climbing activity of Cerastoderma spat

(i) *C. glaucum*: Sixty spat of *C. glaucum* measuring *ca.* 0·6 mm shell length were placed in each of two 500 ml Pyrex glass breakers containing 400 ml of filtered (1·0 mm) UV-treated sea water. A mass of green monofilament nylon netting (Netlon) (2 cm mesh), obtained by folding a 20 × 8 cm piece of material, was immersed in each beaker to imitate the submerged vegetation occurring in the natural habitat. The beakers were loosely covered to prevent excessive evaporation and entry of air borne particles. The spat were fed daily with reasonable quantities of a mixed algal diet consisting of equal packed cell volumes of T-ISO (see Ewart & Epifanio, 1981), *Monochrysis lutheri* and *Phaeodactylum tricornutum*. The numbers of spat clinging to the walls of the beakers and to the Netlon were recorded separately, every other day and at the same time the sea water was changed and all the spat returned to the bottom of the beakers. The numbers of spat which climbed were expressed as percentages of the total number and plotted as 'climbing activity'. This was continued for 56 days beyond which no more climbing was recorded within two-day intervals of water change. The ambient temperature of the laboratory during the experimental period ranged between 18 and 23 °C.

(ii) *C. edule*: Fifty spat of this species, collected from the field and measuring between 1·0 and 6·5 mm in shell length were divided into two lots of 25 each and placed in 250 ml tall form Pyrex glass beakers. The conditions of water, food and temperature were the same as for *C. glaucum* (above) except that no Netlon was used. Records were taken every other day of the number and sizes of spat that climbed the vertical walls of the vessels as well as mortalities.

The effects of starvation and water condition on the climbing activity of older C. glaucum spat

The spat used in this experiment were part of the batch which had ceased climbing under the conditions described above. When the feeding of these spat (14 weeks old by then) was withheld 8 out of 42 (i.e. 19 %) climbed the walls of the beaker by the 4th day. The following experiment was therefore set up to investigate primarily, whether it was starvation which induced climbing in these spat.

Spat, measuring between 8·0 and 10·3 mm in shell length, were fed continuously for 5 days on a mixed algal diet as above. They were divided into 4 lots of 10 and placed in 500 ml Pyrex glass beakers filled with 400 ml filtered (5 μm), but unsterilized sea water. The beakers were held in a water bath maintained at 20 °C. Two of the lots ('A') were fed with a mixed diet as above while the other two ('B') were unfed. Initially, the sea water in all the vessels was changed every other day during which the number of spat clinging to the walls was recorded before they were washed to the bottom. Between the 17th and 29th day after the start of the experiment, the sea water in all the vessels was left unchanged but the feeding of the spat in 'A' was continued and records taken as usual. Thirty-six days after the start of the experiment no further food was administered to the spat in 'A' but the number of spat climbing was recorded as usual until a definite pattern emerged.

OBSERVATIONS AND RESULTS

External anatomy of the foot

External morphology of the foot of the spat is essentially similar in the two species of *Cerastoderma* except that the foot is stouter in *C. edule*, the adult of which is reported to be a better burrower than *C. glaucum* (Brock, 1979). In the spat of both species the foot is pointed anteriorly and has a 'blunt' heel at the posterior end (Fig. 1). The characteristic infoldings of the pedal epithelium impart an irregular outline to the foot. The entire ventral surface of the foot and its distal half dorsally, are ciliated. The ciliation of the pedal epithelium coincides with the position of the underlying pedal 'mucous' glands. The pedal cilia in the young spat of *C. glaucum* (5 weeks old and measuring *ca.* 1·5 mm in length) are responsible for creating the inhalant water current into the mantle cavity as in *Macoma balthica* (L.) (Caddy, 1969) and *Mytilus edulis* (Bayne, 1971). Although such post-larval spat of *C. edule* were not available for comparable observations, it seems reasonable to assume that the pedal cilia of its young spat would perform a similar function as in the sibling species *C. glaucum*.

A single posterior duct (the byssus duct), in *C. glaucum* and at least 3 narrow ducts in *C. edule* (see Fig. 2C), open in front of the heel of the foot into the pedal groove. The latter extends forwards and terminates in the pedal depression situated at about one-third the distance from the tip of the foot.

The foot glands

The histological sections have revealed 4 foot glands in the spat of *C. glaucum* and 3 in *C. edule*. Since histochemical studies have not been conducted, the homologues suggested below are based on the positions, appearance and duct openings of the glands.

Gland 1. This is a stem gland (see Lane & Nott, 1975) which, in young *C. glaucum* spat is situated beneath the gut (1 in Fig. 2A) and opens into the dorsal part of the byssal pit. The gland has not been detected in older spat of this species

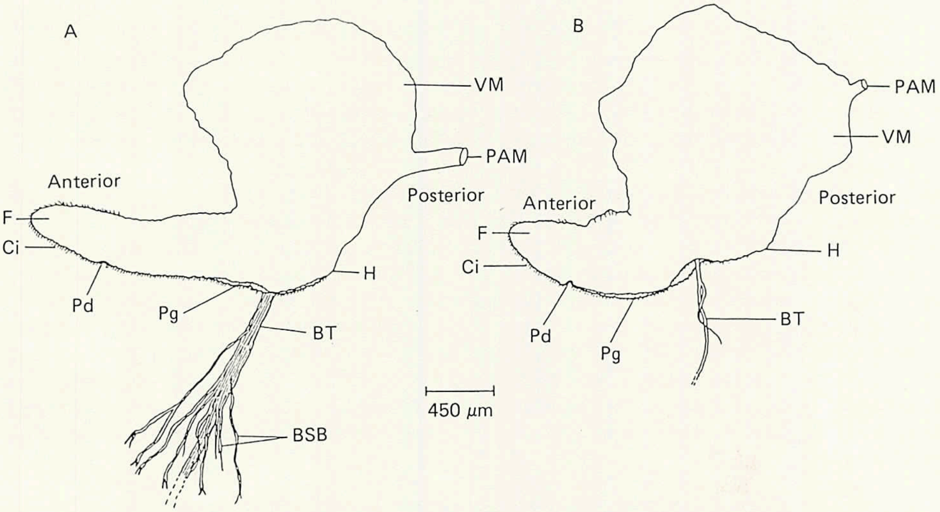

Fig. 1. Dissected spat of *Cerastoderma* showing the foot in outline. (A) *C. glaucum*. (B) *C. edule*. BSB, Byssus side branches; BT, byssus thread; Ci, cilia; F, foot; H, heel; Pd, pedal depression; Pg, pedal groove; PAM, posterior adductor muscle; VM, visceral mass.

(measuring over 8·0 mm in length), in which only its duct persists (dl in Figs. 2B, 3). In younger spat its position, minimal staining and reticulate appearance correspond to gland S1 of *Mytilus edulis* (Lane & Nott, 1975) and gland D3 of *Ostrea edulis* (Cranfield, 1973*a*). The apparent disappearance of gland 1 in older spat of *C. glaucum* suggests that its role in this species is preliminary ('preliminary' byssus gland) and probably useful only during the early post-larval stage. Its weaker, diffuse contribution to the byssus thread probably becomes less important as the spat increases in size and thus requires a stronger thread for support.

In *C. edule*, a massive gland of similar appearance and position to gland 1 in *C. glaucum* is present in all the spat examined (1·5–6·1 mm in length) (1 in Figs. 2C, 5A). It apparently secretes the main component of the homogeneous, non-sclerotized byssus thread into a ciliated byssal pit from where it emerges through one of a delta of ducts in front of the heel of the foot. It may therefore be referred to as the 'main' byssus gland in this species, the remnants of which persist in the adult.

Gland 2. This is also a stem gland and has been detected in all the spat of *C. glaucum* examined, but not in any *C. edule* spat. The gland discharges into the byssal pit (Fig. 4C) and corresponds in position to gland S2 of *Mytilus edulis*, D4 of *Ostrea edulis* and gland 1 of *Pecten maximus* (Gruffydd *et al.* 1975). In *C. glaucum* spat it secretes the main component of the byssus thread which emerges through a single duct anterior to the heel of the foot and may be regarded as the 'main' byssus gland.

The single posterior byssus duct of *C. glaucum* originates from a complex byssal pit (Fig. 4C) homologous to the posterior duct complex of the plantigrade of *Mytilus edulis* (Lane *et al.* 1982). The secretory processes of gland 2 in *C. glaucum* converge into spaces (= lamellar spaces) where they form byssus fibres.

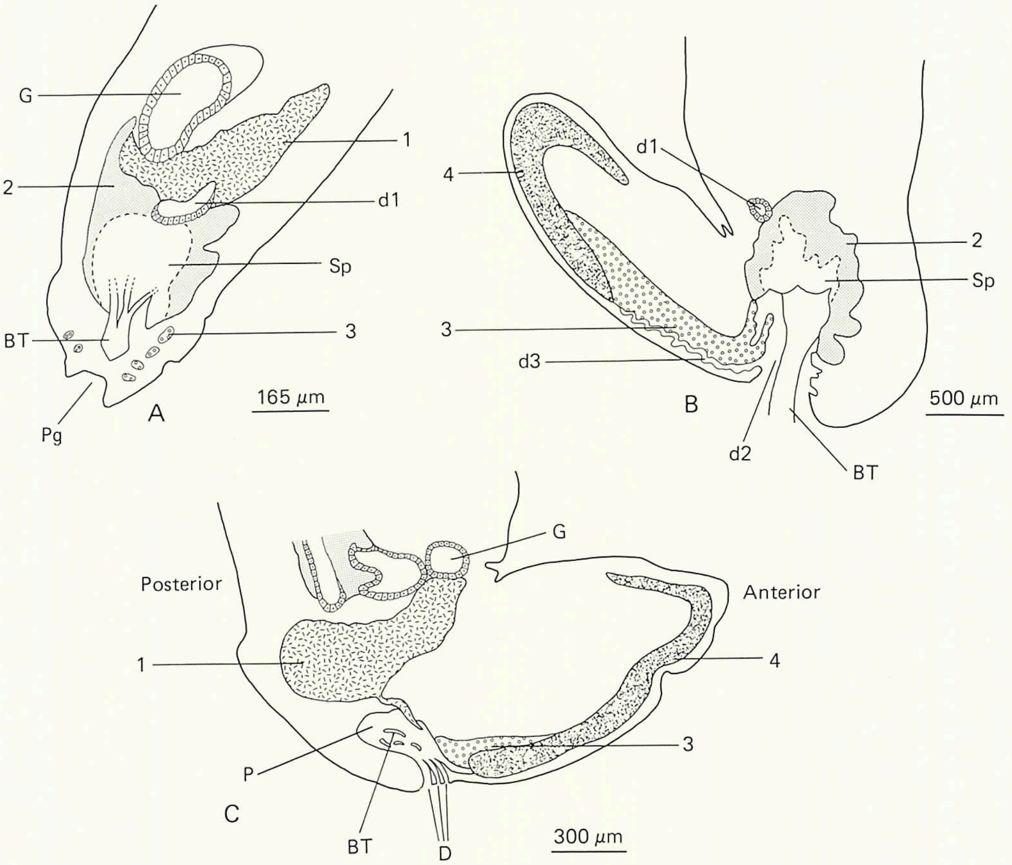

Fig. 2. (A) Low power drawing of transverse section through the lower part of the visceral mass and the foot showing the byssus gland system in *C. glaucum* spat (7 weeks old). (B) Low power drawing of a longitudinal section through the lower visceral mass and the foot of *C. glaucum* spat (20 weeks old) showing the positions of glands 2, 3 and 4 and the remains of the duct of gland 1. (C) Low power drawing of a longitudinal section through the lower visceral mass and foot of *C. edule* spat (*ca.* 9 weeks old) showing the positions of glands 1, 3 and 4.

Abbreviations for Figs. 2–5: 1, gland 1 ('preliminary' byssus gland in *C. glaucum*; 'main' byssus gland in *C. edule*); 2, gland 2 ('main' byssus gland in *C. glaucum*); 3, gland 3 ('auxillary' byssus gland); 4, gland 4 (pedal mucous gland); BF, byssus fibre; BT, byssus thread; CT, connective tissue; D, delta of byssus duct; d1, duct of gland 1; d2, duct of gland 2; d3, duct of gland 3; Epi, epithelium (ciliated); G, gut; LS, lamellar space; MT, muscular tissue; NT, nervous tissue; P, byssal pit; Pg, pedal groove; PO, partial opening of lamellar space; Sp, region occupied by the secretory processes of gland 2, and byssus fibres; Sp2, secretory processes of gland 2; Sp3, secretory processes of gland 3; Sv2, secretory vesicles of gland 2; Sv3, secretory vesicles of gland 3.

The latter emerge separately through the partial openings of the lamellar spaces ventrally into a ciliated byssal pit, where they join to form a longitudinally striated, non-sclerotized byssus thread. In the older spat, following the apparent disappearance of gland 1, the byssus system assumes an arborescent profile consisting of gland 2 and the 'free' byssus fibres (see Figs. 3, 4) as the 'crown', and the main byssus thread as the 'trunk'. Remnants of gland 2 persist in the adults of *C. glaucum*.

Gland 3. This may also be regarded as a stem gland since it opens into the distal end of the byssus duct (in *C. glaucum*) as well as into the pedal groove (3 in Figs. 2B, 4B). In *C. edule* one of its openings forms part of the delta of ducts in front of the heel (3 in Figs. 2C, 5A). The association of this gland with the byssus duct suggests that it adds to the main thread secretion like gland 2 and gland S4 respectively of *Pecten maximus* and *Mytilus edulis* (Gruffydd *et al.* 1975).

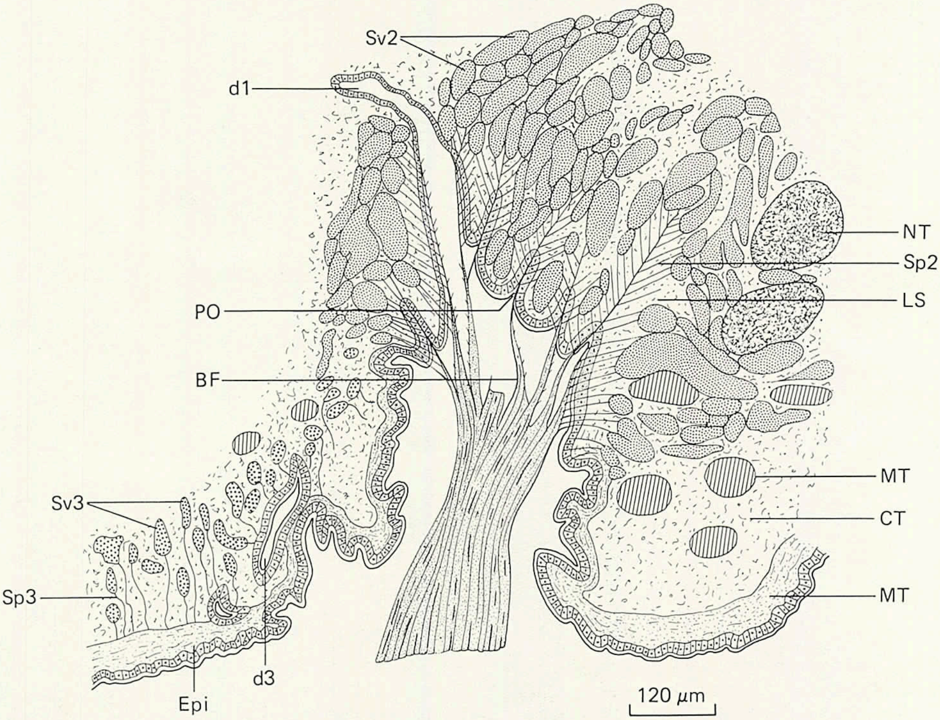

Fig. 3. High power drawing of a longitudinal section through the lower visceral mass and foot of *C. glaucum* (20 weeks old) showing the byssus (stem) gland system. (See legend to Fig. 2 for abbreviations.)

Gland 4. This is a pedal gland. (See 4 in Figs. 2B, 4B (*C. glaucum*) and 4 in Figs. 2C, 5A (*C. edule*).) It opens onto the tip of the sole of the foot in both species of *Cerastoderma*. Glands 3 and 4 overlap considerably in the mid-ventral region of the foot; the former gland overlying the latter. The exact homologue of gland 4 of *Cerastoderma* is difficult to find in the other bivalves, but its position corresponds to those of the pedal glands of the pediveliger of *Mytilus edulis* (Lane & Nott, 1975) and glands 3–5 of *Pecten maximus* (Gruffydd *et al.* 1975). In the spat of *Cerastoderma*, the association of gland 4 with the pedal depression and the ciliation of the foot suggests that its functions would be similar to those proposed for the pedal glands in *Mytilus edulis* and *Pecten maximus* by the above authors; namely, weak adhesion of the foot to the substratum, formation of attachment plaques for the byssus thread, and facilitation of pedal locomotion by

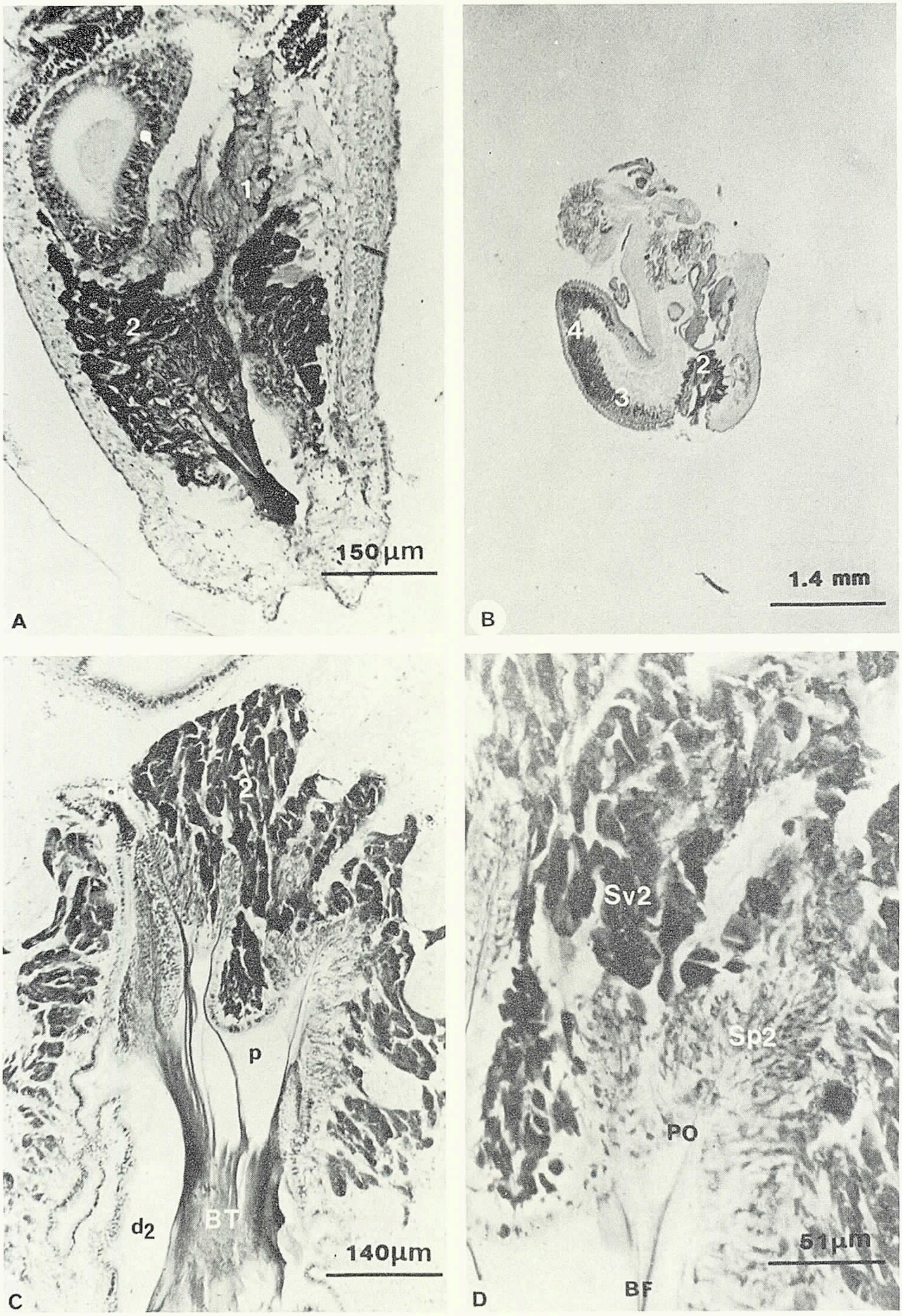

Fig. 4. Photomicrographs of the byssus system of *C. glaucum*. (A) T.S. through the lower visceral mass and foot of 7 weeks old spat. (B) L.S. through the lower visceral mass and foot of 20 weeks old spat. (C) L.S. through the byssus (stem) gland system of 20 weeks old spat. (D) Higher magnification of L.S. through gland 2 showing secretory vesicles and processes. (See legend to Fig. 2 for abbreviations.)

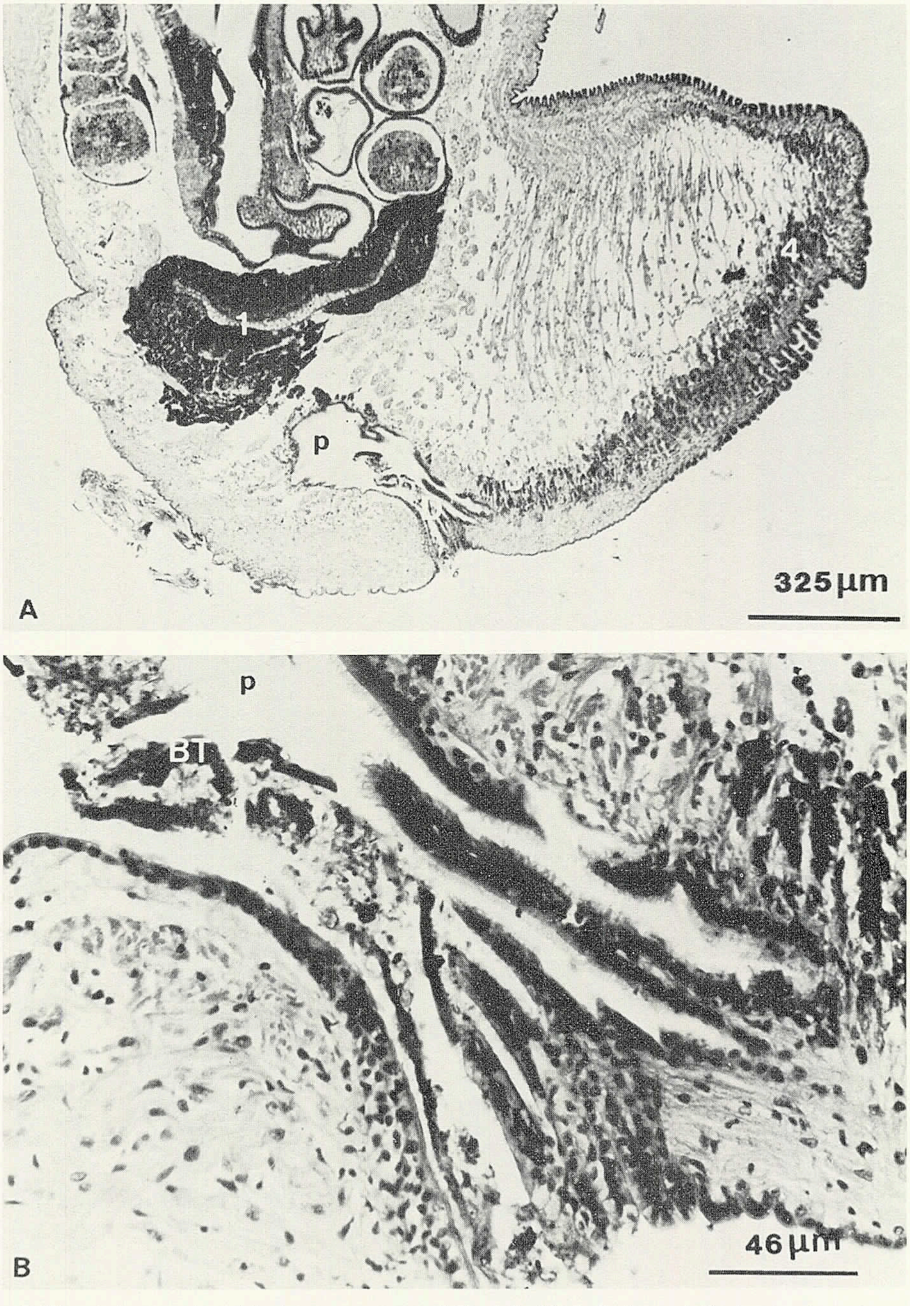

Fig. 5. Photomicrographs of the byssus systems of *C. edule*. (A) L.S. through the lower visceral mass and foot of 9 weeks old spat. (B) Higher magnification of (A) showing the association of the byssus duct with the byssal pit.

ciliary gliding. Gland 4 persists in the adults of both species of *Cerastoderma* and probably plays a role in burrowing.

The byssus thread and its functions in Cerastoderma spat

Physical features

The post-larval spat of both species of *Cerastoderma* secrete a non-sclerotized transparent 'byssus' thread which may be trailed behind as they crawl or climb. When broken off the thread can be formed anew. The thread secreted by the spat of *C. edule* is thinner and smoother compared with the relatively thicker and longitudinally striated thread of *C. glaucum*. At the point of emergence from the byssus duct the thread secreted by spat measuring between 2·0 and 4·0 mm in length measured *ca.* 10–15 μm and *ca.* 25–40 μm in *C. edule* and *C. glaucum* respectively.

The byssus thread itself consists of one main branch (or stem) with or without side branches. The side branches of the thread of *C. glaucum* are shorter and more numerous than those of *C. edule* in which only one or two side branches were occasionally seen. The side branches of the former species are forked at the tips where they attach to the substratum.

The byssus thread in *C. glaucum* spat is apparently stronger than in *C. edule* since the former can remain clinging to glass walls and Netlon threads even when the sea water medium is drained off. Such clinging spat are dislodged only with a strong jet of water. *C. edule* spat on the other hand, drop off easily upon the slightest disturbance of the culture vessel. The strength of the byssus thread of *C. glaucum* is further emphasized by the fact that it can stand a considerable pulling force. A pulling operation performed with a pair of forceps under a dissecting microscope resulted in the protrusion of a paired pouch on either side of the base of the byssus thread. A gentle pressure on the lower half of the visceral mass also protruded the pouch in many freshly dissected *C. glaucum* spat but not in *C. edule* spat. In live, crawling animals this pouch forms a pair of protrusible lips through which the byssus thread emerges.

Spat mobility

The spat of both species of *Cerastoderma* are very mobile and observations on live animals in laboratory cultures have revealed three forms of mobility namely: crawling, climbing and floating.

(i) Crawling. All the spat of both species measuring up to 10 mm or more which were observed in the laboratory were capable of crawling. Spat older than 3 weeks and measuring more than 0·5 mm in length usually trailed a byssus thread during crawling. Like other bivalves, during crawling the foot is first extended forward to probe the substratum. A 'grip' is then effected at the point of the pedal depression (= pedal sucker) after which the rest of the body is pulled forward by the action of the pedal and adductor muscles.

(ii) Climbing. The spat of both species of *Cerastoderma* were capable of climbing vertical glass walls to varying degrees. *C. glaucum* spat measuring up

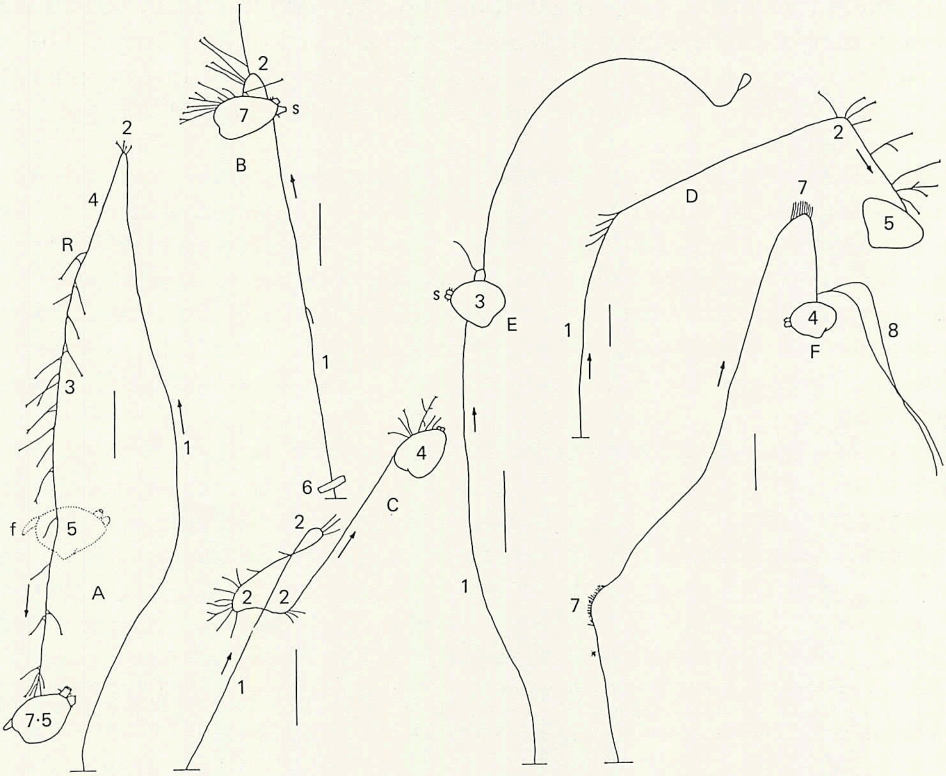

Fig. 6. Annotated illustrations of byssus threads trailed by climbing or floating spat of *Cerastoderma*. (A–D) *C. glaucum*. (E, F) *C. edule*. Arrows indicate direction of thread formation. Scale bars represent 10 mm of byssus threads length (shell lengths not to scale: A, 7·5 mm, B, 7·0 mm, C, 4·0 mm; D, 5·0 mm, E, 3·0 mm, F, 4·0 mm). Horizontal lines indicate the bottom of the culture vessel. Notice side branches or mucous strands mainly on one side of the main thread and also their association with loops indicating turning or 'stop' points. 1, Fast, uninterrupted ascent; 2, turning or 'stop' points; 3, slow descent; 4, fast, uninterrupted descent; 5, position of spat 2 days earlier; 6, piece of debris to which thread is attached; 7, mucous strands for attachment to wall of culture vessel; 8, long side branches probably for enhancing buoyancy; f, foot extended for probing; R, possible reinforcement at the base of side branches in larger specimens; S, siphon.

to 15 mm in length climbed vertical surfaces while *C. edule* spat capable of climbing measured up to only 4·0 mm.

Observations showed that *C. glaucum* spat climb faster than *C. edule*. During the peak climbing activity period of the former species (see below) some could climb as high as 95 mm within 10 min. This distance was usually covered by *C. edule* of comparable size overnight. The probing and anchorage functions of the foot were observed during climbing in both species. Again a byssus thread was trailed behind by the climbing spat older than 3 weeks.

Fig. 6 consists of annotated illustrations of some climbing *Cerastoderma* spat and their byssus threads. Fast climbing spat usually secrete a single, more or less straight thread bearing no side branches. In *C. glaucum* a tuft of side branches is always found at the point where the animal itself is attached. As it moves further on, it leaves the tuft of side branches behind and trails the main thread which may bear single side branches depending on the speed of movement. The tufts of side branches are frequently associated with loops in the main thread (Fig. 6A–D), which indicate changes in the direction of movement of the spat. Before the climbing spat changes its direction it stops and probes with the foot prior to 'deciding' on the next move. Whilst the foot is probing and therefore not anchoring the animal, the side branches are then secreted presumably for support. In *C. edule* the stop points on the climbing tract are indicated by mucous strands which tend to be associated with the loops in the main thread (Fig. 6F).

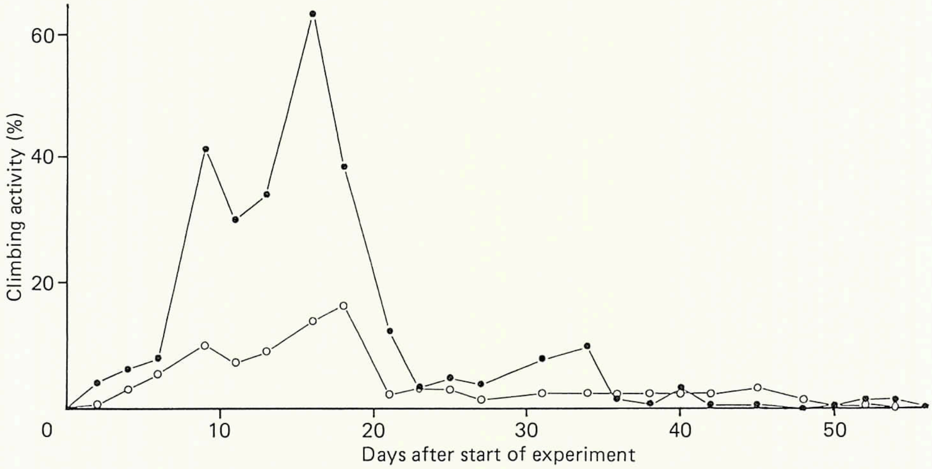

Fig. 7. The climbing activity of *C. glaucum* spat on glass wall (solid circles) and Netlon (open circles). (the spat were 21 days old at the start; 0·63 mm in mean length. They were fed with a mixture of *Monochrysis* and *Phaeodactylum*.). Values represent the means of 2 replicates.

Whenever *C. glaucum* spat climbed to the water surface, they either (1) 'toured' the meniscus; (2) climbed down the wall slowly back to the bottom or (3) floated. The threads which trailed behind during the 'meniscal tour' had numerous side branches mainly on the upper side. This emphasizes the supportive role of the side branches. The *C. edule* spat on the other hand, usually floated for a while and dropped to the bottom. Some individuals of this species climbed out of the water and eventually died from dehydration if not returned to the water.

(iii) Floating. Specimens of the two species which were observed floating in laboratory cultures measured up to 3·0 mm in length. The valves of the floating spat gaped, with their ventral margins pointing uppermost, and the animals still attached to their byssus threads. This posture is similar to that reported to be assumed by other bivalves during bysso-pelagic drifting (see Sigurdsson *et al.* 1976). The few, but rather long side branches of the thread secreted by *C. edule* provide better buoyancy for floating. Hence more individuals of this species floated on their own as opposed to *C. glaucum* spat which frequently floated in clumps of up to about 10 individuals. Examination of such floating clumps revealed that they were interconnected by byssus threads.

Results of the laboratory experiments on climbing activity

(i) *C. glaucum*. Fig. 7 shows that active climbing by the spat of *C. glaucum* on both the glass walls and the Netlon occurred within the period between 9 days and 18 days after the start of the experiment peaking on the 16th day at 77·6 % (values on wall and Netlon combined). The spat were 37 days old at this time and had a mean shell length of 2·0 mm. It should be noted that although the climbing activity decreased dramatically after the peak climbing period, the spat did not cease climbing completely until the 56th day after the start of the experiment when they were 77 days old and had a mean shell length of 6·9 mm. After this time their climbing became sporadic. It is difficult to determine any special preference for either the glass wall or the Netlon since the spat were not equally exposed (in terms of surface area) to the two materials. However, the fact that they did climb and remained attached to the Netlon indicates that this material can be utilized for the collection of spat in the field. This has been positively demonstrated and will be reported elsewhere.

Table 1. *The climbing activity of C. edule spat on glass walls*

Specimens were collected from the field and measured between 1·0 and 6·5 mm in length. Results from 2 replicate vessels combined.

Time from the start (d)	No. on glass walls	No. at the bottom	Climbing activity (%)	Cumulative mortality (%)
2	9	41	18·0	0
4	7	41	14·6	4
6	3	42	6·7	10
8	2	43	4·4	10
10	2	43	4·4	10
12	0	40	0	20
14	0	39	0	22

(ii) *C. edule*. The results shown in Table 1 indicate an apparent decrease in the climbing activity with time: 18 % on the 2nd day to 4·4 % on the 10th day. No firm relationship with age can be made in this case since the precise ages of the spat used in this experiment were not known. However, the mean length of all the spat of this species which climbed the vertical glass walls during the experiment (14 days duration) was 2·4 mm. The largest climbing specimen measured 4·0 mm although the dissection of one specimen measuring 6·1 mm in length revealed remnants of a byssus thread.

Unlike *C. glaucum* in which mortality was minimal during the experimental period, substantial mortalities were recorded with *C. edule* (up to 22 % by the 14th day). About 50 % of the recorded mortalities of this species involved individuals which climbed above the water level. Such a problem was not encountered with *C. glaucum*. Furthermore, withholding food from *C. edule* spat which had ceased climbing, did not induce them to climb again, (cf. *C. gnaucum* below).

The effects of starvation and poor water condition on the climbing activity of C. glaucum spat

The results are illustrated in Fig. 8 which indicated the following:

(1) Starvation induced climbing activity (up to 30 %) in the spat of *C. glaucum* which had previously ceased climbing.

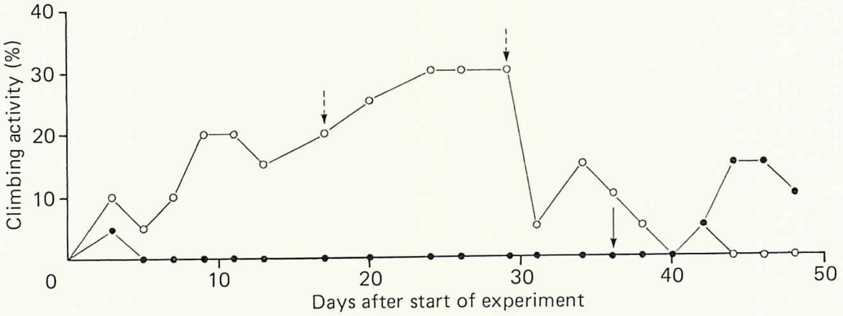

Fig. 8. The effects of starvation and poor water condition on the climbing activity of *C. glaucum* spat (approx. 16 weeks old). Values represent the means of 2 replicates. Solid circles for spat fed initially; open circles for spat starved throughout. Broken arrows demarkate the period when the seawater medium was not changed. Solid arrow indicated the time from which all the spat were starved.

(2) There was a drop in the climbing activity of the starved spat after the water change on the 29th day beyond which there was little recovery and after the 42nd day none of the starved spat climbed again. This may be attributed to physical weakness after the prolonged starvation.

(3) Over a 12-day period, poor water conditions (i.e. unchanged sea-water medium) did not induce climbing activity in the spat receiving food, and only slightly enhanced the climbing of the starved spat.

It is evident from the results of the climbing experiments that whereas the younger and smaller spat of *C. glaucum* showed a tendency to climb vertical walls even when fed, the older and larger spat tended not to climb, so long as they were fed continuously. Spat of this species collected from the field, measuring up to 15 mm in length have been observed climbing the walls of plastic containers on the 3rd day of starvation.

DISCUSSION

The post-larval spat of many bivalves achieve dispersal by bysso-pelagic drifting and thereby enhance their chances of finding a suitable substrate for final settlement (Sigurdsson *et al.* 1976; Blok & Tan-Maas, 1977; Lane *et al.* 1982; Board, 1983). The structural adaptation for this behaviour is found in the possession by the post-larval spat of a byssus gland the secretion of which is in the form of a long, transparent, elastic, non-sclerotized thread with which they transport themselves in a manner analogous to the gossamer flight of young spiders. According to Sigurdsson *et al.* (1976), this byssus drifting is functional up to at least 2·5 mm size in some species while Carriker (1956) reports the byssus of *Mercenaria mercenaria* becoming functionless at a shell length of approximately 7 mm.

The present study has shown that the spat of both species of *Cerastoderma* secrete a byssus thread with which they primarily attach to objects in the water as in other bivalves. However, the byssus gland system of *C. edule* is structurally simpler than that of *C. glaucum*. The unbranched thread secreted by the former is similar to that typical of the post-larvae of many bivalves (see Sigurdsson *et al.* 1976). Baggerman (1953) reports that *C. edule* larger than 600 μm in length were regularly transported over the cockle bed and that spat measuring 1–2 mm were also transported. Verwey (1981) reports similar observations. The present observations suggest that the spat of *C. edule* use their byssus threads to achieve horizontal dispersal in the tidal habitat. Byssal drifting by this species prior to final settlement can be regarded as a prolongation of the pelagic phase as a means of locating a suitable substrate for favourable settlement. As such it is dependent on tidal currents and it is noteworthy that Franklin (1972) attributed the vast accumulation of *C. edule* spat in unsatisfactory situations in the field to the sinking of the spat in areas of weak currents.

With regard to *C. glaucum*, in addition to the role of attaching the spat to objects, the more elaborate byssus thread is employed for climbing up submerged aquatic vegetation. In their typical lagoonal habitat there is little water movement and hence byssopelagic drifting would be minimal. In the relatively confined conditions in the lagoon intraspecific competition may be intense and the muddy bottom may be detrimental to the survival of the newly settled spat; hence vertical dispersal by means of byssal climbing would seem to be more important than horizontal dispersal by drifting. The smallest specimen collected on the submerged vegetation during present field studies measured 0·6 mm. Since the settlement size of the species is 0·2–0·3 mm (see also Kingston, 1972,) it could be inferred that the spat normally settle at the bottom initially before they climb upwards. This was corroborated by laboratory observations in which the spat settled at the bottom of the vessels and later resumed climbing activity which peaked when they were about 2 mm long.

The association of juvenile *C. glaucum* with submerged or floating vegetation has been thought to provide shade, and oxygen which would otherwise be low at high temperatures (Russell, 1972). In view of the enhanced climbing of vegetation by the juveniles in the field during the spring algal bloom, this association must also serve a food searching role enabling juveniles to compete with the benthic adults for food.

The drifting and climbing activities of the two species apparently cease when the animals attain a size beyond the supporting capability of the byssus thread.

Hence the weaker thread of *C. edule* supports the drifting of individuals up to 2–4 mm in length, beyond which they finally settle and burrow into the top few centimetres of the substratum; while the stronger thread of *C. glaucum* supports the climbing individuals of up to 15 mm or more, after which they may either lie on top of or bury themselves in the top layers of the substratum, or become entangled in a mass of submerged vegetation.

The differences in the physical features of the byssus threads of the two species can be used for corroboration of specific identification. The separation of *C. edule* and *C. glaucum* at the specific level is now very well acknowledged but identification can be difficult in sympatric populations. The more reliable electrophoretic methods of identification (Jelnes *et al.* 1971; Brock, 1978) involve sacrificing the animals; while the morphological methods (Petersen, 1958; Boyden, 1971, 1973; Brock, 1978) run into difficulty when applied to specimens from the same locality, especially the juveniles (see Rygg, 1970). The byssus threads secreted by the spat of the two species are so distinct (size, complexity and strength, as described earlier) that if their spat are mixed and held in a glass beaker of clean sea water, it is possible to tell them apart once they climb on the walls.

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