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Regeneration of the inhalant siphon and siphonal sense organs of brackish-water (Baltic Sea) Macoma balthica (Lamellibranchiata, Tellinacea)

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Sublittoral *Macoma balthica* (L.) (14 mm size class) from the Southern coast of Finland (6 ‰ S) has smaller inhalant siphon (0.8 mg as dry weight) than intertidal *M. balthica* in England (4 mg, respectively).

When one third of the siphon was removed, it was restored to the normal size within 3 months. The condition factor (dry weight/shell length^3) of the operated animals after the experiment did not differ from that of wild *Macoma*. When half of the siphon was amputated twice with an interval of 3 months, the siphon remained smaller than normal 6 months after the first amputation. The condition factor of these animals, too, was normal.

The regeneration of the tip of the siphon is comparable to that reported in *Scrobicularia plana* (da Costa). The muscles at the end of the siphon contract to close the wound. The tip also rolls inside to shelter. A very thin microvillated epithelium is spread over the wound, usually within 48 h. 48 h after wounding traces of forming fingers may be seen at the tip. One week after mutilation these seem to be fully reformed.

Two types of sense organs on the siphons of *M. balthica* are described in general: goblet organs and smaller hill organs. Comparison with sense organs in other tellinaceans is made.

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1. Introduction

The siphons of *Macoma balthica* (L.) are very flexible and extensible as are those of other tellinacean siphons. Buried in mud, *Macoma* extends its inhalant siphon through the sediment into the water above. Cropping of the siphon tips of tellinaceans by juvenile flatfish is common (Trevallion 1971, Gilbert & Suchow 1977, de Vlas 1979). Also crabs (Hughes 1969) and birds (Ansell 1981) feed on tellinacean siphons.

Siphons are very sensitive to different kinds of stress. When *Abra longicallus* (Scacchi) is not allowed to bury, its siphons may autotomize (Wikander 1980). Autotomy of the siphons of *Solecurtus scopula* (Turton) and *S. chamasolen* (da Costa) caused by rough handling was frequently seen by Atkins (1937). When sand around *Tellina tenuis* (da Costa) was disturbed the siphon autotomized frequently (Trevallion 1971). In experiments with small concentrations of heavy metals (Eldon et al. 1980) the siphons of *M. balthica* suffered histological damage and pieces of them were broken off. Permanent damage of siphon tissues of *M. nasuta* (Conrad) were induced with the insecticide Sevin (Armstrong & Millemann 1974) and of *Scrobicularia plana* (da Costa) with 1-naphthol (the first hydrolytic product of Sevin) (Akberali et al. 1982).

Siphon regeneration after amputation has been described at least in the tellinaceans *Tellina tenuis* da Costa (Trevallion 1971), *Scrobicularia plana* (da Costa) and *Donax serra* Röding (Hodgson 1982a). The siphons of *Macoma balthica* are very sensitive to vibrations. They are richly innervated and rich in sense organs, at least near the tips. It would be profitable to the animal if damaged or lost parts of siphons could regenerate so as to function normally after injury.

The aim of this study was to examine how soon the normal tip of the inhalant siphon of *M. balthica* is reformed, whether the siphon grows in length when part of it is amputated and if this affects the condition of the animal.

2. Material and methods

2.1. Experiment A. Relation of siphon size to the size of the animal

About 150 *Macoma* of different sizes were collected with a van Veen bottom sampler from a mud bottom, 7-8 m depth (6‰ S), near Tvärminne Zoological Station, on the southern coast of Finland at the beginning of July 1982. They were kept

in an aquarium in aerated running brackish water at 10-12°C, first on a bare bottom for 4 weeks and then in sand (5 cm sand and 7 cm water) at 6-8°C for another 4 weeks. They were sampled in early September. After keeping for 1-2 days in pure water they were anaesthetized in 0.1 % sodium pentobarbital in brackish water. The inhalant siphon was cut off under a preparation microscope. The preparation was much easier in narcotized animals than it was without anaesthetization. The cutting base can be determined exactly as the site where the muscular siphon base becomes thinner and changes into the sheath of the siphon (Yonge 1949). The siphon tip was checked to see whether it had intact "fingers" and had not broken during digging up and handling. The siphons were dried at 100°C for 24 h. Siphon dry weights (Cahn 25 Automatic Electrobalance) and other measurements (see Pekkarinen 1983) were made from these animals and from freshly collected animals, kept in clean water for two days. Siphon indices (100 × siphon dry weight/soft body dry veight and 100 × siphon dry weight, mg/shell length, mm) of appropriate size classes were used as further control values in experiments B and C.

2.2. Experiment B. Animals amputated once in three months

M. balthica were collected at the beginning of June 1981. At this time of year most *Macoma* have spawned and they have almost reached the condition maximum determined as soft part dry weight/(shell length)^3 (Pekkarinen 1983). About 100 medium-sized (mean shell lengths 13-14 mm) *Macoma* were used in the experiment. After two days' rest in an aquarium on a bare plastic bottom in aerated running natural brackish water (6-8°C), two control groups, each of 25-29 specimens, were established. Bivalves in one control group were anaesthetized with 0.1 % sodium pentobarbital in brackish water until slightly relaxed, which took 45 min - 3 hours. They were placed in the test aquarium. The animals in the other control group were put into the test aquarium in an intact condition.

The test aquarium was a plastic container measuring 55 × 55 × 20 cm. The aquarium was divided into numbered squares measuring 5 × 5 cm, with plastic walls 5-6 cm high, so that 121 cells were formed. In the cells there was washed dune sand (sifted with a 1 mm mesh sieve) to a height of 4.5-5 cm, and a 7-10 cm layer of brackish water (6-8°C). For better coverage the water was sprayed on the small cells and the aquarium was aerated. The photoperiod was 12 h light and 12 h dark.

Individuals of one test group of 24 bivalves were anaesthetized as above until both siphons were visible and the inhalant siphon could be recognized and cut with scissors and tweezers. Dry weights of the removed bits were determined after drying at 100°C for 20-24 h. Those individuals which did not relax within three hours were abandoned. Often such individuals were in one way or another exceptional. Some selection was therefore made. Some individuals burrowed down into the sand on the day of the operation. By the next day half of the operated animals were buried. Within two days almost all had burrowed.

In the other test group (17 individuals) siphons were cut without anaesthetization. In order to encourage the siphons to extract, they were warmed to 15-18°C in a Petri dish. This group may have been a little unhomogenous with respect to their condition, because those which first extracted their siphons, for whatever reason, were taken.

After three months, i.e. at the beginning of September, the bivalves were gently forced to the surface of the sand in their cells by the ejection of water. The animals were left to clean their gut and mantle cavity in clean water in numbered plastic ice cube boxes for about one or two days. The animals were weighed after blotting their shells, and they were anaesthetized as above (experiment A). The inhalant siphon was prepared as in A and its intactness (i.e. whether it had fingers) was checked. The dry weight of the siphon (see experiment A) and wet weights of the body and shell were measured. The dry weight of the soft body was measured after drying at 100°C for 48 h. The following condition indices were used: condition factor = soft body dry weight, mg/(shell length, cm)^3 and "fatness" = soft part wet weight × 100/ (weight of whole animal — shell weight).

2.3. Experiment C. Animals amputated twice in 6 months

Macoma for this experiment were collected at the beginning of July 1981. The arrangement was similar to that in B but in both test groups the operation was made under anaesthesia. Three months after the first operation the bivalves of one test group were gently forced to the surface as above, anaesthetized and operated again and put back into their cells. After 6 months from the start, i.e. at the beginning of January 1982, they were sampled as in B.

2.4. Experiment D. Regeneration of the siphon tip

Parts of the siphon were amputated from several *Macoma* as in B and C. Samples of operated siphons were taken at different time intervals: just after cutting, 6 h, 24 h, 48 h, 72 h, 5 d, 7 d, and 1-3 mo after the amputation. Normal and operated siphon tips were photographed, and they were fixed in Bouin's fluid, or 3 % glutaraldehyde in 0.1 M phosphate buffer, pH 7.2, for 1.5 h. Natural photographs were taken from unstained or stained (methylene blue or Nilblue) siphons. Paraffin sections of Bouin-fixed material were stained with haematoxylin - eosin, Masson - Gomori (chromotrope - fast green, Gray 1954) or with Crossmon's haematoxylin - acid fuchsin - orange - light green (Burck 1969). Samples fixed in glutaraldehyde were postfixed in 1.5% OsO_4 in phosphate buffer, dehydrated and embedded in Epon. Semi-thin sections were stained with toluidine blue. Samples for scanning electron microscopy were fixed in glutaraldehyde, dehydrated and dried through an ethanol series and critical point and coated with gold. The SEM preparations were examined and photographed with a Jeol JSM-35C.

3. Results

3.1. Experiment A. Relation of siphon size to the size of the animal

The relationship between the dry weight of the inhalant siphon and the dry weight of the soft body of *M. balthica* kept in the laboratory is shown in Fig. 1a. The relationship between the dry weight of the siphon and shell length is linear in the size range studied, 7-19 mm, (Fig. 1b).

For calculations of "siphon indices", (Figs 2a and 2b) of *Macoma* kept in the laboratory (L) and of wild *Macoma* from the sea (S) the clams were classified in 2 mm classes from class 1 = 6.0-7.9 mm to class 8 = 20.0-21.9 mm. The animals in size class 3 taken from the sea had a significantly smaller siphon than animals of similar size kept in the laboratory, but this was exceptional in the general graph (c.f. Fig. 2a L and S). When the relationship siphon dry weight/shell length is used, there is a tendency among freshly collected

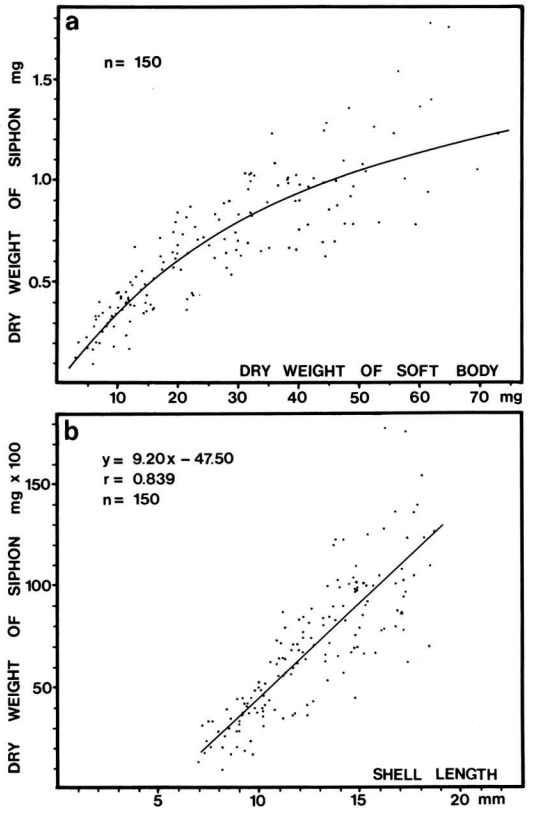

Fig. 1. Relationship between inhalant siphon size and body size in *Macoma balthica* kept in the laboratory from July to September (experiment A). a) Relation between the dry weight of the siphon and the dry weight of the soft body. The curve has been drawn free-hand. b) Relationship between the dry weight of the siphon and shell length.

animals to have a smaller siphon (in classes of smaller shell length) than animals kept in the laboratory (Fig. 2b L and S).

3.2. Experiment B. Animals amputated once in three months

No animal died just after anaesthetization. Only three animals died during the experiment, one in each test group and one in the group of unanaesthetized controls. The shells of the animals in all the groups had grown less than expected from the earlier growth rings, and disturbance rings were observed in several shells.

The mean shell length of the animals in this experiment was about 13-14 mm (Fig. 3). Although the animals in group A (amputated without anaesthetization) were smaller than the respective control animals (C) the difference was not statistically significant. When a siphon comparison is made, the animals in group A will be classified as size class 4 above. The other three groups (C-AN) will belong to class 5. The mean shell length in group A differed significantly from the mean shell length of wild animals analysed in September 1981 (Pekkarinen 1983). Condition characteristics of these animals (September 1981, Pekkarinen 1983) such as "fatness", condition factor and water content, were used as values by means of which the condition of the animals in this experiment were compared (Fig. 3).

The mean water contents (% of the soft part) in the four groups did not differ significantly from each other, being about 77-78 % (Fig. 3). These mean water contents were, however, smaller than that of wild *Macoma* in September (79.3 %). Only in group C was the difference not significant. Also "fatness" in the animals in this experiment was lower than in freshly collected *Macoma*. "Fatness" was greatest in the group of animals amputated under narcosis (AN) and this group differed from its control group (CN) in this respect. Condition factors in all these groups did not differ from the condition factor in freshly collected *Macoma*, i.e. the groups had a similar amount of dry material (in relation to shell length^3).

The siphons of *M. balthica* react very rapidly to vibrations, e.g. those caused by scissors during cutting, so that only smaller fragments of the siphon could be taken off without anaesthetization (about 30 % in group A). Approximately 40 % of the siphon was taken off in the anaesthetized group (AN). The siphon indices after the experiment and the mean sizes of fragments removed are given in Fig. 4. Control values of appropriate animal size classes are derived from Fig. 2: In Fig. 4a the upper dotted line represents the control value for group A (size class 4, Fig. 2a L) while the lower dotted line represents the control value for groups C, CN and AN (class 5). In Fig. 4b the upper dotted line is for C, CN and AN, and the lower line for A, respectively. The wild siphon control value for A (S, class 4 in Fig. 2) would be even higher in Fig. 4a but lower in 4b. Although the siphons in the control groups (C and CN) seemed to be larger than the operated siphons (A and AN), there were no significant differences. If the removed parts with cross-hatched mean are individually added to the siphons left after the experiment, the total index (white column + cross-hatched column) calculated as siphon dry weight/soft body dry weight is significantly greater than the mean size of the control siphon in both anaesthetized and unanaesthetized groups (A > C, AN > CN). Similarly, the sum of the siphon and the removed fragment as siphon dry weight/shell length, is

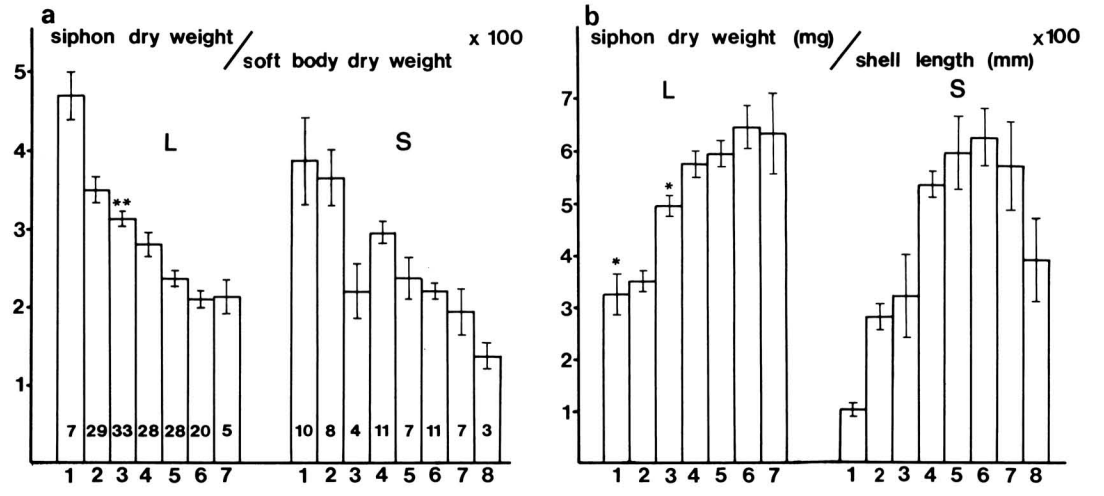

Fig. 2. "Siphon indices" for different size classes of *M. balthica* kept in the laboratory (L) or taken from the sea (S): a) Relationship of the siphon dry weight to the dry weight of the soft body and b) relationship of the siphon dry weight to the shell length. Classification according to the shell length is as follows: 1 = 6.0 - 7.9 mm, 2 = 8.0 - 9.9 mm, 3 = 10.0 - 11.9 mm, 4 = 12.0 - 13.9 mm, 5 = 14.0 - 15.9 mm, 6 = 16.0 - 17.9 mm, 7 = 18.0 - 19.9 mm, 8 = 20.0 - 21.9 mm. Means ± *SE*s are given. Numbers inside the columns represent numbers of specimens. Corresponding size classes of animals kept in the laboratory and animals taken from the sea were compared using Student's *t* test. Two-sided probability levels: * = $p < 0.05$, ** = $p < 0.01$.

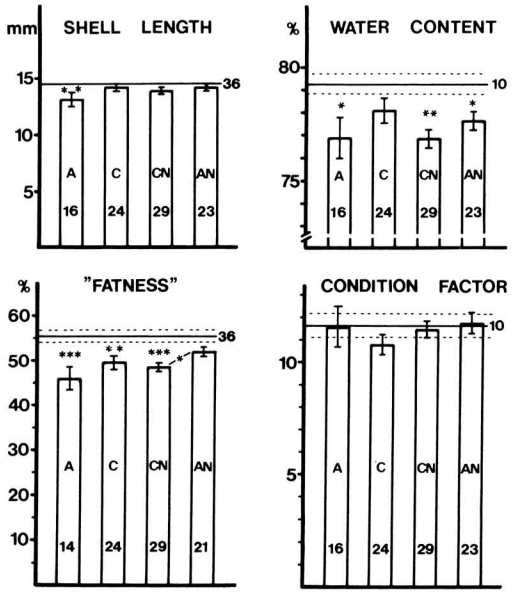

Fig. 3. Sizes and condition characteristics of *M. balthica* three months after the amputation of the inhalant siphon in experiment B. A = animals amputated without anaesthesis, C = unnarcotized control animals, CN = narcotized control animals, AN = animals amputated under narcosis. Means ± *SE*s and numbers of specimens are given. Horizontal control lines are mean values (± *SE*s) for natural *Macoma* in September 1981 (Pekkarinen 1983). Comparison made with Student's *t* test (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

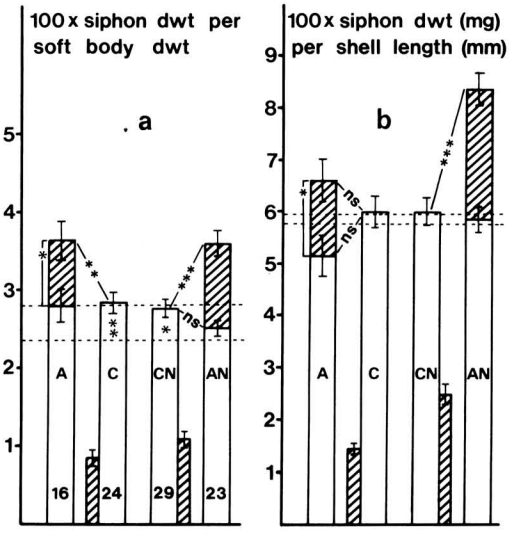

Fig. 4. a) and b) Siphon indices of *M. balthica* after three months in experiment B calculated as in Figs 2a and 2b. Groups as in Fig. 3. The cross-hatched small columns beside the control columns represent the mean sizes of the amputated portions of siphons. The fragments removed were individually added to the siphons, and total siphon indices for these sums were calculated (white column + the cross-hatched area at the top). Dotted horizontal lines are control values in respective size classes 4 and 5 in Fig. 2a L and Fig. 2b L.

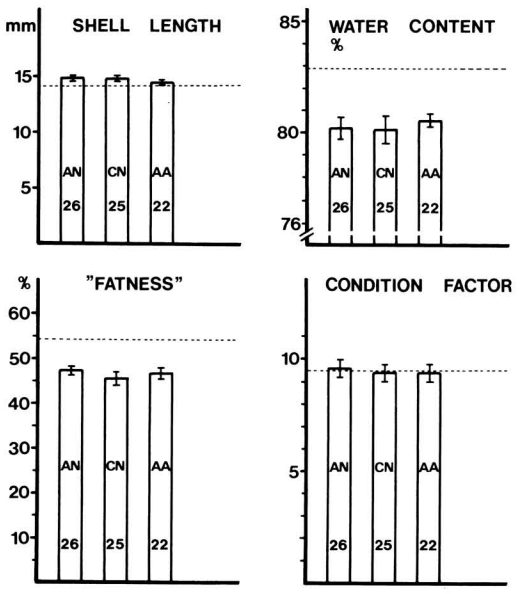

Fig. 5. Sizes and condition characteristics, as in Fig. 3, of *M. balthica* after six months in experiment C. AN = animals amputated once (narcotized), CN = narcotized control animals, AA = animals amputated twice with an interval of three months. The dotted horizontal lines are natural control levels extrapolated from the figures in November 1981 and February 1982 to early January (Pekkarinen 1983).

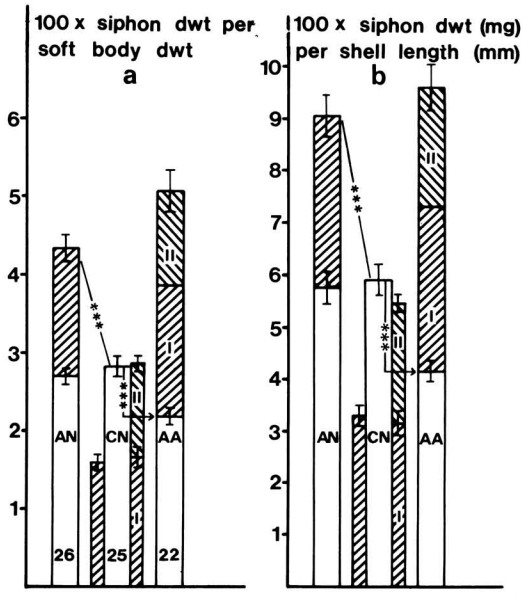

Fig. 6. a) and b) Siphon indices of *M. balthica* after six months in experiment C, calculated as in Figs 2a and 2b and 4a and 4b. Groups as in Fig. 5. The mean size of the first fragment removed from the siphon is indicated with the ascending cross-hatched column I and the second fragment with the descending cross-hatched column II.

much greater in the group amputated under anaesthesia than in the respective control group (AN > CN). The difference was not so evident in the unanaesthetized groups (A ≥ C). The size of the removed fragment is, however, significant in group A, when the siphon is compared with the sum of the siphon and cut-off fragment.

3.3. Experiment C. Animals amputated twice in six months

The experiment was commenced at the beginning of July with 25-28 animals in each group. Dead animals (0-2 individuals/group) were excluded from the analyses. Shell growth did not differ between the groups. Many shells displayed disturbance rings.

The mean shell lengths of the test animals, 14-15 mm (Fig. 5), were comparable to the shell lengths of *Macoma* analysed in November and February, 1981-1982 (14.2 mm) (Pekkarinen 1983). The mean water contents of the soft parts of the animals in groups AN, CN and AA (once amputated animals, anaesthetized control animals, twice amputated animals, respectively), i.e. 80.2-80.5 %, were higher than in experiment B in September, but the extrapolated control value for January (Pekkarinen 1983) would be about 83 % (dotted line in Fig. 5). The "fatness" of the animals, at 45-47 %, was still lower than in most groups in experiment B. The extrapolated control value in early January would be about 54 %. On the other hand, the mean condition factors in all the groups were exactly the same as the extrapolated control figure for January, i.e. 9.5. The three groups did not differ from each other in any of these respects (Fig. 5).

When over half of the siphon was amputated, the size of the siphon was normal six months later (AN = CN, Fig. 6). When about half of the siphon was removed twice with an interval of three months, the siphon remained smaller than the control siphon six months after the first amputation (AA < CN). An amount equivalent to one total siphon was removed in this group (I + II = CN, Fig. 6).

3.4. Experiment D. Regeneration of the siphon tip

The tip of the inhalant siphon of *M. balthica* has six blunt fingers (Fig. 7), which are very mobile. At least two types of sense organs are present on the surfaces of the siphons. Goblet organs (c.f.

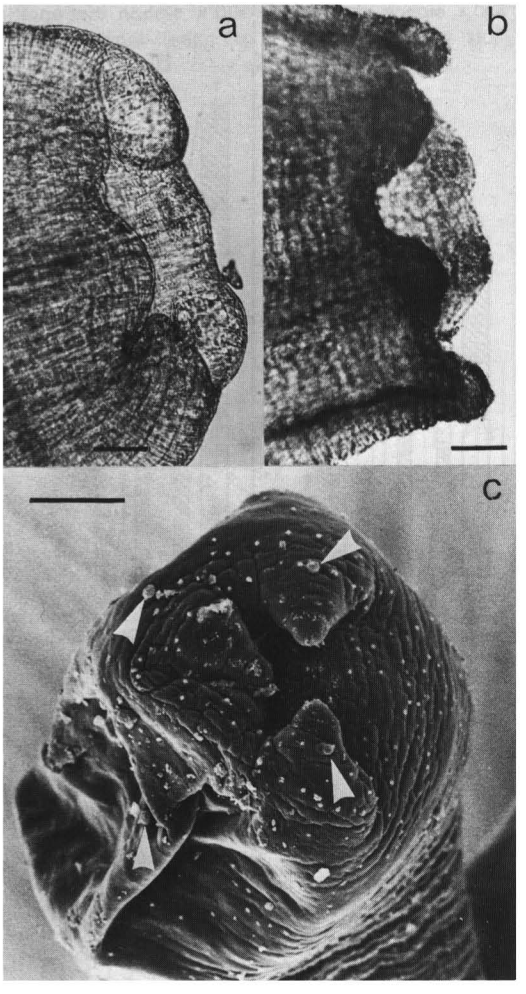

Fig. 7. Tips of inhalant siphons taken from *M. balthica*. a) Fingers of a siphon with swollen haemocoelic lumina. b) Normal fingers one month after cutting off the siphon tip. c) A SEM photograph of fingers which close the siphon. Two fingers are retracted under the others. Goblet organs are indicated with arrows, the white dots being hill organs. Scale in all pictures 100 μm.

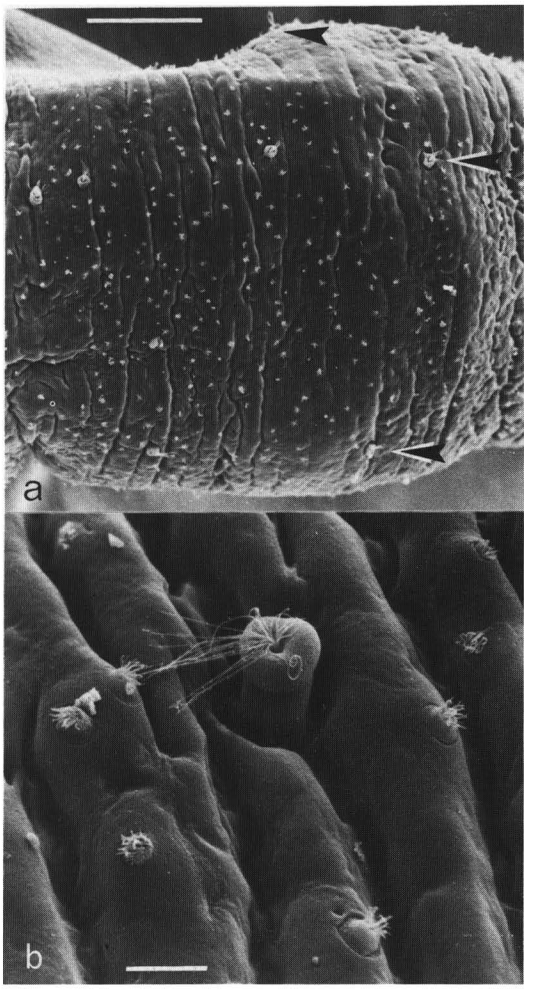

Fig. 8. a) Distal part of an inhalant siphon of *M. balthica*. Two rows of goblet organs and one organ of the third row (topmost arrow) are visible. Smaller hill organs are scattered throughout the wall. Scale bar 100 μm. b) The goblet organ bears long cilia at the centrum. The diameter of the organ is about 20 μm, but this organ has shrunk during fixing and drying. Hill organs are small hills, about 7μm in diameter, supplied at the top with cilia. Scale bar 10 μm.

Becherförmigen Organe, Eisig 1879, Seitenorgane, Rawitz 1892) are aligned in six rows on the outer surface of the siphons representing the course of the main longitudinal nerves (Fig. 8). The most distal goblet organs are located just at the necks of the fingers (Fig. 7c). Numerous hill organs (c.f. Hügeln, dreiteiligen Organe, Rawitz 1892) (Fig. 8) are scattered in particular on the distal half of the inhalant siphon. Smaller numbers are present on the inner epithelium of the siphon and on the exhalant siphon.

When the siphon is cut, the wounded wall soon rolls inside the siphon tube, and the muscles contract to close the wound. Healing begins during the first day. After 24 h the wound may be closed in some siphons (Fig. 9b). After two days traces of forming fingers may be seen (Fig. 9c-d). *Macoma* was seen to use its siphon in conjunction with deposit-feeding during the next day after wounding. A very thin microvillated epithelium covers the wound (Fig. 10). Mitotic figures were not detected in the preparations. Loosened cells

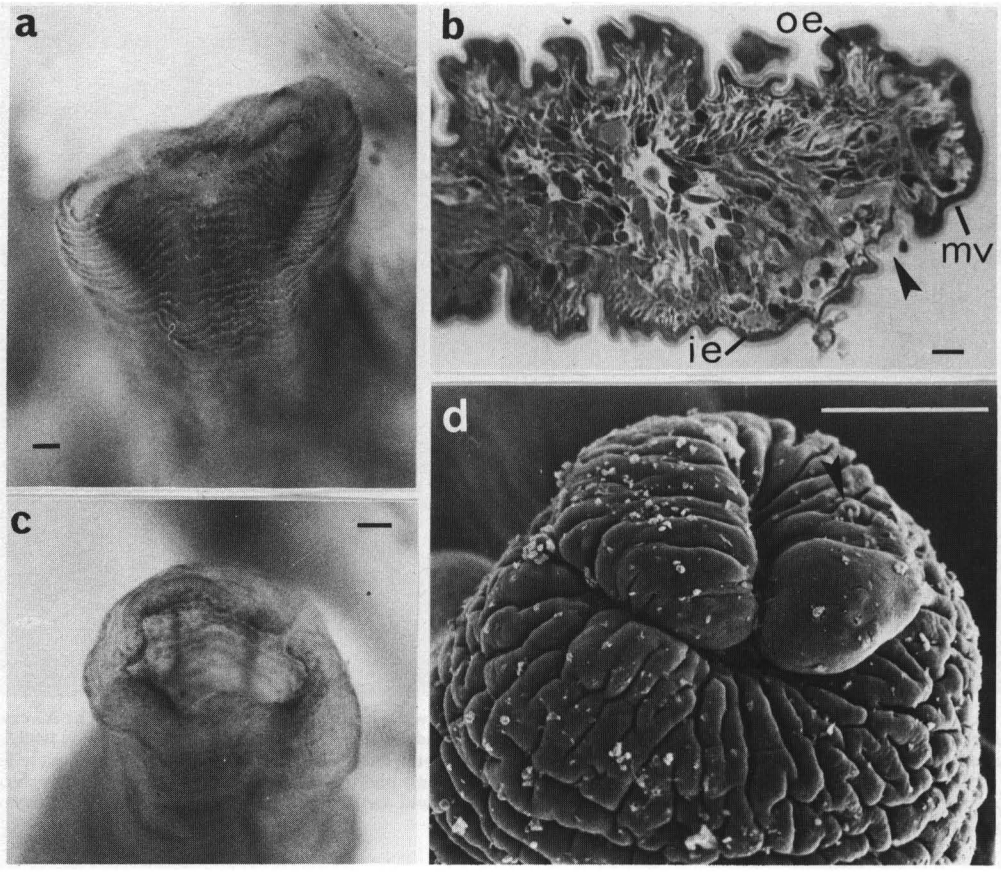

Fig. 9. Inhalant siphons of *M. balthica* various times after cutting off the tip. a) Immediately after cutting. The epithelia of the siphon are slightly stained with Nilblue, so that the wound seems to be a shade lighter. b) The end of a siphon wall 24 h after cutting. The wound (arrowed has closed in this section. Epon section, stained with toluidine blue. ie = inner epithelium, oe = outer epithelium, mv = microvilli. c) A siphon 48 h after cutting off the tip. Nerves and regenerating fingers have stained darker with methylene blue than the other tissue. d) A SEM photograph of a siphon 48 h after cutting off the tip. The loosened cell mass is still visible in the opening of the siphon. A goblet organ is indicated by the arrow. Bars 100 μm in a, c, d, and 10 μm in b.

and remnants of membranes (microvilli) can be seen near the wound for several days (Figs 9b, 9d, 10d). Loosened cells are also sometimes seen on intact siphons. Generally the tip of the siphon was fully reformed after seven days. The regenerated siphons seemed to bear sense organs in the same way as intact siphons. If the siphon is cut obliquely or raggedly, repair is delayed (Fig. 10d).

The number of ciliated centra inside the goblet organs varies. These may be as many as five. The organs usually bear dozens of cilia. Goblet organs with very few cilia were sometimes observed near the siphon tip (Fig. 11c-d). It is not known whether the small buds occasionally apparent in the epithelium of siphons which have regenerated for two or three days are developing goblet organs (Fig. 11a-b).

4. Discussion

The dry weight of the inhalant siphon especially of smaller *M. balthica* at Tvärminne is much smaller than that of intertidal *M. balthica* in England (Reading & McGrorty 1978). *Macoma* of shell length 14 mm in England have an inhalant siphon weighing 4 mg (c.f. 0.8 mg in this study). The difference may be due to the presence of a thinner siphon wall rather than to the smaller length. An example of the extensibility of the siphon can be cited: The longest siphon observed by the author on any occasion measured 115 mm.

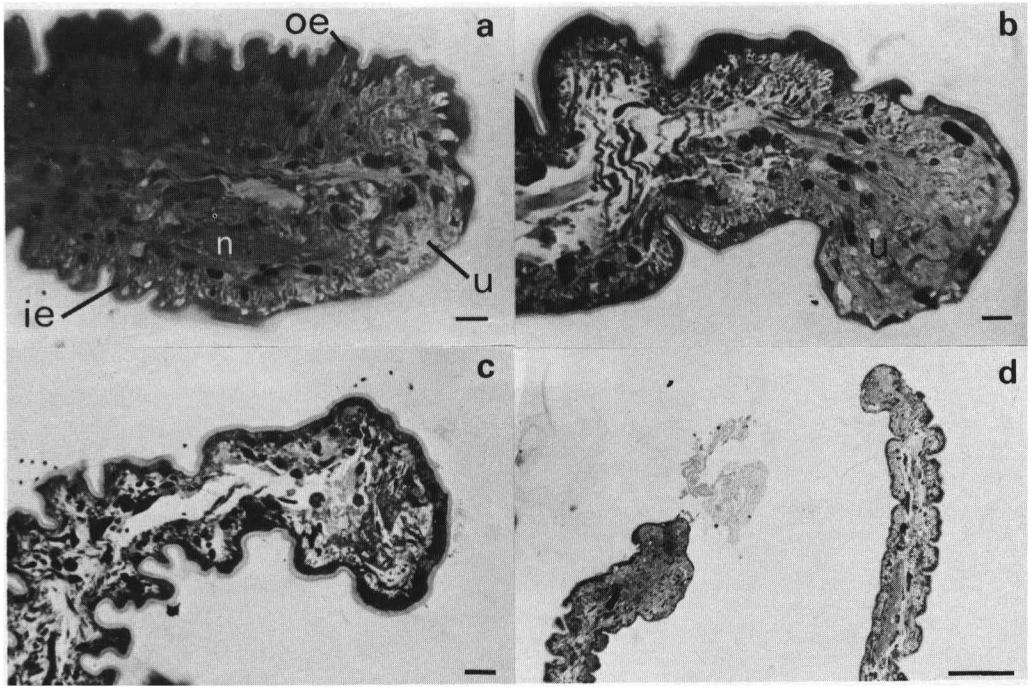

Fig. 10. Semi-thin Epon sections, stained with toluidine blue, of siphon walls in various stages of regeneration. a) A very thin microvillated epithelium covers the wound after 48 h. u = undifferentiated tissue, n = nerve. b) The end of a siphon wall 5 days after cutting. c) The tip of an intact siphon wall. d) Longitudinal section from a siphon which has been cut obliquely 5 days earlier. There is much loosened tissue left near the tip. One side of the siphon is still shorter than the other. Much of the undifferentiated cell mass is present in the wall of the shorter side. The wound was not even closed in all the sections of this siphon. Bar 10 μm in a-c and 100 μm in d.

If this measures 3 mm in the contracted state, then it is extended 38-fold when stretched to 115 mm.

The siphon dry weight appears to change in proportion to variations in the dry weight of the soft body; in other words, the lighter the body the lighter the siphon. Smaller animals kept in the laboratory in experiment A had a higher dry weight and a better condition factor than animals of similar size taken from the sea (Pekkarinen 1983, experiment I). However, the relation of siphon dry weight to soft body dry weight did not differ, except in size class 3, which was abnormal in respect of group S (experiment A, Fig. 2a). This class included only 4 individuals, and possibly, some of these had suffered recent siphon losses in the sea. This class was also exceptional in respect of its tissue water content (Pekkarinen 1983, Fig. 6). Some indication of the better condition of the smaller animals kept in the laboratory is also given by the relation of siphon dry weight to shell length (Fig. 2b).

The siphon index calculated as siphon dry weight/soft body dry weight overestimates siphon size in group A in experiment B (Fig. 4). Again, the index· siphon dry weight/shell length somewhat underestimates this size. It is only possible to make valid comparisons between animals of highly similar size using such siphon indices (c.f. Figs. 2 and 4).

Regeneration of lost siphon parts in *Macoma balthica* is in agreement with the other tellinaceans studied (*Tellina tenuis*: Trevallion 1971, *Scrobicularia plana* and *Donax serra*: Hodgson 1982a). If 50 % of the siphon of *Scrobicularia plana* has been removed, and the animals are not fed, regeneration takes place at the expense of body condition (Hodgson 1982a). When 30-40 % of the siphon of *M. balthica* was amputated, the siphon had regrown within three months and the condition factor of the animals was normal (experiment B). However, their water content and "fatness" were smaller than in the wild. Tissue water content and "fatness" were smaller, too, in the control animals. This suggests that amputation did not affect their condition (expressed as dry weight of soft part/shell length^3) at all, but the condidions in the laboratory possibly delayed gonadal development in both amputated and control

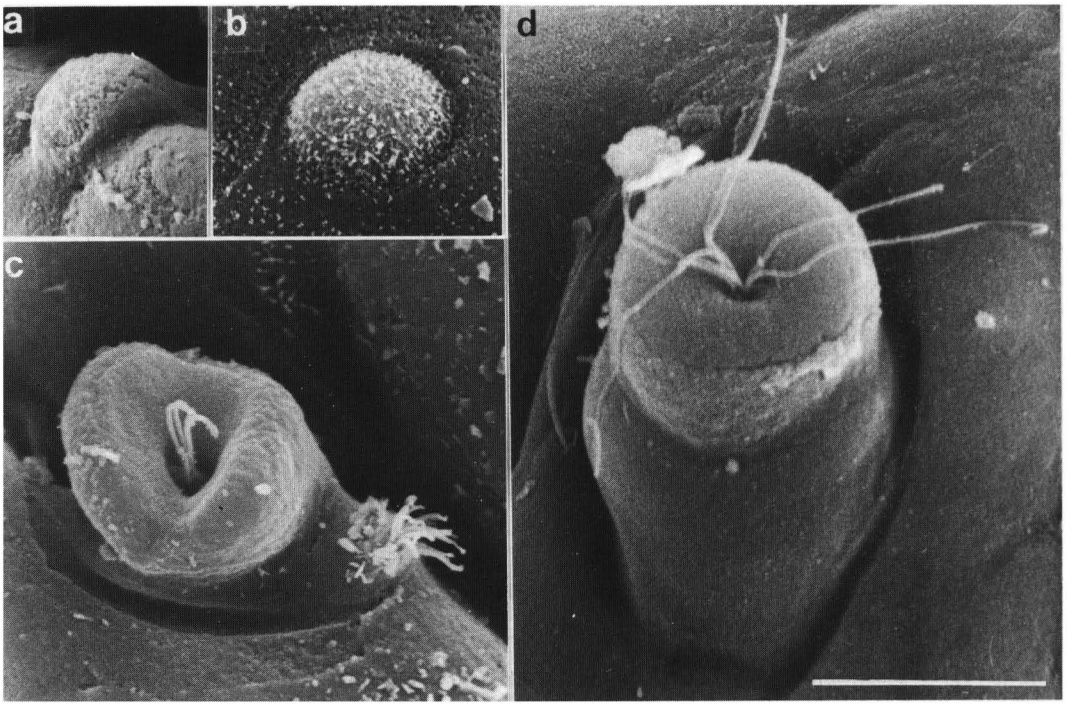

Fig. 11. a) and b) Small buds near the ends of siphons two days and three days after cutting off the tip. c) A goblet organ with only three or four cilia besides a hill organ near the end of a siphon regenerated for three days. d) A goblet organ with few cilia near the end of an intact siphon. Scale bar 10 μm for all pictures.

animals. Gonadal smears were not prepared. The animals in both experiments (B and C) were taken to the laboratory in early summer just after spawning. Normally the percentual water content of the soft part increases during the autumn and winter. Some increase of tissue water content had taken place in the animals in experiment C compared with B, but again the increase was slower than normal. Their condition factor was normal, however. The high water temperature (about 15 °C) in late summer may perhaps be critical for the normal onset of gonadal development.

One is obliged to ask why the siphon remained smaller than normal in the animals amputated twice. If one third of the siphon is removed, it can be assumed on the basis of experiment B to be restored within three months. The first fragment removed, however, was larger in experiment C. So the siphon may not have become fully restored before the second amputation. There may also have been competition with the gonads for energy. Nutritional circumstances in the aquarium do not, of course, entirely correspond to natural conditions.

The regeneration of the tip of the siphon in *M. balthica* seems to take place at the same rate as in *Scrobicularia plana* (Hodgson 1982a). The first reaction, the contraction of the muscles near the wound to prevent loss of haemolymph, was similar to that of *Scrobicularia*. The injured margin is also rolled inside for protection. Siphon tip amputation was made in most cases under anaesthesia. Anaesthesis disturbs the normal muscular function of the siphon for some time, although some muscular activity remains. This may be the reason why *Macoma* was not seen to use its siphon in deposit-feeding earlier than the next day after amputation. *S. plana* was observed to do so a few hours after wounding (Hodgson 1982a, b).

In conjunction with wound healing in the Pacific oyster, *Crassostrea gigas* (Thurnberg), fusiform leucocytes first form a pseudoepithelium (Des Voigne & Sparks 1968, 1969). Within 168 h after wounding, part of this pseudoepithelium has formed cilia. Although the exact process in the siphon of *Macoma* is not known, the healthy epithelium seems to spread as a very thin cover over the wound.

It is not known how the fingers at the siphon tip in *Macoma* are formed. Are they formed by contraction of the longitudinal muscles between the fingers or do they really grow out of the tip? Or, again, are the spaces between the fingers formed by phagocytosis of the tissue by amoebocytes? The tip of the siphon of *Tellina tenuis* has six small projections, the regeneration of which requires no reorganisation, the cut end having the same appearence as the former tip (Trevallion 1971). The pinnately-branched tentacles at the siphon tip of *Donax serra* Röding have been commonly seen in various stages of regeneration during collection (Ansell 1981). It appears that in the siphon of *Macoma* the damaged tissue remnants are sloughed off so that the wound is not so rough. Fig. 7c suggests that the fingers cannot form in any other way than by growing out of the tip.

The "lateral organs" (Seitenorgane, Rawitz 1892) of tellinaceans provide and interesting subject in the examination of tellinacean evolution, in addition to those described by Pohlo (1982). According to Rawitz (1892) and Yonge (1949) these organs are present in *Gari depressa* (Pennant) (= *Psammobia vespertina* Lam.) and *Solecurtus strigillatus* L., but they are absent in *Tellina nitida* Poli and *T. planata* L. and *Donax trunculus* L. (Table 1). However, Moueza & Frenkiel (1974) describe bouquets of sensory cells connected with the longitudinal nerves and with the outer surface of the siphon of *Donax trunculus*. Apparently using information from Yonge (1949), Coan (1971) states in his description of Northwest American Tellinidae that this family lacks rows of sensory cells similar to those of *Psammobia*. In *Macoma balthica* analogous organs are present. However, these organs are smaller and unlike the buds (Knospen) in *Gari depressa*. Moreover, *Egeria radiata* Lam. (Purchon 1963) and *Iphigenia brasiliensis* Lam. (Narchi 1972) (both members of Donacidae) have uncoloured papillae, surrounded by pigment, along the nerve courses of siphons. Longitudinal rows of white spots appear on the siphons of *Solecurtus gibbus* Conrad (Morse 1919). The spots of different rows are arranged similarly in relation to encircling lines on the siphons. According to Graham (1934) the siphons of *S. chamasolen* (da Costa) have exceedingly large number of fine tentacles, some apparently scattered at random over the general surface of the distal separate parts, but many are arranged in definite rows, overlying the course of the nerves within. Pohlo (1973) depicts rows of small papillae on the siphon of *Tagelus californianus* (Conrad). Also *T. dombeyi* (Lam.) and *T. longisinuatus* Pilsbry & Lowe have similar rows of papillae on their siphons (Villarroel & Stuardo 1977). Rows of sensitive papillae on siphons may also appear in members of other superfamilies than Tellinacea (at least in *Mesodesma mactroides* Deshayes, Mactracea, two rows on both siphons; Narchi 1981). Rawitz (1892) suggests that the lateral organs of the siphons are analogous to the lateral line organs of fishes, detecting delicate movements in the water. *Scrobiculaia plana* may lack these receptors, hence its siphons are not very sensitive to vibrations (Hodgson 1982b). Because there are structural differences between the sense organs in different species within Tellinacea, there may be functional differences, too.

Table 1. Distribution of siphonal sense organs within Tellinacea. Presence or absence of sense organs (buds, papillae goblet organs etc., see text) arranged as longitudinal rows is indicated with + or -. Presence of smaller sense organs (hill organs, minute papillae) scattered on the siphon wall is indicated with *. Division into families based primarily on Coan (1971, 1973a, 1973b).

	Sense organs	Source
Tellinidae		
Tellina nitida Poli	−	Rawitz (1892)
T. planata L.	−	" "
T. crassa Pennant	−	Graham (1934)
Macoma balthica (L).	+ *	This study
Semelidae		
Scrobicularia plana (da Gosta)	−	Hodgson (1982b)
Donacidae		
Donax trunculus L.	−	Rawitz (1892)
D. denticulatus L.	−	Wade (1969)
Egeria radiata Lam.	+	Purchon (1963)
Iphigenia brasiliensis Lam.	+	Narchi (1972)
Psammobiidae		
Gari depressa (Pennant) (=*Psammobia vespertina* Lam.)	+ *	Rawitz (1892)
G. tellinella (Lam.)	+	Graham (1934)
Solecurtus striqillatus L.	+	Rawitz (1892)
S. gibbus Conrad	+ *	Morse (1919)
S. chamasolen (da Costa)	+ *	Graham (1934)
S. scopula (Turton)	− *	" "
Tagelus californianus (Conrad)	+	Pohlo (1973)
T. dombeyi (Lam.)	+ *	Villarroel & Stuardo (1977) Hoffman (1914)
T. longisinuatus Pilsbry & Lowe	+	Villarroel & Stuardo (1977)

The tip of the siphon is usually reformed in one week. When the siphon grows in length after

amputation or as the animal grows, new sense organs must develop. It is not known at what physical point the siphon grows in length. The general structure of the siphon wall of *Macoma balthica* is described in Eldon et al. (1980). The tissue at the base of the siphon was compact and cell nuclei were seen abundantly in the preparations. Mitoses, however, were not seen. Sense organs are fewer near the base of the siphon than on the distal half of the siphon. When the siphon of *Scrobicularia plana* regenerates there is a lag phase over the first 24 h during which little or no growth occurs (Hodgson 1982a). This period corresponds to the closure of the lesion. Small goblet organs and buds observed in experiment D near the mutilated tip of the siphon of *Macoma* in the second and third days suggests that the siphon grows there and forms new sense organs. The mass of undifferentiated cells near the tip of the siphon wall some days after wounding also supports this view (Fig. 10).

Due to an abundance of sense organs on the siphons and its siphon regeneration ability, *Macoma balthica* can withstand certain adverse factors in its environment (predators, pollutants etc.).

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References

Akberali, H. B., Trueman, E. R., Black, J. E. & Hewitt, C. 1982: The responses of the estuarine bivalve mollusc Scrobicularia to the first hydrolytic product of the insecticide Sevin^{R}. — Est. Coast. Shelf Sci. 15: 415-421.

Ansell, A. D. 1981: Functional morphology and feeding of Donax serra Röding and Donax sordidus Hanley (Bivalvia: Donacidae). — J. Moll. Stud. 47: 59-72.

Armstrong, D. A. & Millemann, R. E. 1974: Pathology of acute poisoning with the insecticide Sevin in the bent-nosed clam, Macoma nasuta. — J. Inv. Pathol. 24: 201-212.

Atkins, D. 1937: On the ciliary mechanisms and interrelationships of lamellibranchs. Part III: Types of lamellibranch gills and their food currents. — Quart. J. Micr. Sci. 79: 375-421.

Burck, H.-C. 1969: Histologische Technik. Leitfaden für die Herstellung mikroskopischer Präparate in Unterricht und Praxis. 2nd ed. — 183 pp. Georg. Thieme Verlag. Stuttgart.

Coan, E. V. 1971: The Northwest American Tellinidae. — Veliger 14, suppl.: 1-63.

—»— 1973a: The Northwest American Semelidae. — Veliger 15: 314-329.

—»— 1973b: The Northwest American Psammobiidae. — Veliger 16: 40-57.

DesVoigne, D. M. & Sparks, A. K. 1968: The process of wound healing in the Pacific oyster Crassostrea gigas. — J. Inv. Pathol. 12: 53-65.

DesVoigne, D. M. & Sparks, A. K. 1969: The reaction of the Pacific oyster Crassostrea gigas to homologous tissue implants. — J. Inv. Pathol. 14: 293-300.

Eisig, H. 1879: Die Seitenorgane und Becherförmigen Organe der Capitelliden. — Mitt. Zool. Stat. Neapel 1: 278-343, Tafel VII.

Eldon, J., Pekkarinen, M. & Kristoffersson, R. 1980: Effects of low concentrations of heavy metals on the bivalve Macoma balthica. — Ann. Zool. Fennici 17: 233-242.

Gilbert, W. H. & Suchow, E. F. 1977: Predation by winter flounder (Pseudopleuronectes americanus) on the siphons of the clam Tellina agilis. — Nautilus 91: 16-17.

Graham, A. 1934: The structure and relationships of Lamellibranchs possessing a cruciform muscle. — Proc. Roy. Soc. Edinb. (II) 54: 158-187.

Gray, P. 1954: The microtomist's formulary and guide. — 794 pp. The Blakiston Company, Inc. New York.

Hodgson, A. N. 1982a: Studies on wound healing, and an estimation of the rate of regeneration, of the siphon of Scrobicularia plana (da Costa). — J. Exp. Mar. Biol. Ecol. 62: 117-128.

—»— 1982b: Some behavioural and electrical responses of Scrobicularia plana (Bivalvia: Tellinacea) to siphonal wounding. — J. Moll. Stud. 48: 87-94.

Hoffmann, F. 1914: Beiträge zur Anatomie und Histologie von Tagelus dombeyi (Lamarck). — Jenaische Zeitschr. Naturwiss. 52: 521-566, Tafel XII - XIV.

Hughes, R. N. 1969: A study of feeding in Scrobicularia plana. — J. Mar. Biol. Ass. U. K. 49: 805-823.

Morse, E. S. 1919: Observations on living lamellibranchs of New England. — Proc. Boston Soc. Nat. Hist. 35: 139-196.

Moueza, M. & Frenkiel, L. 1974: Contribution a l'etude des structures palleales des Tellinacea. Morphologie et structure du manteau de Donax trunculus L. — Proc. Malac. Soc. Lond. 41: 1-19.

Narchi, W. 1972: On the biology of Iphigenia brasiliensis Lamarck, (Bivalvia, Donacidae). — Proc. Malacol. Soc. Lond. 40: 79-91.

—»— 1981: Aspects of the adaptive morphology of Mesodesma mactroides (Bivalvia: Mesodesmatidae). — Malacologia 21: 95-110.

Pekkarinen, M. 1983: Seasonal changes in condition and biochemical constituents in the soft part of Macoma balthica (Lamellibranchiata) in the Tvärminne brackish water area (Baltic Sea). — Ann. Zool. Fennici 20: 311-322.

Pohlo, R. H. 1973: Feeding and associated functional morphology in Tagelus californianus and Florimetis obesa (Bivalvia, Tellinacea). — Malacology 12: 1-11.

—»— 1982: Evolution of the Tellinacea (Bivalvia). — J. Moll. Stud. 48: 245-256.

Purchon, R. D. 1963: A note on the biology of Egeria radiata Lam. (Bivalvia, Donacidae). — Proc. Malacol. Soc. Lond. 35: 251-271.

Trevallion, A. 1971: Studies on Tellina tenuis da Costa. III. Aspects of general biology and energy flow. — J. Exp. Mar. Biol. Ecol. 7: 95-122.

Reading, C. J. & McGrorty, S. 1978: Seasonal variations in the burying depth of Macoma balthica (L.) and its accessibility to wading birds. — Est. Coast. Mar. Sci. 6: 135-144.

Rawitz, B. 1892: Der Mantelrand der Acephalen. Dritter Teil. Siphoniata. Epicuticulabildung. Algemeine Betracht-

ungen. — Jenaische Zeitschr. Naturwiss. 27: 1-232, Tafel I-VII.

Villarroel, M. & Stuardo, J. 1977: Observaciones sobre la morfologia general, musculatura y aparato digestivo en Tagelus (Tagelus) dombeii y T. (T.) longisinuatus (Tellinacea: Solecurtidae). — Malacologia 16: 333-352.

de Vlas, J. 1979: Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. — Neth. J. Sea Res. 13: 117-153.

Wade, B. A. 1969: Studies on the biology of the West Indian beach clam, Donax denticulatus Linné. 3. Functional morphology. — Bull. Mar. Sci: 19: 306-322.

Wikander, P. B. 1980: Biometry and behaviour in Abra nitida (Müller) and A. longicallus (Scacchi) (Bivalvia, Tellinacea). — Sarsia 65: 255-268.

Yonge, C. M. 1949: On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. — Phil. Trans. Roy. Soc. London 234B: 29-76.

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