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Life cycle and mode of infestation of *Myzostoma cirriferum* (Annelida), a symbiotic myzostomid of the comatulid crinoid *Antedon bifida* (Echinodermata)

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ABSTRACT: Eight different stages succeed one another in the life cycle of the myzostomid *Myzostoma cirriferum*, viz. the embryonic stage, 4 larval stages, and 3 postmetamorphic stages. Fertilization is internal. Embryogenesis starts after egg laying and takes place in the water column. Ciliated protrochophores and trochophores are free-swimming. Ciliated metatrochophores (i.e., 3 d old larvae) bear 8 long denticulate setae and form the infesting stage. They infest the host *Antedon bifida* through the feeding system of the latter: they are treated by hosts as food particles and are caught by the host's podia. By means of their setae, metatrochophores attach on the host's podia and are driven by the latter in the pinnule groove where they eventually attach and undergo metamorphosis. Juveniles and early males remain in the pinnules. They attach to the ambulacral groove through parapodial hooks and produce localized pinnular deformations. Late male and hermaphroditic individuals move freely on their host. They occur outside the ambulacral grooves and are located respectively on the pinnules, the arms or the upper part of the calyx of the host, depending on their stage and size. The success of the *Myzostoma cirriferum-Antedon bifida* symbiosis is ensured by the usually high density of the hosts' populations, the way the myzostomids reproduce (reproduction occurs year-round) and their effective mode of infestation.

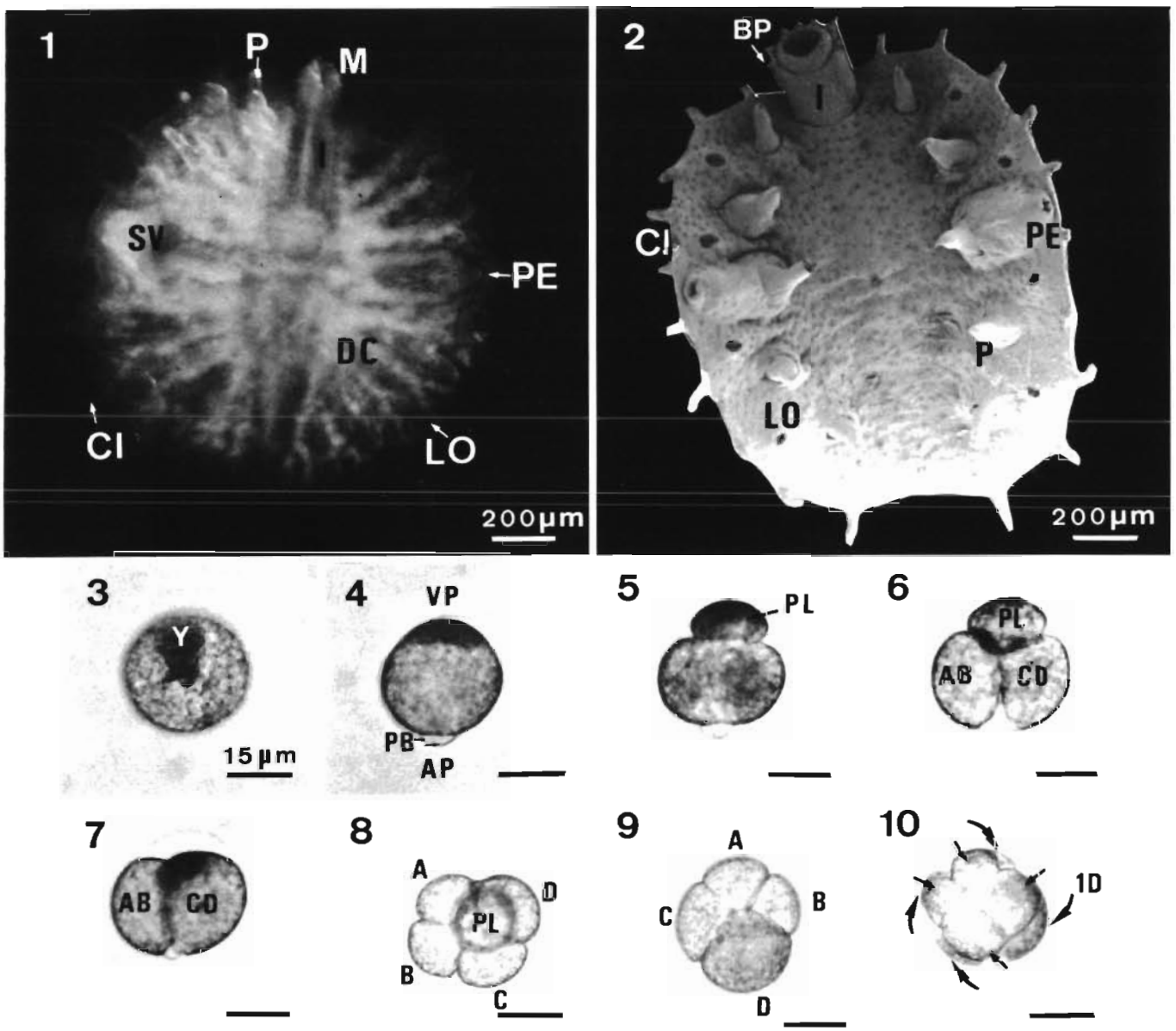
INTRODUCTION

Myzostomids are tiny invertebrates having affinities with polychaetes (Wheeler 1896, Kato 1952). There are more than 120 species which are all obligatory symbiotes of echinoderms, most of them being associated with crinoids (Grygier 1990, Jangoux 1990). Until recently, reports on the myzostomid life cycle were very limited, the most complete being those of Jägersten (1939, 1940) on *Myzostoma cirriferum* Leuckart, 1836 and Kato (1952) on *Myzostoma ambiguum* Graff, 1887. During the last few years, SEM and TEM observations were performed on myzostomids but they focused on one or a few particular developmental stages and never traced the entire life cycle (Grygier 1988, 1989, Eeckhaut et al. 1990, Eeckhaut & Jangoux 1992). Moreover, the specificity of the symbiosis (Jangoux 1990) as well as the usually high levels of infestation (Clark 1921, Jägersten 1940) suggest that myzostomids have a very well host-adapted mode of infestation, which is unknown.

The aim of the present paper is to detail the entire life cycle of *Myzostoma cirriferum* Leuckart, 1836 – viz. from fertilized eggs to fully developed individuals – with special emphasis on the mode of infestation of its comatulid host, *Antedon bifida* (Pennant, 1777).

MATERIALS AND METHODS

Adult *Myzostoma cirriferum* and their host *Antedon bifida* were collected by scuba-diving at Morgat (Brittany, France), from January 1990 to December 1991. The hosts were located on a pile of concrete blocks at a depth of 3 to 10 m, where they formed a



Figs. 1 to 10. *Myzostoma cirriferum*. Adult morphology and early embryogenesis. Fig. 1. OM view of the dorsal surface of an adult individual. Fig. 2. SEM view of the ventral surface of an adult individual. Fig. 3. Just-emitted egg. Fig. 4. Egg with 2 polar bodies. Fig. 5. Formation of the 2-blastomere stage (appearance of the first polar lobe). Fig. 6. Division in the non-polar part of the egg. Fig. 7. Resorption of the first polar lobe. Fig. 8. Embryo before resorption of the second polar lobe. Fig. 9. Embryo after resorption of the second polar lobe. Fig. 10. 8-blastomere stage (arrows indicate blastomeres). AP: animal pole; BP: buccal papilla; CI: cirrus; DC: digestive caeca; I: introvert; LO: lateral organ; M: mouth; P: parapodium; PE: penis; PB: polar body; PL: polar lobe; SV: seminal vesicle; VP: vegetal pole; Y: yolk

dense population of up to 1000 ind. m^{-2} (Lahaye & Bulteel 1987).

The comatulids and their symbiotes were maintained in an open-circuit aquarium at the Biological Station of Roscoff (7 to 18 °C – depending on the time of the year – and 34 ‰ salinity). *In vivo* observations were done on myzostomids that were either maintained on their hosts or placed in petri dishes after having been separated from them. Egg layings by adult *Myzostoma cirriferum* were induced by separating them from their host and by increasing the water temperature to ca 20 °C. Eggs were placed in petri dishes containing ca 50 ml of 0.2 µm filtered seawater with 50 mg l^{-1} of streptomycin sulfate (no. of eggs: ca 4 ml^{-1}; salinity 34 ‰). Once the larval stage was reached, the dishes were gently stirred and maintained at room

temperature (ca 20 °C). The water was renewed every day. For infestation studies, batches of ca 500 larvae were transferred to dishes including either a whole *Antedon bifida* (ca 4 cm in diameter) or a few autotomized or sectioned arms (ca 3 cm long).

Light microscopy was used to determine the stage of postmetamorphic individuals (viz. juvenile, male or hermaphrodite). Bouin-fixed 4 µm thick sections were used for routine histology (Masson Trichrome; de Groat hematoxylin counterstained with phloxin and light green) according to Ganter & Jollès (1969–1970).

For SEM observations, larvae and postmetamorphic individuals were fixed in Bouin's fluid for 24 h, dehydrated through a graded ethanol series, dried by the critical point method from carbon dioxide. They were mounted on aluminium stubs, coated with gold in a sputter coater and observed with a JEOL JSM 6100 scanning electron microscope.

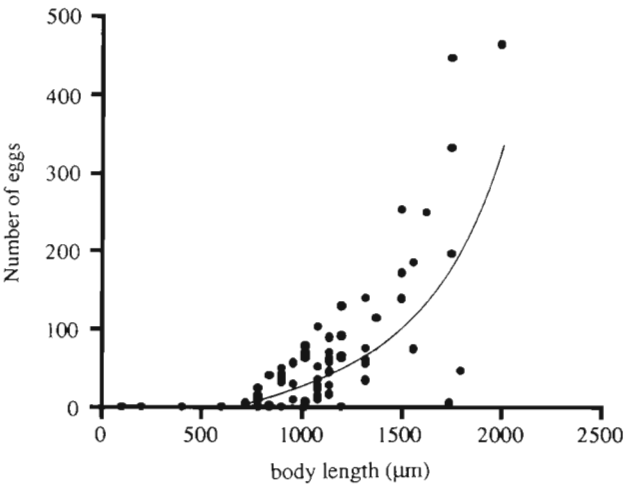


Fig. 11. *Myzostoma cirriferum*. Relation between the body length (B) and the number of eggs (N) laid over a 24 h period (laboratory conditions; December 1991). Equation of the regression line: $N = 3.1\ e^{(0.0023\ B)}$; r = 0.77

RESULTS

Development

Adult morphology. Adult *Myzostoma cirriferum* are translucent disc-shaped animals generally coloured in orange, pink or red (Fig. 1). Their relative transparency makes possible *in vivo* observations of internal organs such as the digestive tract and the paired seminal vesicles in which spermatophores form (Fig. 1). Their body consists of a short anterior introvert and a large posterior trunk (Figs. 1 & 2). When extended, the introvert in the largest individuals reaches ca 700 µm long and 250 µm wide; when retracted, it is housed in a pouch located in the antero-ventral part of the myzostomid trunk (Figs. 1 & 2). The trunk of the largest adults measures 2.4 mm in diameter (observed range 0.7 to 2.4 mm). Five pairs of parapodia are located lateroventrally in 2 rows, one on each side of the body (Fig. 2). Each parapodium is topped by a hook-like seta (Fig. 2). Close to the third pair of parapodia, near the body margin, lies 1 pair of penile apertures (Fig. 2). Four pairs of lateral organs are located between the 5 pairs of parapodia (Fig. 2). Ten paired cirri are located on each body margin of the trunk (Fig. 2). Cirri are needle-like structures ca 20 µm wide and 60 to 100 µm long (when retracted or extended respectively).

Reproductive process, laying and early embryogenesis. The reproductive process of *Myzostoma cirriferum* has been described in detail by Eeckhaut & Jangoux (1991). Reproduction occurs year-round and fertilization is internal. Once fertilized, eggs accumulate in the coelomic cavity which lies dorsally to the digestive system. Eggs are released in the water column, and layings can be induced by separating the myzostomids from their hosts and increasing the water temperature (up to 20 °C). As a result, myzostomids laid egg batches during a period of up to 48 h. The number of eggs varied according to the length of the individual (Fig. 11): myzostomids of less than 0.7 mm long never laid, while those of greater length laid a few (myzostomids whose length is close to 0.7 mm) to some hundred eggs (myzostomids whose length is close to 2 mm). In order to detect if there are definite periods of laying, 10 large myzostomids were separated from their hosts at each sampling period and the eggs laid over a 24 h period were counted (Table 1). With the exception of August, when the average number of eggs laid by 1 myzostomid was rather low (40 eggs), layings were fairly similar, the average numbers being between 147 and 204 (high values for standard deviations in Table 1 are because some individuals presumably had laid part of their eggs before they were field-collected; see also Fig. 11).

The chronology of early embryogenesis of *Myzostoma cirriferum* is summarized in Table 2. At 20 °C, the first maturation division occurs 2 h after laying (from the animal pole emerges the first polar body). The second polar body appears 10 min later (Figs. 3 & 4). The cleavage pattern is spiral. The first cleavage is preceded by formation of the first polar lobe at the vegetal pole (2 h 15 min after laying): the egg constricts perpendicularly to the vegetal-animal (V-A) axis and transforms into a caped-like egg (Fig. 5). Almost simultaneously (2 h 18 min), a furrow, parallel to the V-A axis, sinks in at the animal pole resulting in the formation of a caped 2-blastomere stage (viz. 1 polar lobe, and the AB and CD blastomeres) (Fig. 6). Shortly afterwards (2 h 25 min), the polar lobe merges with the CD

Table 1 *Myzostoma cirriferum*. Number of eggs laid in different months in 1990 (n = 10, individuals measuring from 0.9 to 2.0 mm long; laboratory conditions)

	Jan	Mar	May	Aug	Dec
Mean no.of eggs (m ± SD)	147 ± 102	204 ± 178	177 ± 96	40 ± 17	162 ± 72
Range	18 – 334	18 – 512	24 – 359	8 – 82	47 – 304

Table 2. *Myzostoma cirriferum*. Chronology of early embryogenesis (laboratory conditions). Times indicate when 50 % of the embryos reached the corresponding development stage

Time after laying (min)	Events
120	First division of maturation (1st polar body)
130	Second division of maturation (2nd polar body)
135	Appearance of the first polar lobe
138	First cleavage (formation of a caped 2-blastomere stage)
145	The first polar lobe fuses with blastomere CD (formation of a regular 2-blastomere stage)
158	Appearance of the second polar lobe
159	Second cleavage (formation of a caped 4-blastomere stage)
168	The second polar lobe fuses with blastomere D (formation of a regular 4-blastomere stage)
198	Appearance of the third polar lobe and beginning of the third cleavage (division of blastomere D)
205	Division of blastomeres A, B, and C and fusion between the third polar lobe and blastomere 1D (formation of a regular 8-blastomere stage)

blastomere thus forming the regular 2-blastomere stage (Fig. 7). The second cleavage (2 h 38 min) is preceded by the formation of the second polar lobe arising from the CD blastomere. Almost simultaneously (2 h 39 min), the AB blastomere and the non-polar part of the CD blastomere divide in two, resulting in the formation of a caped 4-blastomere stage (viz. 1 polar lobe and the A, B, C, and D blastomeres) (Fig. 8). Shortly thereafter (2 h 48 min) the polar lobe merges with blastomere D, forming the regular 4-blastomere stage (Fig. 9). During the second cleavage, the 2 polar bodies regress and disappear. The third cleavage (3 h 18 min) is also preceded by the formation of a polar lobe coming from the D blastomere. That lobe, however, is less prominent than those formed previously. The cleavage first concerns blastomere D (3 h 19 min) and shortly later (3 h 25 min) blastomeres A to C. The polar lobe finally merges with blastomere 1D resulting in the formation of the regular 8-blastomere stage (Fig. 10).

Larval development. SEM study allows the recognition of 4 larval stages, viz. a protrochophore, a trochophore, a metatrochophore and a metamorphic larva.

The protrochophore is spherical and measures from 30 µm (18 h after laying) to 40 µm (48 h after laying) in diameter (Fig. 12). It has a prototroch that divides its body into a hyposphere and an episphere (Fig. 12). At the top of the episphere lies an apical tuft of ca 10 cilia (each 10 µm long).

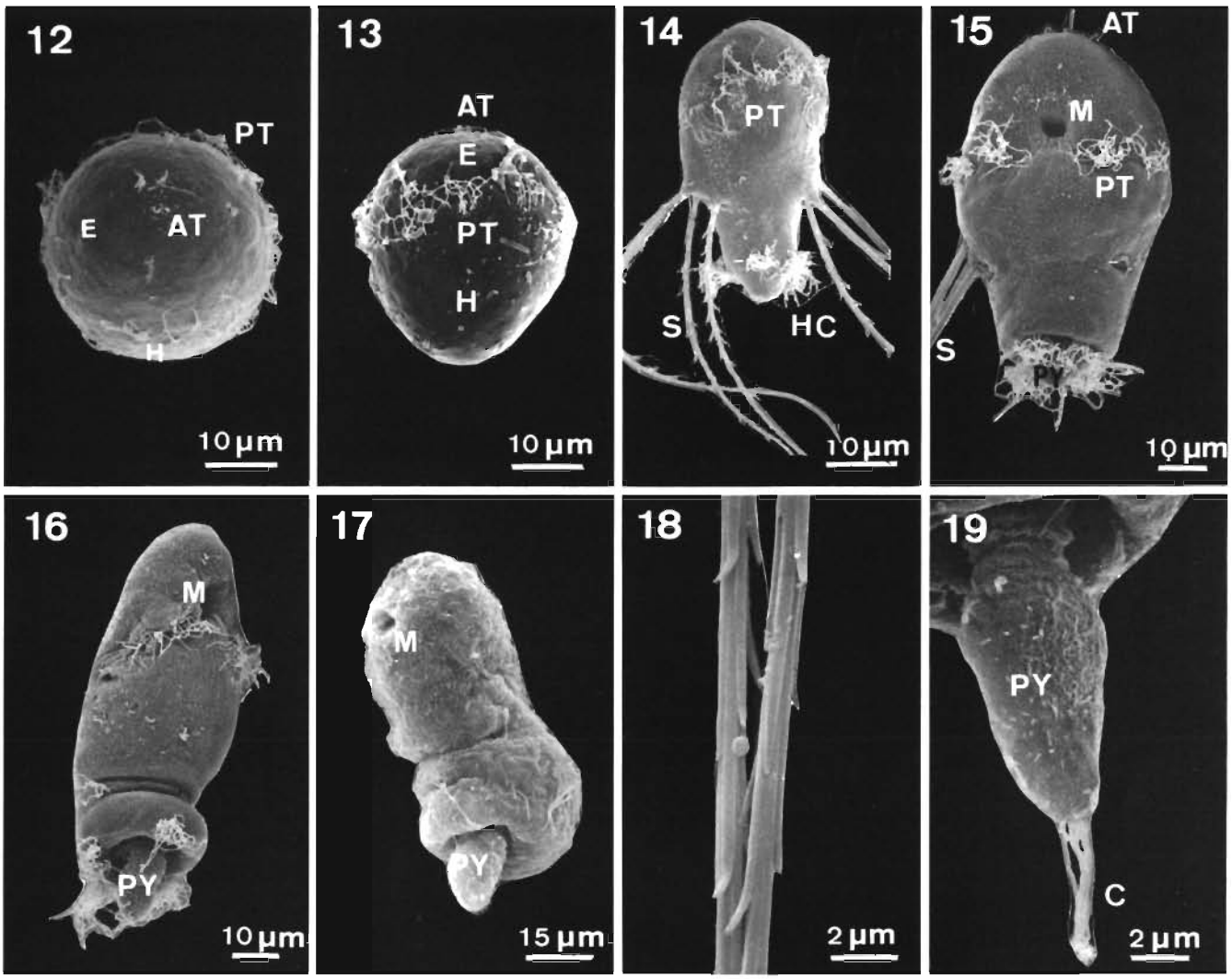
The trochophore measures from 40 µm (48 h after laying) to 50 µm (72 h after laying) in length (Fig. 13). It differs from the protrochophore in having an elongated hyposphere giving the larva a pear-shaped aspect.

The metatrochophore is also pear-shaped and measures from 50 µm (72 h after laying) to 70 µm (10 d after laying) in length but it differs from the previous stages in that it has 4 pairs of lateral setae (Figs. 14 & 18). These are denticulates and their length can reach up to 150 µm (in 10 d old larva) (Figs. 14 & 18). During the fourth day, the metatrochophore acquires an antero-ventral buccal aperture located close to the prototroch, as well as a retractile pygydium 5 to 15 µm long (when retracted or extended respectively) (Fig. 15). At the same time, the prototroch splits into 4 ventral tufts, and a hypospheral ciliary crown appears surrounding the pygydium (Figs. 14 & 15). During the fifth day, a tuft of 10 straight cilia appears at the top of the pygydium (Fig. 19).

Metamorphic larvae lose all setae and cilia (loss of setae precedes loss of cilia). This process does not begin simultaneously for all larvae. Indeed, though a few larvae have already lost their setae from the fifth day, for most of them this occurs on the seventh day (Fig. 20). Metamorphic larvae are bean-shaped with their body folding back ventrally; they measure 70 µm in length (Figs. 16 & 17). When maintained *in vitro*, in the absence of hosts, they generally die when they are 12 to 14 d old.

Postmetamorphic development. Histological and SEM analysis allows us to distinguish 3 postmetamorphic stages: a juvenile, a male and a hermaphroditic stage.

The juvenile stage includes myzostomids from 70 to 500 µm long These are whitish translucent worms. The smallest juvenile observed on *Antedon bifida* was 70 µm long and 30 µm wide (Fig. 21). Juveniles are bean-shaped animals with their body folding back



Figs. 12 to 19. Larval development of *Myzostoma cirriferum* (SEM views). Fig. 12. Protrochophore. Fig. 13. Trochophore. Fig. 14. Early metatrochophore. Fig. 15. Late metatrochophore. Fig. 16. Early metamorphic larva. Fig. 17. Late metamorphic larva. Fig. 18. Details of setae. Fig. 19. Details of the pygydium. AT: apical tuft; C: cilium; E: episphere; H: hyposphere; HC: hypospheral ciliated crown; M: mouth; PT: prototroch; PY: pygydium; S: seta

ventrally and their ventral surface pleated (Figs. 21 & 22). A constriction divides the juvenile body in 2 parts: an anterior part, corresponding to the future introvert, and a posterior part which will form the trunk of the adult (Fig. 22). The mouth opens at the apex of the future introvert which is not yet retractile. The posterior part (two-thirds of the whole body length) bears 1 pair of parapodia. A further step in the myzostomid development is reached at 200 µm long. The body is no longer bean-shaped and the distinction between the introvert and the trunk is stronger (Fig. 23). The introvert is still not retractile but the introvert pouch is differentiating. The major features of this 200 µm juvenile are the appearance of the 5 pairs of parapodia and 4 pairs of lateral organs looking like small slits. Myzostomids of 300 µm long are similar to those of 200 µm, but have 4 pairs of buccal papillae at the apex of the introvert (Fig. 24). At 400 µm long, the juvenile begins to look like the adult; the introvert can almost totally retract into its introvert pouch, the body is wider with 6 pairs of cirri on its margin (Fig. 25).

Myzostomids enter the male stage when they reach a length of ca 500 µm (Fig. 26). At this stage, mature male gametes as well as 4 deferent ducts and 2 seminal vesicles appear in the ventro-lateral parts of the body, on both sides of the ventral nerve cord. Myzostomids are then as wide as they are long, the introvert can totally retract into the introvert pouch, and they have 10 pairs of marginal cirri and 1 pair of penises. When they reach 600 µm, they look very similar to adults but differ from them in both internal morphology and behaviour.

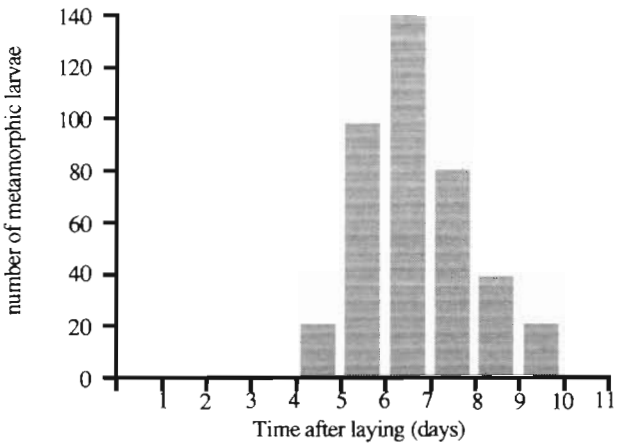


Fig. 20. *Myzostoma cirriferum*. Time (d after laying) of appearance of metamorphic larvae (laboratory conditions)

The hermaphroditic or adult stage (Figs. 1 & 2) is reached when myzostomids are close to 700 µm long. At this stage, mature female gametes appear in the dorso-lateral parts of the body. All individuals from 700 to 2400 µm show the same shape and the same internal organization. Their coloration develops progressively and the digestive caeca become more and more branched.

Behaviour

Larval behaviour. Early protrochophores (18 h old) rotate slowly counterclockwise, and the larvae are not able to elevate in the water column. From 24 h their ciliary activity enables larvae (viz. late protrochophore and trochophore) to swim though a counterclockwise movement allowing them to move upright. With the appearence of setae, the swimming of the 3 d old larva (viz. the metatrochophore) changes: it still rotates but the general trajectory is not straight yet and has a counterclockwise spiral movement. From the fifth day, the larvae become less motile and often remain motionless. Metatrochophores show a great tendency to attach by their setae either on the substrate or on any kind of sestonic particles occurring in the water column. From the seventh day, most larvae begin to lose their setae, returning to a swimming stage. These larvae (viz. metamorphic larvae) swim for a few hours the same way as metatrochophores. They eventually either stay motionless or move slowly without rotating, often in circles.

Assays of host's infestation were performed using larvae at different developmental stages. Whatever the larval stage of *Myzostoma cirriferum*, its swimming is not modified by the presence of the host and larvae do not seem to be attracted by hosts. For each larval stage, larvae are treated by the host as any other food particles (for a detailed description of the feeding behaviour of *Antedon bifida*, see Lahaye & Jangoux 1985). When larvae swim close to pinnules, they are caught by the comatulid podia, mostly by the primary podia. Yet the fate of captured larvae will vary according to the larval stage.

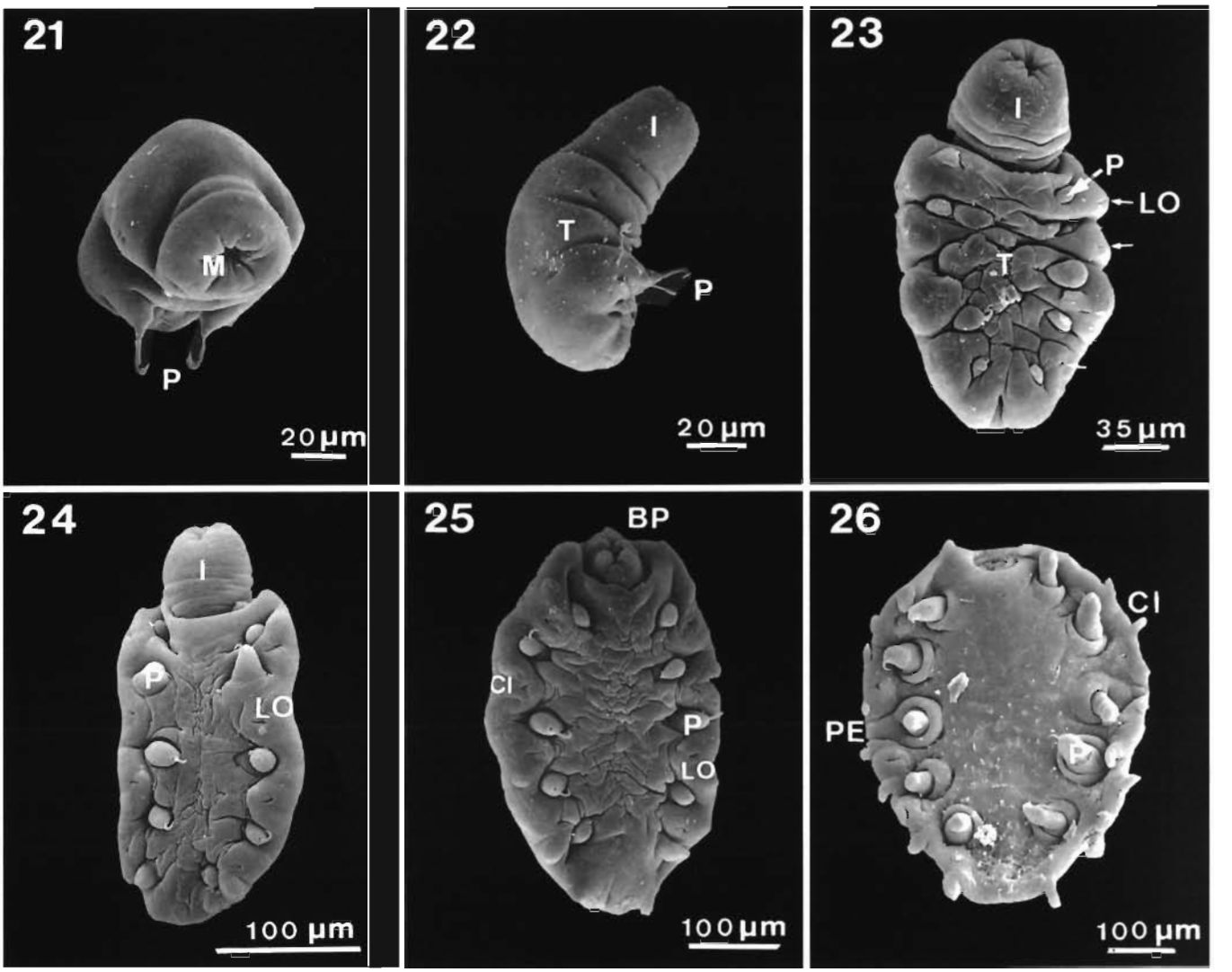
When protrochophores, trochophores or metamorphic larvae are caught by podia, the latter bend, driving the larvae into the ambulacral grooves. In most cases, captured larvae are rejected into the water column through the activity of secondary or tertiary podia while a few are carried to the mouth where they are swallowed. The greater the larvae are, the more are their chances of being rejected.

When metatrochophores are caught by the podia, they attach to them by their setae and, as podia necessarily will bend and wripe on the groove wall, larvae thus will eventually attach to the groove integument (Figs. 27 & 28). Some metatrochophores, however, will either not attach or detach. They will be carried by the groove ciliary current and will be either rejected to the water column as were non-metatrochophoran larvae or transported to the mouth and swallowed. It has been observed that swallowed metatrochophores will always be regurgitated by a vigorous contraction of the host foregut.

Postmetamorphic behaviour. Two types of behaviour can be distinguished in postmetamorphic individuals corresponding to 2 different stages during their development: a pinnular or fixed stage, and a free-moving stage.

Pinnular stage concerns myzostomids from 70 to 600 µm long. They are always fixed in pinnular grooves, generally in proximal pinnules (distal pinnules are rarely infested). They are fixed into the groove by their parapodial hooks, so that their ventral side lies against the bottom of the groove with their anterior part (viz. the future introvert) pointed to the arm of the host (Figs. 29, 30 & 31). Infested pinnules are generally inhabited by a single myzostomid, although 2 can occasionally be present. Individuals smaller than 500 µm are steadily attached to pinnules but become progressively more motile as they grow, the largest pinnular worms being able to move in the ambulacral groove. Fixed myzostomids produce asymmetric pinnular deformations; viz. they occur usually on 1 of the 2 pinnular sides (Figs. 31 & 32). Deformations are roof-like and can cover the groove over its width and over a length depending on the myzostomid size (the greatest length observed was 450 µm). Such roof-like deformation covers either part of or the entire body of the myzostomid. It results in the fusion of several podia and ambulacral lappets.

At the end of the pinnular stage, myzostomids be-



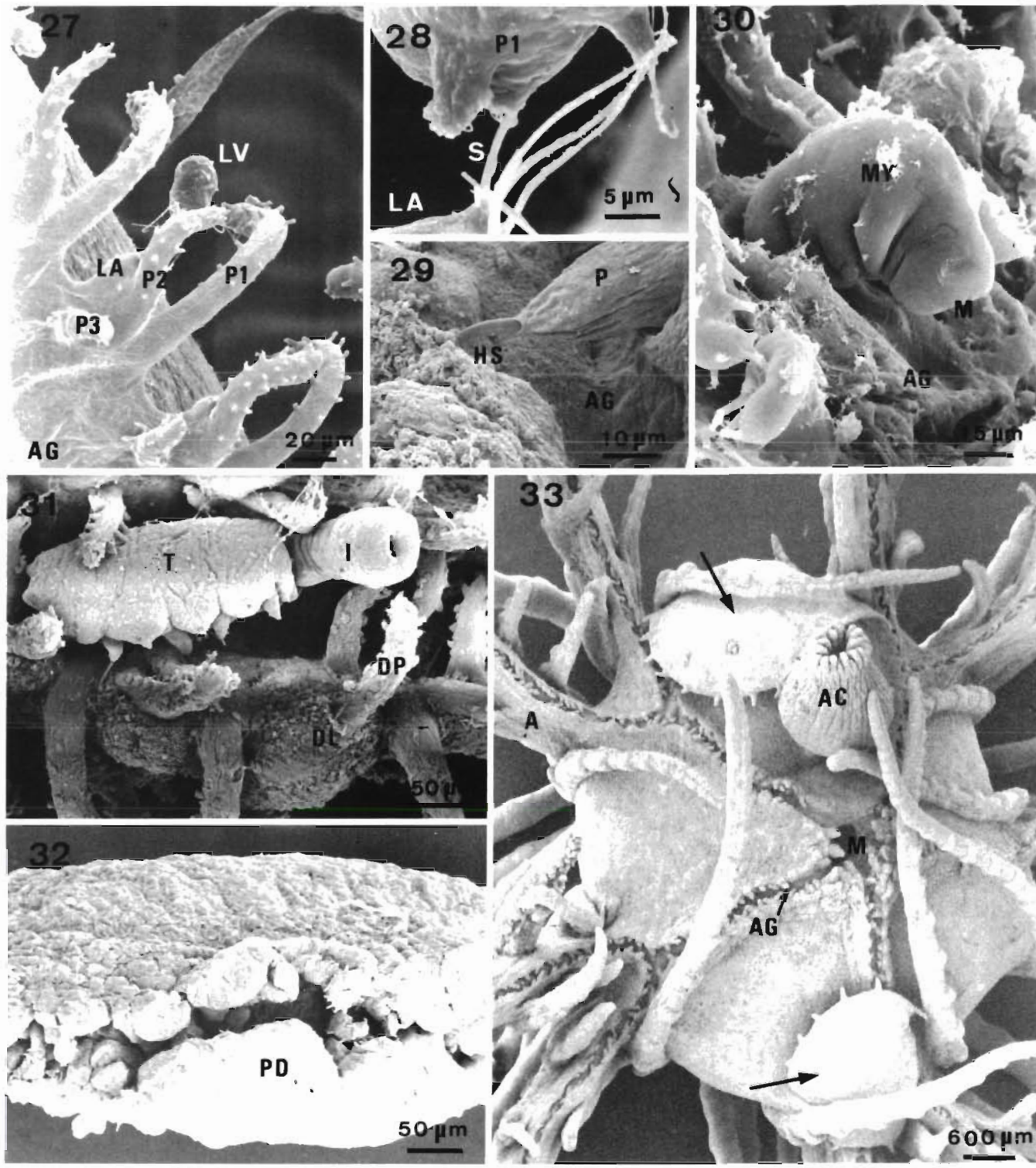
Figs. 21 to 26. Postmetamorphic development of *Myzostoma cirriferum* (SEM views). Figs. 21 to 25. Early to late juveniles. Fig. 26. Early male. BP: buccal papilla; CI: cirrus; I: introvert; LO: lateral organ; M: mouth; P: parapodium; PE: penis; S: seta; T: trunk

come totally free-moving (Fig. 33). Up to a length of 1 mm, myzostomids move all over the host's body but never enter an ambulacral groove. They move very quickly and can wander from one end of an arm to the other, viz. ca 4 cm, in 2 to 3 s. When they are still, they often apply their introvert into a brachial or pinnular groove where they divert food particles. Myzostomids longer than 1 mm are less motile and generally stay on the upper part of the calyx of the host.

DISCUSSION

One of the most remarkable features of myzostomids is their reproductive process which is internal and implies the intradermic penetration of a spermatophore content (Kato 1952, Eeckhaut & Jangoux 1991, 1992, Lehmann et al. 1991). Reproduction in *Myzostoma cirriferum* occurs throughout the year (Eeckhaut & Jangoux 1991) and individuals longer than 0.7 mm are able to lay fertilized eggs year-round. The more the myzostomid length increases, the greater the number of eggs they lay. Once laid, eggs start to cleave. The cleavage pattern in *M. cirriferum* is spiral and the first 3 divisions are characterized by the formation of polar lobes. This last feature has already been reported by Kato (1952) for the species *Myzostoma ambiguum* and is also encountered in early embryos of a few polychaetes (Schroeder 1989) and a few gastropod molluscs (Brahmachary 1989).

The life cycle of *Myzostoma cirriferum* is summarized in Fig. 34. Larvae of this species appear similar to



Figs. 27 to 33. Relations between *Myzostoma cirriferum* and its host, *Antedon bifida*. Figs. 27 & 28. Setal attachment of a metatrochophore to a host's podion. Fig. 29. Parapodial attachment of a pinnular myzostomid to the groove integument of its host. Fig. 30. The smallest observed pinnular myzostomid. Figs. 31 & 32. Pinnular deformations produced by juvenile myzostomids observed on relaxed and contracted pinnule, respectively. Fig. 33. Large hermaphroditic individuals on the host's tegmen. A: arm; AC: anal cone; AG: ambulacral groove; DL: deformed lappets; DP: deformed podia; HS: hook-like seta; I: introvert; LA: lappet; LV: larva; M: mouth; MY: myzostomid; P: parapodium; P1, P2, P3: primary, secondary and tertiary podia; PD: pinnular deformation; S: seta; T: trunk

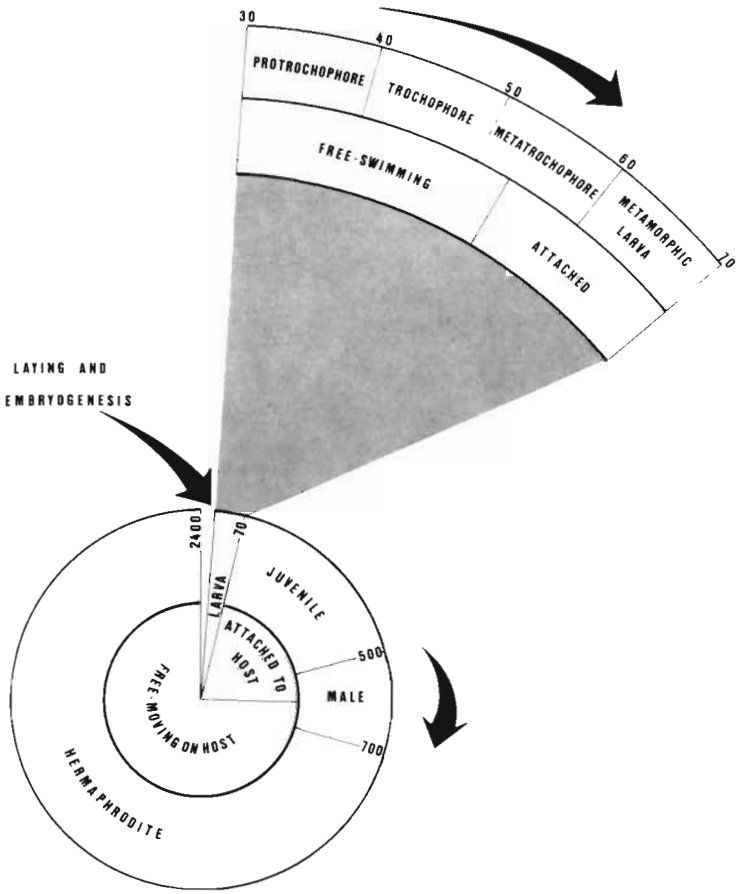


Fig. 34. *Myzostoma cirriferum*. Life cycle (circle) and details of larval development (arc). For both the circle and arc, the outer ring deals with myzostomid morphological stages and the inner ring with myzostomid behaviour (numbers indicate length of individual in µm)

those observed previously in 3 other ectosymbiotic myzostomids of comatulids, viz. *M. ambiguum*, *M. alatum*, and *M. parasiticum* (Kato 1952, Eeckhaut & Jangoux 1992, Jägersten 1939 respectively). The life span of laboratory-reared larvae of these 4 species is about 10 d and, in *M. cirriferum*, the free-swimming larval stage would occur up to the third day. This corresponds to the acquisition of setae which means that larvae can attach to any 'fleshy' substratum they contact and thus have become infesting. To be free-swimming for 3 d appears rather paradoxical. Indeed, while the embryos and developing larvae of *M. cirriferum* are directly situated near the natural hosts they have to infest, the longer the free-swimming stage, the better chance the larvae have of being carried away from the comatulid hosts. However, the high density of the investigated host population could indirectly prevent a too high myzostomid larval dispersal. Indeed, this population can reach 1000 ind. m^{-2} (Lahaye & Bulteel 1987). It forms an epibenthic stratum of a few cm thick extending over numerous square meters. Such a dense population could generate favourable hydrodynamic conditions enabling small particles and, all the more, myzostomid larvae to stay between host individuals. Platel (1962) reported a low level of myzostomid infestation for a population of *Antedon bifida* where individuals were scattered on the substratum. It is thus probable that the denser the comatulid population, the easier the infestation. (In the investigated host population there is a 100% infestation of adult comatulids and the infestation rate can reach up to 71 myzostomids per host; Eeckhaut unpubl.) During the first 3 d, larvae should be confronted by another problem: they should be considered by comatulids as any other small particles and should thus be caught as food particles. However, as we observed, the captured larvae can be rejected by secondary and tertiary podia to become free again. Larvae probably take advantage of this mechanism of rejection which could prevent a lot of them from being swallowed by their host.

With the appearance of setae, metatrochophores can attach either on the comatulid pinnules or on the neighbouring substrate. Pinnule-attached metatrochophores will eventually lose their setae and rapidly acquire their first pair of parapodia to attach more firmly to the pinnule. The total loss of setae in reared metatrochophores was observed, but *in vitro*-produced metamorphic larvae never acquired 1 pair of parapodia. According to Chia (1978) the metamorphosis in symbiotic invertebrates is dependent upon some stimuli from the host. If the larvae are not correctly stimulated, the stage of competency (viz. the stage during which the larvae can metamorphose) takes more time and can end in their death. In *Myzostoma cirriferum*, the stage of competency is probably reached in 5 d old larvae, viz. in metatrochophores having differentiated the mouth aperture and the pygydium. These larvae will have been adequately stimulated if they have already attached in pinnular grooves, and they will thus metamorphose totally and quickly. As a consequence, the life span as metamorphic larvae is very short (viz. they acquire their first pair of parapodia very rapidly becoming thus a juvenile). Yet metatrochophores that attached to the neighbouring substrate could not be correctly stimulated (as are those produced in laboratory conditions). They will thus metamorphose partially and give rise to metamorphic larvae with longer life span. To be able to delay metamorphosis would be an advantage for myzostomids. Indeed, long-lived metamorphic larvae are

still able to swim for some time after they lost their setae. This means they still have some chance to be caught by a comatulid, to be appropriately stimulated, and to complete their metamorphosis.

The population of postmetamorphic *Myzostoma cirriferum* on a given host always appeared very well structured: small myzostomids (viz. juveniles and early males) attach in pinnular grooves and large ones (viz. late males and hermaphrodites) always occur outside the grooves and move on the whole surface of the comatulids. The fact that small individuals are situated in pinnular grooves has 2 advantages for the myzostomid population. Firstly, they are in a place where alimentary particles transit and where they can feed easily. Secondly, to be attached in pinnules prevents these immature individuals from being in contact with large mature ones. Indeed, when moving, adult individuals can emit their spermatophore to any conspecific they touch (Eeckhaut & Jangoux 1991). Yet, as they never move in ambulacral grooves, they consequently never contact an immature myzostomid. The more adult individuals grow, the more motionless they are, and largest hermaphroditic individuals are concentrated on the upper part of the calyx of their host. As a result, the reproductive process is even more efficient; when a large adult emits its spermatophore, there are more chances that it will be emitted on another large adult and consequently that the spermatozoons used in this process reach more mature oocytes.

Among polychaetes, the invertebrate group closest to the myzostomids, the process of intradermic penetration of a spermatophore content was only reported in some archiannelid species (Westheide 1984). According to Westheide (1984), the existence of small polychaete species as archiannelids is only possible if successful fertilization is better insured than in the larger macrobenthic species which discharge their gametes into the water. This implies an adaptation of the reproductive behaviour resulting in the occurrence of direct sperm transfer and internal fertilization. In *Myzostoma cirriferum*, internal fertilization must certainly be of the utmost importance for the survival of the species: it is a small invertebrate and, as a consequence, the adults only possess a small number of gametes. However, it is a symbiotic invertebrate which usually means that it has to produce a substantial number of infesting larvae at the next generation. Yet the reproductive potential of *M. cirriferum* is rather low (largest individuals rarely produce more than a few hundred eggs), and its survival as a symbiote appears to be permitted both by the fact that it reproduces year-round, and by its effective mode of infestation.

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