

Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata)

J. F. CADDY¹

Queen Mary College, London, England

Received February 6, 1969

CADDY, J. F. 1969. Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata). Can. J. Zool. 47: 609-617.

Postlarval *M. balthica* is well adapted for interstitial life in particulate sediments, although metamorphosis to the adult form and function is not complete until a shell length of 2 mm is reached.

Spatfall at 300-310 μ shell length is followed by a plantigrade stage in which the ciliated plantiform foot is used as an organ of feeding, locomotion, and rejection of pseudofaeces. The inhalant current is produced by the ciliation of the foot and inner demibranch, and enters through the pedal gape. This is already separated from the lumen of the inhalant siphon by the cruciform apparatus. Food sorting in the early postlarvae is exclusively by the palps, which are well developed in the midline to overhang the mouth, and already have simple sorting ridges on their inner surfaces.

Siphon development proceeds by infolding of the fusions of the mantle edge around the siphonal apertures. In early postlarvae the pseudofaeces are transported to the pedal gape by the mantle ciliary tract, and swept from the mantle edge by the foot. At approximately 1 mm shell length, rejection of pseudofaeces occurs via the inhalant siphon, which only gradually takes over its adult function as exclusive route of the inhalant current at between 1 and 2 mm.

Introduction

Studies on the early life history of lamellibranchs such as *Venerupis* (Quayle 1952), *Venus* (Ansell 1962), *Mytilus* (Bayne 1964), and *Pandora* (Allen 1961) have demonstrated that metamorphosis of the larva to the adult form is a gradual process in vagile species. Ansell, for example, says: "The change from a free-living veliger stage to a fixed or sedentary adult form is a critical period for bivalves. . . may involve a rapid loss of the velum followed by a relatively slow adjustment and growth of the body organs to the adult form, as in actively burrowing species, or a drastic change in body form as in fixed species." It is evident for *Macoma* that the postlarva is not merely in transition from a well-adapted planktonic stage to a similarly well-adapted benthic stage, but possesses anatomical and behavioral adaptations peculiar to this stage in its life history.

Material and Methods

Weekly surface plankton tows for larvae were made with a No. 12 mesh plankton net at high tide throughout the spring and summer of 1963.

Postlarval *M. balthica* were obtained from the shore at low tide on the Thames estuary after spatfalls during the spring and autumn months. Surface scrapings of the muddy soil around high water neaps were passed through a fine plankton net (0.1-mm mesh) to remove silt, and the larvae of *Macoma* were picked out under a binocular

microscope. Densities of juveniles of up to 5000/m² (June 1964) provided plentiful material. All behavioral observations were made under a binocular microscope by daylight.

The extreme shell transparency of young specimens enabled observations to be made on ciliary tracts in the mantle cavity without disturbing the live animal. Pathways of particles in the mantle cavity were demonstrated by addition of small amounts of fine silt or carmine particles to the inhalant stream. Suspensions of milk in seawater were also useful in illustrating ciliary tracts in the mantle cavity (Crisp and Southward 1956).

For histological examination, specimens were fixed in Bouin's fluid, stained, when required, in Ehrlich's acid haematoxylin, and then either cleared and mounted in Canada balsam, or 7- μ sections cut after embedding in 56° wax. Small specimens were lightly stained before embedding for greater ease of orientation in the wax. Final staining and differentiation were carried out on the mounted sections.

Size at Metamorphosis

Descriptions of larval *M. balthica* by Werner (1939), Jørgensen (1946), and Sullivan (1948) were consulted in identifying planktonic stages. As Jørgensen found, it was impossible to differentiate the early veligers (D-shaped larvae) of *M. balthica* from those of other bivalves in the plankton. However, the late larvae (veliconchae) were readily distinguished by their yellow shells and red umbones, features also distinctive of the larval (prodissoconch) shells of early postlarvae. Veliconchae (Fig. 1A) were uncommon in the plankton, and were only encountered just before the spatfall in April-May

¹Present address: Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

of 1963 and 1964. A smaller, second spatfall was detected in November 1964 from weekly samplings of the surface soil. No plankton hauls were made in the autumn months.

In *M. balthica*, the limits of the first and second prodissoconch shell are readily recognizable in late larvae and early postlarvae (Fig. 1B) until obscured by hinge growth. The margin between first and second prodissoconch shell (Pd I and Pd II respectively) is delineated by a shallow groove and a change in shell texture. Pd I has a punctate appearance, while Pd II has characteristic concentric striae. The transition between Pd II and dissoconch shell is marked by an increased opaqueness and coarseness of striae.

Metamorphosis in bivalves involves loss of the velum and increased mobility of the foot. This has generally been considered to coincide with the onset of deposition of dissoconch shell. However, mature planktonic larvae from Whitstable (Fig. 1A) already showed some deposition of dissoconch shell before spatfall, although a functional velum was still present. The mean size of prodissoconch shells found in postlarval *M. balthica* at Whitstable was 301 μ long, smaller than the largest planktonic larva found (330 μ ; Table D). The smallest benthic stages (19 April 1964) were approximately 310 μ long. Evidently, metamorphosis occurs at around 310–330 μ shell length.

The first spring spawning at Whitstable occurred March 12–29, 1964 (Caddy 1967); the

first major spatfall was recorded between April 11 and 19. This allows a tentative estimate for the duration of planktonic life of 2–5 weeks.

Jørgensen (1946) stressed that the shells of planktonic stages of lamellibranchs vary considerably in size at metamorphosis. Table II illustrates this variation but shows that Pd I is larger for *M. balthica* at Whitstable than recorded previously, although Pd II is within the range of recorded sizes from elsewhere in the zoogeographical range of the species. Ockelmann (1965) has shown that Pd I size is related to the size of the mature oocyte. A large Pd I and large oocyte (97 μ diameter: Caddy 1967), and a small Pd II suggest that *M. balthica* undergoes a shorter planktonic life at Whitstable than in other localities studied. The mean sizes of Pd I and Pd II for spring-spawned *M. balthica* were smaller than for autumn-spawned animals.

TABLE I

M. balthica. Number of mature larvae in plankton

	Length, μ				
	240	260	280	300	320
23 April 1963		4	5	1	
3 May 1963			2		
11 April 1964	6	6	8	1	2
16 April 1964			2	5	1
19 April 1964		1			3

ABBREVIATIONS USED IN FIGURES

Aa	Anterior adductor muscle	Op	Outer palp
Ab	Abfrontal cilia	P	Palp
Bg	Byssus gland	Pa	Posterior adductor muscle
Ca	Ctenidial anlage	Pd I	Prodissoconch I
Cm	Cruciform muscle	Pd II	Prodissoconch II
Ct	Ciliary tract	Pe	Periostracum
Dg	Digestive gland	Pf	Pseudofaeces
D	Dissoconch	Pg	Pedal ganglion
Es	Exhalant siphon	Pr	Pedal retractor muscle
F	Foot	R	Rectum
Fr	Frontal cilia	Re	Rudiment of exhalant siphon musculature
Gf	Gill filament	Ri	Rudiment of inhalant siphon musculature
Ic	Infrabranchial chamber	Rs	Siphonal rudiments
Id	Inner demibranch	S	Siphonal space
Il	Inner mantle lobe	Sb	Suprabranchial chamber
Ip	Inner palp	Sm	Stomach
Is	Inhalant siphon	Sp	Sensory pit
K	Kidney	Sr	Siphonal retractor muscle
L	Lateral cilia	Ss	Siphonal septum
Me	Mantle edge	St	Statocyst
Ml	Middle mantle lobe	Tc	Tissue connection
Ms	Mantle sinus	Vg	Visceral ganglion
Od	Outer demibranch		
Oe	Oesophagus		
Oi	Outer mantle lobe		

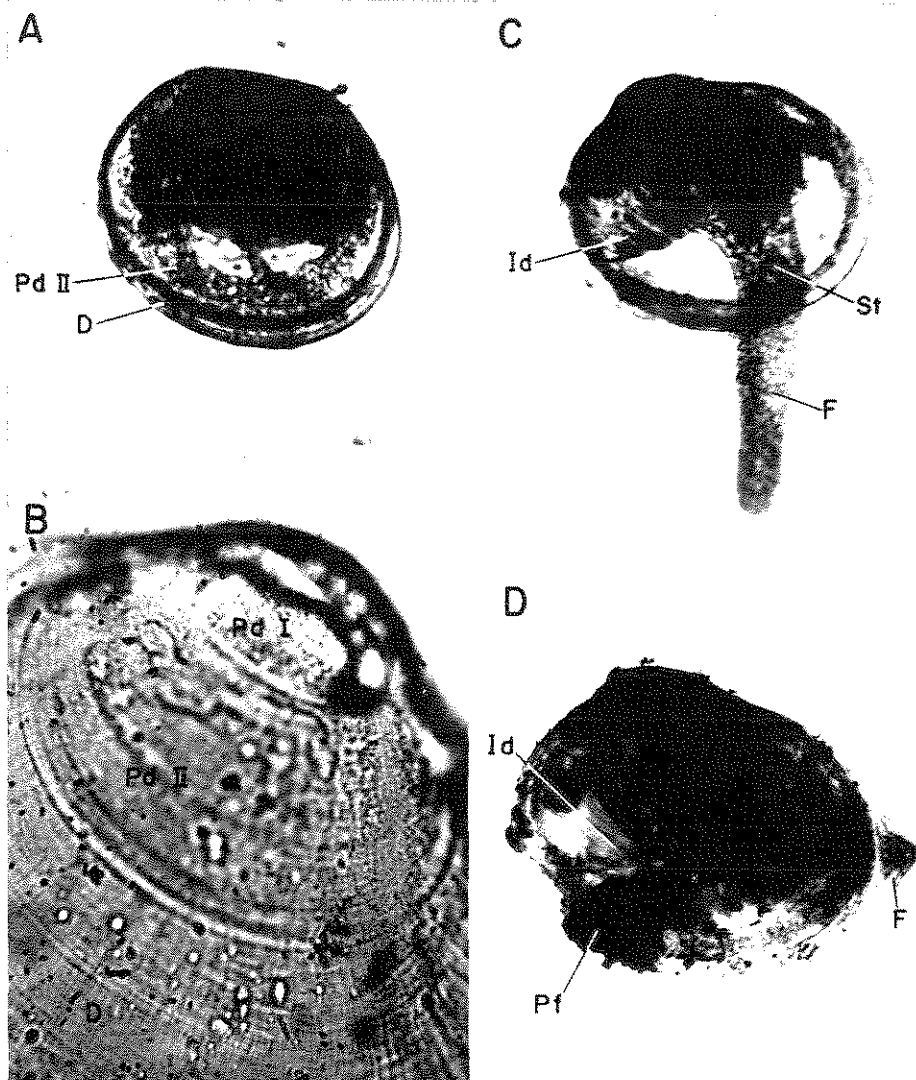


FIG. 1. Early postlarval *M. balthica*. A. 310 μ planktonic larva (collected 16.4.64) showing early deposition of dissoconch shell. B. Umbonal region of the shell of 900 μ *M. balthica* showing first and second prodissoconch shell. C-D. Characteristic phases of activity in postlarval (500 μ) *M. balthica*. C. Extreme protraction of the foot; locomotory activity. D. Position of foot during feeding response, showing pedal ciliation and accumulation of pseudofaeces in the posterior region of the mantle cavity. Note particles of dirt adhering to shell.

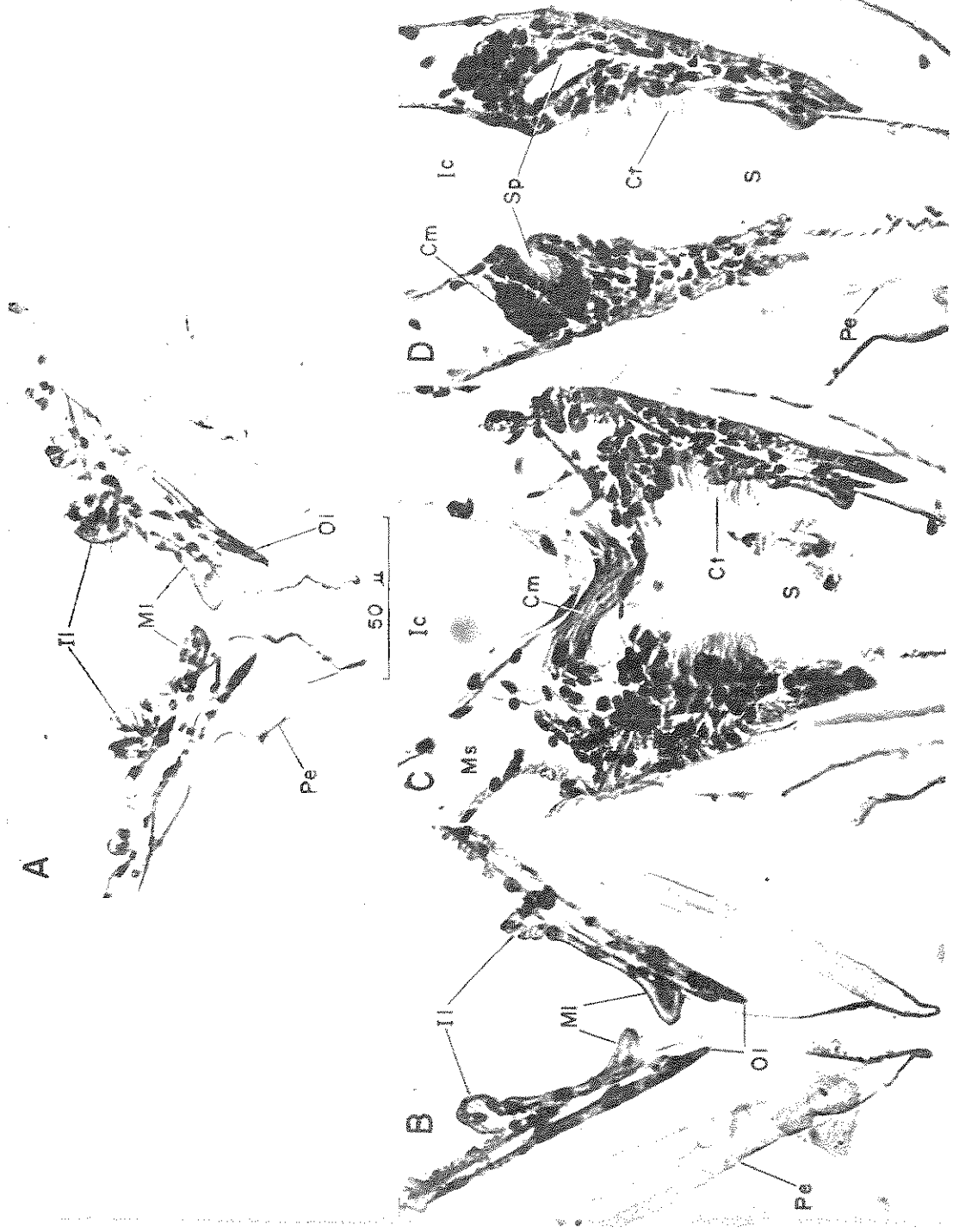


TABLE II
Lengths of prodissoconch shell in *Macoma balthica* (L.)

Author	Locality	Pd I length	Pd II length
Werner, 1939	German Waddensea	150	310
Sullivan, 1948	Prince Edward Island	—	255
Jørgensen, 1946	Øresund	126-150	294
Caddy, 1967	Whitstable: spring	176 (± 36)	285 (± 40)
	autumn	186 (± 32)	301 (± 49)

Quayle (1952) and Ansell (1962) described the complete anatomy of an immature bivalve. The following account is confined to a description of the mantle organs in early settlement stages of *M. balthica* and their functional transition to the adult form.

Development of Mantle Organs

Superficial examination of the arrangement of mantle organs in early postlarvae reveals marked differences from the adult morphology described by Yonge (1949). In the early postlarvae, several important adult organs were not present or were present only in a rudimentary form.

Figures 1C and 1D illustrate the arrangement of mantle organs in postlarvae 500 μ long. There is a well-developed foot, a number of gill filaments, but no differentiated muscular siphons.

Mantle Edge and Siphons

Sections of the mantle edge of an early postlarva shows rudiments of the inner (I), middle (M), and outer (O) mantle lobes described by Yonge (1949) (Figs. 2A, 2B). A prominent ciliated tract (Ct) runs along the inner mantle edge between the inner and middle lobes of the mantle (Figs. 2C, 2D). At this stage, the waste canal (Yonge 1949) found in the posterior region of the adult mantle is absent.

In postlarvae of *M. balthica*, this postero-ventral area of the mantle edge is the point where two fusions have occurred between left and right inner mantle lobes. The inhalant and exhalant apertures have already been separated by the siphonal septum (Ss) (Fig. 5E), and the inhalant aperture has been closed ventrally by

the cruciform muscle (Cm) (Fig. 2C). These fusions involve the inner mantle lobe alone—the sole contributor to Tellinacean siphonal structures (Yonge 1949). This differs from the Veneracea where the middle lobes are also involved (Quayle 1952; Carriker 1961; Ansell 1962), and the Myacea where all three are involved.

Figure 3 illustrates successive stages in the development of *M. balthica* siphons based on whole mounts of young specimens fixed with the siphons in the retracted position. When protracted (in vivo), the juvenile siphons are in the plane of the mantle edge and not readily seen. Only when a size of 1 mm is reached do the siphons protrude beyond the shell margin. When retracted, the distal ends of each siphon are contracted, and the siphonal lumen is only visible as a translucent area in the center of the siphonal musculature. In the smaller specimens the rudiments of the siphonal musculature (Re, Ri) and of the cruciform muscle (Cm) are only visible as thickenings of the mantle edge (Figs. 3A, 3B).

The position of the siphonal septum is marked by the point of impingement of the inner demibranch (Id) onto the mantle edge (Fig. 3A). This point marks the division between the muscular precursors of the exhalant siphon posteriorly (Re) and the inhalant siphon (Ri) and the cruciform apparatus anteriorly. These two rudiments become more distinguishable as development of the siphonal complex continues (Figs. 3A-3E).

Rapid growth of the fused mantle edge leads to infolding around the siphonal apertures (Figs. 3C-3E). As the siphonal retractor muscles become functional in the mantle wall, the point of attachment of the demibranch to the siphonal

FIG. 2. Transverse sections of the mantle edge of 700 μ *M. balthica* (A-D proceeding posteriorly). A. Through palp region. B. Through demibranch region. C, D. Through cruciform apparatus.

septum is drawn within the line of the mantle edge when the siphons are in the retracted position (Figs. 3B–3F). Thus, the two siphon rudiments come to lie in the retracted position along the line of the future pallial sinus (Figs. 3E, 3F). With further development, the siphons occupy a large proportion of the mantle cavity

lumen on retraction (Fig. 3F). As a result, in the retracted position the gill changes its orientation from an initial position lying approximately dorsoventrally in the posterior part of the mantle cavity (Fig. 3A), moving upwards and anteriorly to lie almost anteroposteriorly in the upper part of the mantle cavity (Fig. 3F).

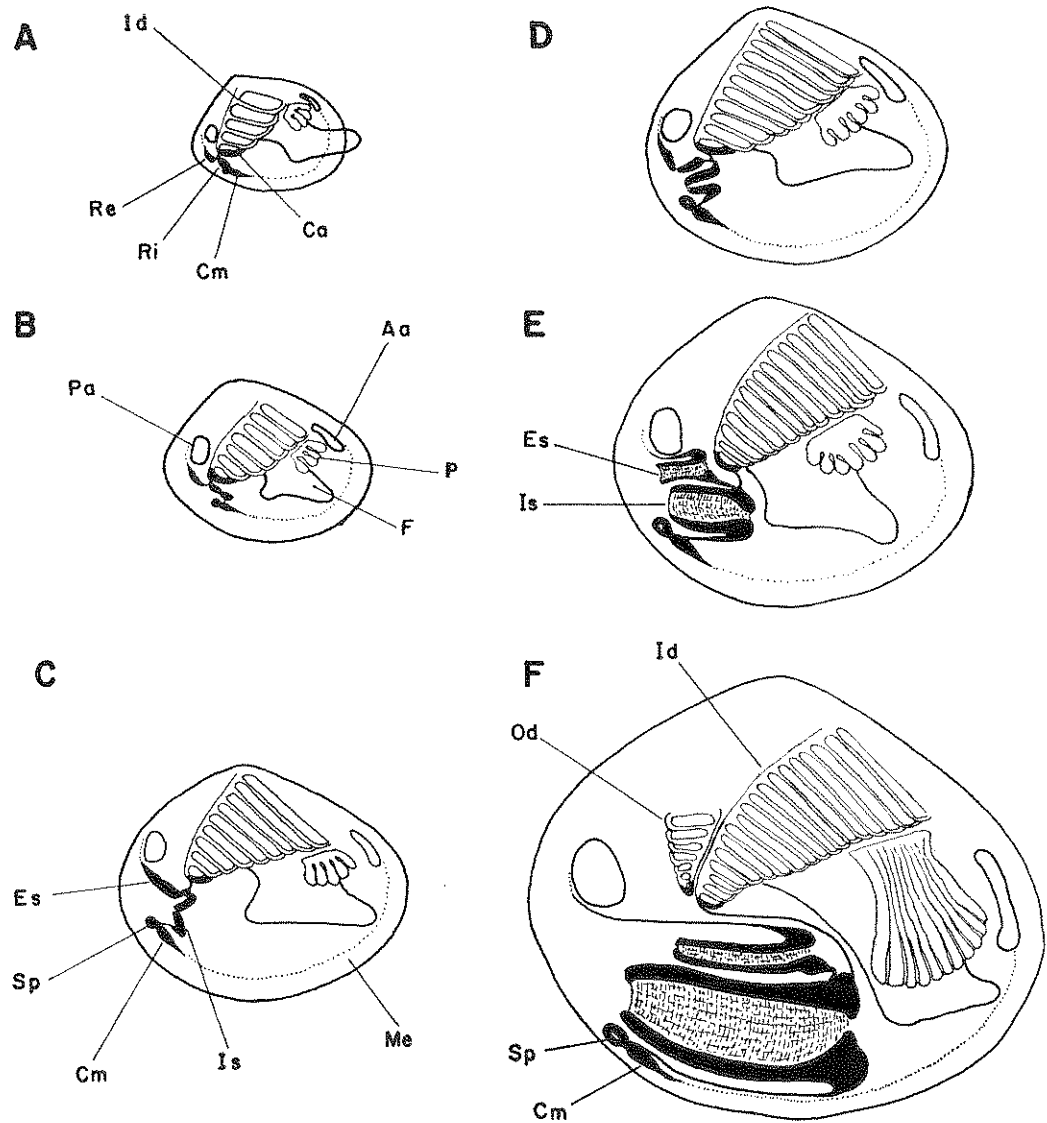


FIG. 3. Diagrammatic representation of siphonal development in postlarval *M. balthica* based on whole mounts of fixed specimens with retracted siphons. A. 0.45 mm shell length—5 filaments on inner demibranch. B. 0.60 mm shell length—7 filaments on inner demibranch. C. 0.83 mm shell length—9 filaments on inner demibranch. D. 0.87 mm shell length—11 filaments on inner demibranch. E. 1.30 mm shell length—14 filaments on inner demibranch. F. 1.80 mm shell length—18 filaments on inner demibranch. Six outer demibranch filaments (E and F not to scale).

Since it retains its attachment to the siphonal apparatus, the inner demibranch is necessarily drawn down to reoccupy its original position when the siphons are protruded.

The more rapid development of the inhalant siphonal musculature compared with the exhalant siphon in young *M. balthica* contrasts with descriptions for other bivalves (*Venerupis*, Quayle 1952; *Cardium*, Baggerman 1954; *Venus*, Ansell 1962) where the exhalant siphon invariably develops more rapidly. This more usual state of affairs was also observed by the author in juveniles of *Syndosmya alba* and *Spisula subtruncata* from the Oresund, Denmark.

Cruciform Apparatus

The cruciform apparatus in *M. balthica* and a number of other tellinids was described by Graham (1934). In the adult, this consists of two parts: (1) two interdigitating muscle bundles crossing diagonally between the mantle margins; (2) a pair of sensory sacs at the posterior point of attachment of the muscles to the mantle edge.

In the adult, these two sacs are in communication with the siphonal space by means of a short duct. Examination of postlarval *M. balthica* revealed the precursors of these sensory sacs to be a pair of shallow pits (Sp) (Fig. 2D) in the mantle edge posterior to the cruciform muscle, as was predicted by Graham (1934). No evidence was found for the suggestion of Yonge

(1949) that the muscle preceded the sensory pit, at least in ontogeny.

Development of Gills and Palps

In early postlarval *M. balthica*, the gill is represented by the inner demibranch alone. This has four gill filaments at the time of spatfall (Fig. 4). The filaments are suspended dorsally from the visceral mass and, in the earliest postlarvae examined (450 μ), were attached distally to the sides of the foot by a tissue connection (Tc) (Fig. 5B). Posterior to the foot, the ctenidial anlagen (Ca) (Quayle 1952) are fused to form the floor of the suprabranchial chamber (Fig. 5C), so that the suprabranchial (Sb) and infrabranchial (Ic) chambers are separated by the gill filaments. This division between the supra- and infra-branchial chambers persists posteriorly, where the siphonal septum divides the two siphonal lumina.

"Reflection" of the inner demibranch occurs as described by Ansell (1962) for *Venus striatula*: by increasing in length, the inner demibranch becomes folded into the adult shape. However, *M. balthica* differs from *Venus* in that tissue fusion of the distal ends of the filaments to the body wall occurs before reflection is complete. Further observation will be needed to determine the point in ontogeny when tissue fusion occurs. No marginal groove is formed in *M. balthica* (Yonge 1949).

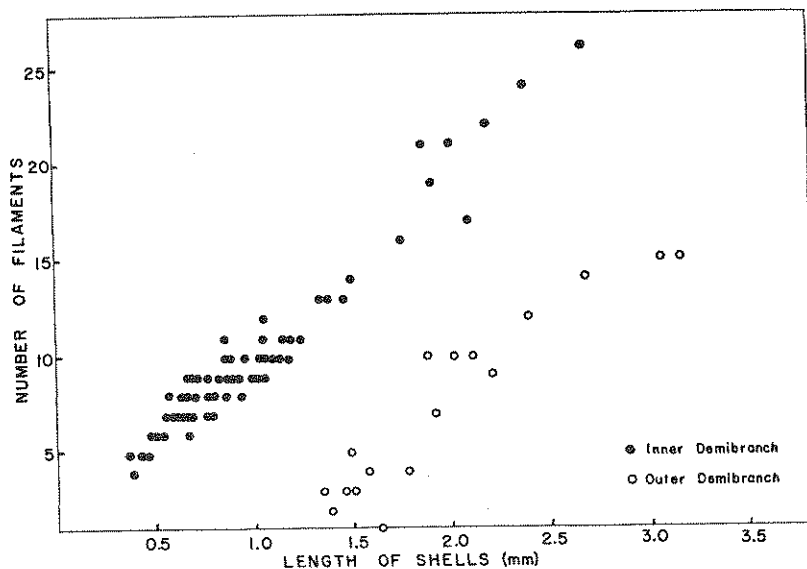


FIG. 4. Relationship between shell size and number of filaments in postlarval *M. balthica*.

First traces of outer demibranchs were noticed when the juveniles reached a length of 1.4–1.6 mm (approximately 16 filaments on the inner demibranch—Fig. 4). The outer demibranch remains unreflected in the adult, so that the gill presents the appearance of a flat sorting surface. At this stage the ciliation of the filaments already shows a division into frontal, abfrontal, and lateral cilia (Fig. 5D).

The early postlarva possesses well-developed palps, elongated in the midline to form extensive lips above and below the mouth. The inner surfaces already show a number of ridges with extensive ciliation, and serve as the main sorting area at this stage (Fig. 5A). Further palp development principally involves the formation of complex secondary foldings, with emphasis on the lateral sorting wings.

Foot

Figure 6 illustrates the well-developed pedal cilia on the lateral and ventral surfaces of the foot. It also shows the prominent byssus gland opening by a duct onto the posterior spur of the foot. No evidence was found for the formation of byssus threads in young of this species: the coating of sticky material invariably covering the shell of young specimens of *M. balthica* (noted in the larvae by Jørgensen 1946) may serve a similar purpose in anchoring the young animal to sand grains and other debris (Fig. 1D). The other prominent pedal organ is a well-developed statocyst (St), dorsal to the pedal ganglion. An interesting feature of the juvenile foot is the flat plantar surface (Fig. 5A, 5B) noted previously in juvenile *Pandora* by Allen (1961).

Locomotor and Feeding Behavior

Locomotion

Small specimens of *M. balthica*, placed in a petri dish containing muddy sand, buried themselves using the same movements described for the adult by Yonge (1949). In 5–10 seconds they reached a depth of 1–3 mm, and then moved horizontally through the soil without making contact with the surface. A similar type of behavior was noted for adult specimens of *M. balthica* by Brafield and Newell (1961) but here the siphons reached the soil surface during locomotion. Small specimens before siphonal

development must make use of interstitial water for respiratory purposes.

An alternative method of locomotion was shown by small specimens on a clean glass surface. This consisted of a rapid gliding motion with the foot fully extended with its broad plantar surface in contact with the glass. The animal remained in a vertical position during this response, balanced on the ventral edges of the gaping shell valves. A similar type of locomotion was noted for young specimens of *Lima* by Lebour (1937), although the juvenile *Lima* pulls itself along by means of the extensile mantle tentacles. In *M. balthica* the pedal cilia are largely responsible for this type of locomotion. Bayne (1964) observed a similar behavioral response in *Mytilus* plantigrades which, he considered, facilitated passive distribution by water currents. The existence of a plantigrade stage in *M. balthica* was supported by the presence of large numbers of young specimens less than 1 mm in length in the plankton at high tide during June 1964. Postlarval *M. balthica* was also noted by Jørgensen (1946) in plankton from the Gullmarfjord.

Feeding

When particulate material was introduced into the dish, two responses frequently ensued in the early postlarva, the first of which appeared to be a feeding response.

(1) The animal protruded the foot just beyond the slightly gaping shell valves with the pedal cilia beating actively. This position was maintained for some time as a rapid current of water entered the mantle cavity between the shell margins (Fig. 6A). This strong inhalant current often caused particulate material to accumulate along the ventral shell margins.

(2) When a large amount of debris had accumulated, the foot was protruded anteriorly, and while extended, swept rapidly in a posterior direction clearing the debris from the shell margin. On withdrawal of the foot, the shell valves closed rapidly, causing a current of water to dislodge the remnants of debris and pseudo-faeces from the pedal gape.

Although these two behavioral responses seem to be the main ones associated with feeding, early bottom stages show some uptake of particulate material during most phases of activity.

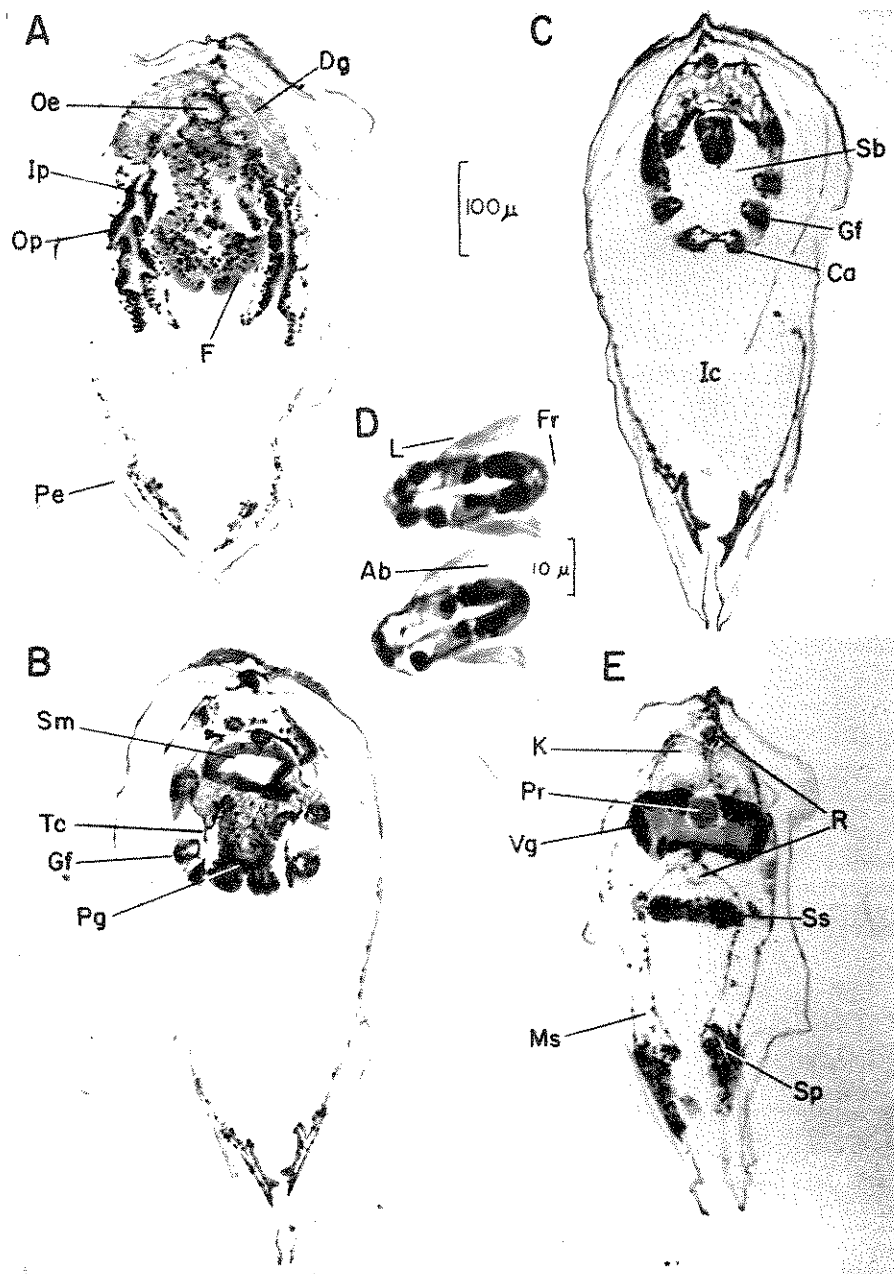


FIG. 5. Transverse sections of 700 μ *M. balthica* illustrating arrangement of mantle organs (A-D proceeding anteroposteriorly). A. Transverse section of palp region showing bilobed foot; sorting ridges on palps (see Fig. 2A for details of mantle edge). B. Transverse section of foot behind palp region. Distal ends of "reflected" filaments of inner demibranch already attached to upper side of foot by a tissue connection. C. Transverse section of inner demibranch posterior to foot demonstrating a common attachment in the midline region. D. Cross section of gill filaments, showing well-developed lateral, frontal, and abfrontal ciliation. E. Obliquely transverse section through cruciform apparatus (see Fig. 2D for details of mantle edge).

tial water
tion was
glass sur-
g motion
ts broad
lass. The
n during
edges of
: of loco-
imens of
: juvenile
: extensile
edal cilia
of loco-
milar be-
es which,
bution by
antigrade
I by the
specimens
ankton at
arval *M.*
(1946) in

duced in-
nsued in
appeared

just be-
with the
ition was
urrent of
ween the
inhalant
terial to
rgins.
bris had
nteriorly,
posterior
the shell
the shell
: of water
i pseudo-

nses seem
feeding,
ptake of
hases of

Lateral gill cilia evidently contribute towards the inhalant current but are aided to a large extent by pedal cilia, which beat strongly away from the apex of the foot (Fig. 6A). By means of its great mobility, the foot is capable of determining the direction of entry of the inhalant current (noted also by Allen 1961 for *Pandora*). The inhalant aperture is equivalent to the pedal gape in these early stages, and occupies almost half of the shell circumference. The exhalant stream is restricted to that region above the siphonal septum where the exhalant siphon later develops. Exhalation and inhalation proceeded alternately, one following the other after a short interval.

Particles entering the mantle cavity of early postlarvae (Fig. 6A) show more random movement than in the adult, but most particles impinge on the frontal surface of the inner demi-branch to be swept forward by cirri on the posterior filaments (Atkins 1937). From here they pass obliquely upward and forward across the face of the gill to the suprabranchial groove. On reaching the anterior end of the gill, particles are carried downward to pass between the two palp lobes where sorting takes place. Details of the action of the palps could not be clearly discerned because of their opacity; however, rapid agitation of particles in the preoral region of the mantle cavity suggested that energetic ciliary

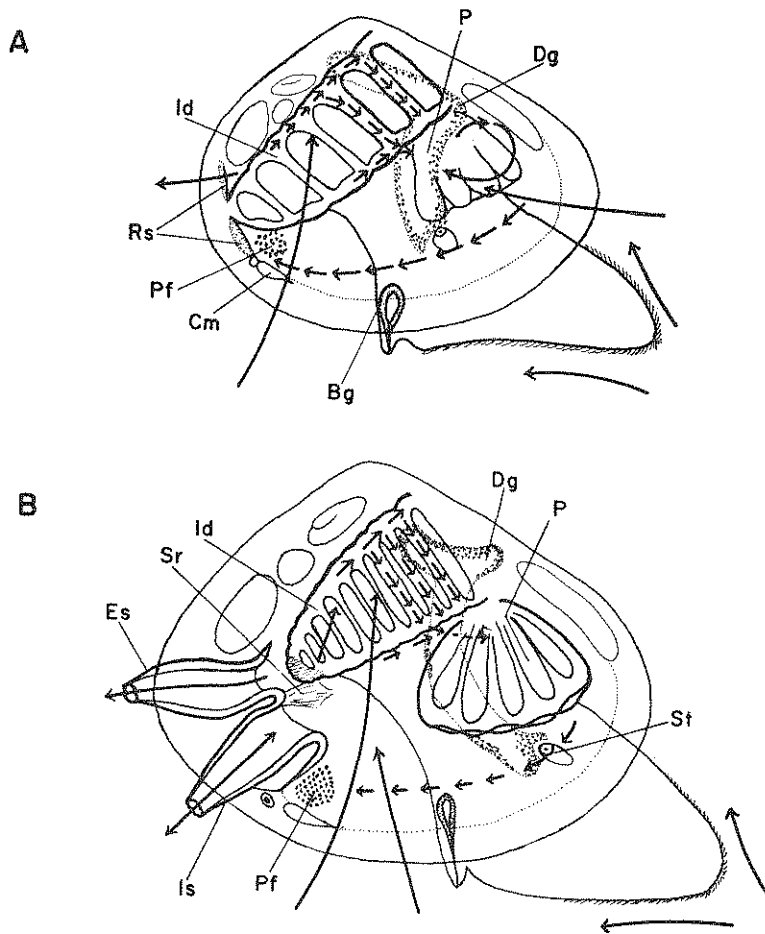


FIG. 6. Feeding mechanism of postlarval *M. balthica* at two stages of development. (Long arrows indicate directions of water currents; short arrows indicate ciliary tracts.) A. Before development of protrusible muscular siphons (0.7 mm). B. Siphons developed (1.4 mm).

action was taking place. The considerable elongation of the palps in the midline is no doubt a response to the burden of sorting which is placed entirely on the palps at this stage.

Rejected material from the palps passes rapidly posteroventrally along the sides of the foot towards the cruciform apparatus, where it accumulates during feeding, eventually to be rejected via the pedal gape (Fig. 1D). This response explains the absence of the waste canal, found in this region of the adult and associated with rejection of pseudofaeces via the inhalant siphon. The ciliary tract along the mantle edge (Fig. 2C, 2D) appears to be responsible for this rejection current.

As the siphons develop, they are protruded beyond the shell margins in feeding (Fig. 6B). The exhalant siphon continues to function as it has since spatfall; however, the inhalant siphon is dependent for its functioning on closure of the ventral shell margins, which, at this stage, are usually kept apart to admit the inhalant stream. The first function of the prospective inhalant siphon seems to be as a passage for the rejection of pseudofaeces (Fig. 6B) and only gradually does it take over its adult role as the exclusive route of the inhalant current.

Discussion

A number of workers have stressed the similarities of habit and adaptations of adult *Macoma* and *Nucula* to life in fine particulate soil (Yonge 1949; Stasek 1962). This functional similarity to *Nucula* is even more pronounced in the juvenile stages. Before development of protrusible siphons, the juveniles live in the surface layers of the soil, apparently drawing water and food particles from the interstitial spaces as described for *Nucula* (Yonge 1939) and *Acila* (Stasek 1961). This similarity extends to the orientation of the inhalant current, which enters the mantle cavity via the pedal gape. At this stage, the heavily ciliated foot acts in a similar way to produce the inhalant current as the palp proboscides of *Nucula*. This is unlike the situation described by Yonge for adult *Macoma* where water enters the mantle cavity exclusively via the inhalant siphon. Protruded between the shell valves, it produces and orientates the inhalant current, drawing particles into the mantle cavity. Another resemblance to the

nuculid type is the flat plantar surface of the foot, which is perhaps an adaptation to horizontal progression through the soil.

Spatfall in *M. balthica* at Whitstable occurs at a size of 300–330 μ , after a planktonic life of 2–5 weeks. However, transition from a juvenile to an adult mode of feeding is gradual. The inhalant current becomes progressively restricted to the posterior part of the pedal gape. A corresponding change in the gill orientation takes place, so that the inhalant current impinges at a constant angle onto the surface of the demibranch. During this transition the already developed inhalant siphon functions largely as a route for the rejection of particles from the mantle cavity. Only with closure of the pedal gape is it able to take over its full adult function.

The survival value of siphons in young specimens of *M. balthica* is emphasized by their rapid development. Muscular siphons are present at a size of 1.5 mm, although they protrude only slightly beyond the shell margins at this stage. The faster development of the inhalant compared to the exhalant siphon may well be an adaptation to life in unstable intertidal substrates. Rapid development of the inhalant siphon enables the young animal to maintain its position in the turbulent intertidal zone while still feeding on material in the surface layers of the soil.

Acknowledgments

This study was part of a doctoral dissertation submitted to the University of London, carried out under the supervision of Dr. J. E. Smith, whose advice and criticism are gratefully acknowledged. The assistance and advice of members of the staff of the St. Andrews Biological Station during the preparation of this paper are greatly appreciated. The author would also like to thank K. W. Ockelmann for helpful correspondence and encouragement.

The work was carried out with a grant from the Science Research Council of the United Kingdom.

ALLEN, J. A. 1961. The development of *Pandora inaequivallis* (Linné). *J. Embryol. Exp. Morphol.* 9: 252–268.

ANSELL, A. D. 1962. The functional morphology of the larva, and the post-larval development of *Venus striatula* (da Costa). *J. Marine Biol. Assoc. U.K.* 42: 419–443.

- ATKINS, D. 1937. On the ciliary mechanisms and interrelationships of lamellibranchs. III. Types of lamellibranch gill and their food currents. *Quart. J. Microsc. Sci.* 79: 375-421.
- BAGGERMAN, B. 1954. Spatfall and transport of *Cardium edule* L. *Arch. Néerl. Zool.* 10: 315-342.
- BAYNE, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. *J. Anim. Ecol.* 33: 513-523.
- BRADFELD, A. E. and NEWELL, G. E. 1961. The behaviour of *Macoma balthica* (L.). *J. Marine Biol. Assoc. U.K.* 41: 81-87.
- CADDY, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). *Can. J. Zool.* 45: 955-965.
- CARRIKER, M. R. 1961. Interrelation of functional morphology, behavior and autecology in early stages of the bivalve *Mercenaria mercenaria*. *J. Elisha Mitchell Sci. Soc.* 77: 168-241.
- CRISP, D. J. and SOUTHWARD, A. J. 1956. Demonstration of small-scale water currents by means of milk. *Nature*, 178: 1076.
- GRAHAM, A. 1934. The cruciform muscle of lamellibranchs. *Proc. Roy. Soc. Edinburgh*, 54: 17-30.
- JØRGENSEN, C. B. 1946. Lamellibranchia. In *Reproduction and larval development of Danish marine bottom invertebrates*. By G. Thorson. *Medd. Komm. Danmarks Fish. Havunders. Ser. Plankton*, 4: 277-311.
- LEBOUR, M. V. 1937. Larval and post-larval *Lima* from Plymouth. *J. Marine Biol. Assoc. U.K.* 21: 705-710.
- OCKELMANN, K. W. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proc. First Europ. Malac. Congr. (1962)*, pp. 25-35.
- QUAYLE, D. B. 1952. Structure and biology of the larva and spat of "*Venerupis pullastra*" (Montagu). *Trans. Roy. Soc. Edinburgh*, 62: 255-297.
- STASEK, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia: Nuculidae), with an evaluation of the role of the Protobranch organs of feeding in the evolution of the Bivalvia. *Proc. Zool. Soc. Lond. Vol. 137, Pt. 4*, pp. 511-538.
- 1962. Aspects of tentidial feeding in immature bivalves. *Veliger*, 5: 78-79.
- SULLIVAN, C. M. 1948. Bivalve larvae of Malpeque Bay, P.E.I. *Bull. Fish. Res. Board Can.* 77.
- WERNER, B. 1939. Über die Entwicklung und Artunter-scheidung von Muschellarven des Nordseeplanktons, unter besonderer Berücksichtigung der Schalenentwicklung. *Zool. Jahrb. Abt. Anat.* 66: 237-270.
- YONGE, C. M. 1939. The protobranchiate Mollusca: a functional interpretation of their structure and evolution. *Phil. Trans. Roy. Soc. Ser. B*, 230: 79-147.
- 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Phil. Trans. Roy. Soc. Ser. B*, 234: 29-76.

face of the
on to hori-
able occurs
tonic life of
a juvenile
radial. The
ly restricted
e. A corres-
ation takes
spines at a
the demi-
he already
s largely as
s from the
f the pedal
ilt function.
in young
hasized by
siphons are
ough they
tell margins
ent of the
siphon may
stable inter-
of the in-
animal to
lent inter-
erial in the

dissertation
ion, carried
. E. Smith,
gratefully
advice of
drews Bio-
ion of this
ithor would
for helpful

grant from
the United

f *Pandora in-*
Morphol. 9:

hology of the
nt of *Venus*
soc. U.K. 42: