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Aspects of the feeding biology of the fanworm *Bispira volutacornis* (Polychaeta: Sabellidae)

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The detail of the characteristic double whorled branchial crown of the tubiculous polychaete *Bispira volutacornis*, with its internal skeleton of large vacuolated cells and ciliated radioles, is consistent with the feeding apparatus of sabellids at large. Studies show that ingested particulate matter has at least one dimension less than 15 μm. Feeding seems to be most readily accommodated at current speeds from 1 cm s^{-1} to 3 cm s^{-1} with the crown apex angled downstream. Particulate matter passes through the alimentary canal in 7.7 h at 14°C, for an average sized specimen of 97 segments. Whilst the tube provides protection against predatory fish and crustaceans (with ample evidence of sub-lethal cropping of the branchial crown), it also has a role in irrigation and respiration. The worm will retreat within the tube when current flow exceeds 8.7 cm s^{-1}.

INTRODUCTION

The tubiculous polychaete, *Bispira volutacornis* Montagu, a member of the subfamily Sabellinae is an epibenthic suspension feeder in north-west Europe. Its conspicuous appearance makes it a notable member of the shallow sublittoral around Ireland and Britain. Structures associated with the branchial crown, the collar and the nature of the chaetae are the most distinguishing taxonomic characteristics of this sabellid (Nicol, 1930). Literature on *B. volutacornis* is restricted almost exclusively to faunal records and descriptions of the external morphology, with knowledge of its biology and ecology being very fragmentary (Fauvel, 1927; Dewarumez et al., 1992). The authors were prompted by the relative paucity of information on this presumptive key species to look at different aspects of its biology and ecology. This paper focuses on aspects of the feeding biology of this fanworm.

MATERIALS AND METHODS

Polychaetes were collected up to depths of 10 m, by diving in Lettercallow Bay on the west coast of Ireland (53°17.4′N 9°42′W). On returning to the laboratory menthol crystals were used to relax specimens. One hundred specimens were dried on filter paper and weighed, their crowns were dissected off and reweighed to determine crown weights in relation to overall weight. For light microscopy, upper abdominal sections were fixed in 10% formalin (24 h) followed by 70% ethanol, embedded in paraffin wax, (Bancroft & Stevens, 1977) sectioned (5 to 10 μm) and stained using Ehrlich's haematoxylin and eosin. Particulate matter in the gut was measured using a computer based image analysis® program. For scanning electron microscopy, tissues were fixed by immersion in 4% gluteraldehyde, in cacodylate buffer (pH 7.2 with 0.02 M) for 1 h at room temperature. After rinsing in buffer, the tissues were post-fixed for 1 h in 1–2% osmium tetroxide (OsO_4), and washed with seawater. Tissues were dehydrated in graded ethanol and dried by the critical point method, mounted on aluminium stubs and spluttercoated. The crown skeletal structure was prepared for study by soaking overnight in a 0.25% aqueous solution of $MgSO_4$ and stained with methylene blue.

Observations on behaviour were made after a 4-day acclimation period. A horizontal flume, with a 'sump' located in the centre of the working channel, set at 12°C, was employed for flow observations. Specimens were monitored for every increase in current of 0.005 m s^{-1}, from 0 m s^{-1} to 0.1 m s^{-1}, with a 15 min adjustment period between each current change.

Both natural, *Bispira* tubes, and introduced settling surfaces, roughened plastic corrugated sheets—held at a 90° angle to the sea floor, in Lettercallow Bay were investigated for epiphytes and epizoids. Fifty *Bispira* tubes were examined along with 12 corrugated sheets over a three-month period, with the remainder (28 sheets) left undisturbed for a 24 month period.

For feeding experiments specimens were put inside glass tubes and orientated in the required position by means of thin wire loops. Held at 14°C, they were fed a carmine suspension, and time until defaecation was recorded, with individual worms tested several times in succession. Over a 6-day period, luminophores (fluorescently stained sand grains as used by Mahaut & Graf, 1987) of different size (>250, 180 to 250, 125 to 180, 90 to 125, <90 and <50 μm) were used to follow particle crown pathways, under UV light. Faeces were also examined to see if any particles were ingested. A recovery time of 12 h was allowed in-between the addition of luminophores.

RESULTS

Bispira volutacornis occupies a tough, leathery tube, overlain by an opaque greyish layer, made up, chiefly, of

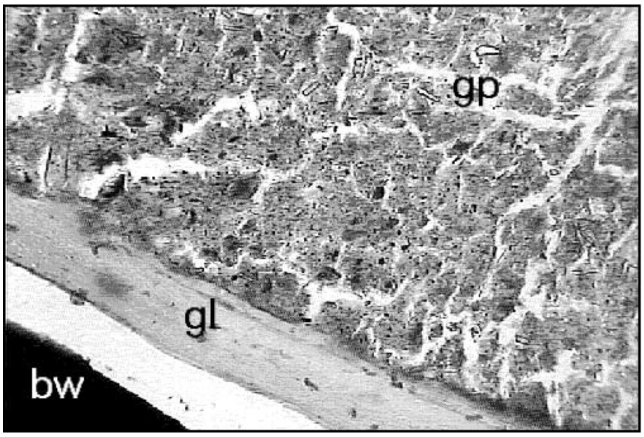

Figure 1. A histological section of the tube with *Bispira volutacornis* in place. bw, body wall of *Bispira volutacornis*; gl, gelatinous lining; gp, granular portion.

sedimentary material (Figure 1). The tube tapers posteriorly with a terminal or sub-terminal pore. Ventral shield glands secrete the inner gelatinous base-lining, whilst the outer layer comprises medium sized particles collected and sorted by the branchial crown and stored temporarily in paired sacs located between the ventral collar folds and the triangular mouth.

In its normal feeding posture, *Bispira volutacornis* extends the anterior part of the body so that the basal portion of its branchial crown is just free of the tube mouth. The crown shows great colour variation, ranging from white radioles in young specimens, to completely orange, purple or brown radioles, with radiolar tips sometimes lacking pigmentation in adults. In adults, the crown constitutes 17% of the total average body weight and contributes some 33% to average body length. The branchial crown is supported by an internal skeleton of large vacuolated cells that are also found, in varying degrees, in the pinnules, radioles, palps and lips. The branchial skeleton consists of two ventral projections which spiral into the basal lobes, that are joined dorsally by a short transverse bar of skeletal material (Figure 2). Anteriorly, each lobe bears bipinnate radioles which, when fully developed, arise from the basal lobes which extend back and spiral independently on the ventral surface to give the double whorled branchial crown. From this branchial skeleton, single skeletal rods extend into the palps. In an 'adult', there are ~60 to 80 radioles in each spiral, increasing to 120 radioles in older worms. In juveniles, the radioles are less numerous, and the lobes may not have yet begun to spiral. The number of radioles may vary between the two spirals of the same crown, where each is united for the first 3 mm of its length by a thin basal web that runs around the abfrontal face of the crown base. Distal to the basal web, the radioles are entirely separate and bear irregularly dispersed eyespots, with some having up to three pairs. The two branchial lobes unite at their bases to encircle the mouth, except for a mid-ventral separation. *Bispira volutacornis* is a faculative suspension feeder, where a food-collecting current is created by the co-ordinated action of various rows of cilia on the fully extended branchial crown. Ciliated structures include the pinnules, the radioles, the basal folds, the lateral lips, the palps (Plate 1) and the entrance to the ventral sacs. Cilia sizes varied from 0.1 μm width and 6 μm length on the tip of the palp to 0.4 μm width and 25 μm length on the latero-frontal cilia on the pinnules. The ventral sacs are, however, covered in what appear to be sensory papillae. In still water, paired whorls of radioles on the branchial crown expand, with the individual radioles arched and held apart at their distal tips. This rounded cone of radioles, with the inner whorls overlapping towards the centre, is positioned symmetrically over the tube, with the plane of the base of the crown perpendicular to the long axis of the tube. In flowing water (1 to 3 cm s^{-1}) the apex of the crown is angled downstream, with the leading edge of the crown raised and the plane of the base of the crown perpendicular to the long axis of the tube. The spiral tiers of the crown intersect the ambient flow at approximately 20° to 30°. At speeds ranging between 4–7 cm s^{-1}, the radioles are held much closer together, as though ready for withdrawal. At higher currents the whole crown is aligned perpendicular to the tube. At speeds greater than 8 cm s^{-1} specimens withdrew more frequently and crowns were retracted when flow exceeded 8.75 cm s^{-1}. This points to a tolerance threshold above which the polychaetes are forced to seek shelter in their tubes.

Introduction of different sized luminophores to the crown have shown that particles >250 μm are too large for transportation along the branchial grooves; those in the lower range of 90 to 250 μm are collected, bound in mucus strings and rejected upwards via the ciliated grooves on

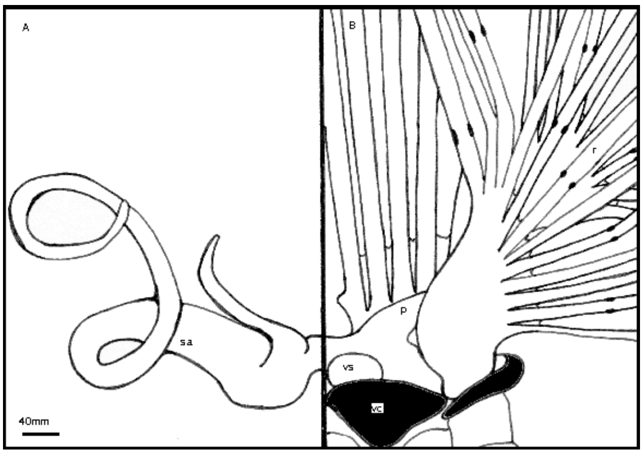

Figure 2. Internal skeleton (A), which supports the branchial crown (B) of *Bispira volutacornis*. p, palp; r, radiole; p, skeletal axis; vs, ventral sac; vc, ventral collar.

Plate 1. Cilia on palps. p, palps.

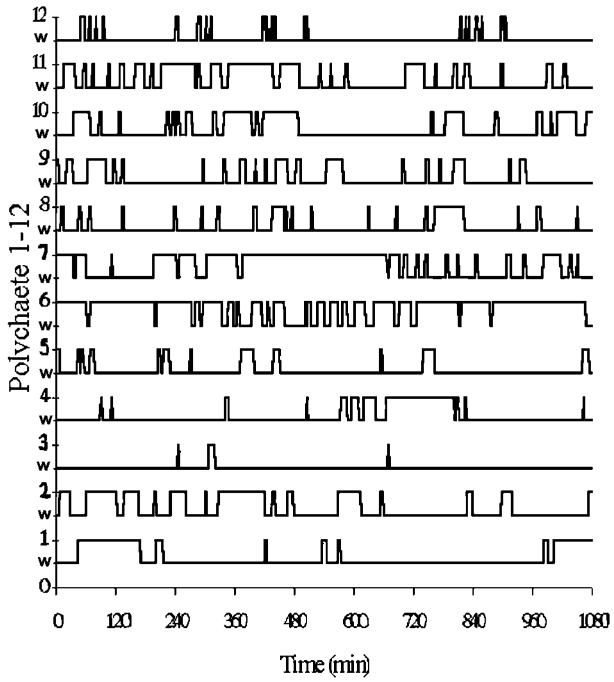

Figure 3. Behaviour of 12 specimen of *Bispira volutacornis*. Each plot represents a single specimen numbered 1 through 12. Specimen #1 begins with its crown withdrawn, w mark on the y-axis, after 40 min the crown reappears, seen on the plot as an increase to the 1 mark on the y-axis. Each w represents a 'withdrawn' state, contrary to this, when a worm remerges, from the tube, the plot rises to the # mark.

the palps and are finally vented in the upward flowing water-current through the crown. Particles 50 to 90 μm are sent to the ventral sacs for tubebuilding with the excess material being rejected upwards into the path of the larger particles.

From histological sections of the gut, benthic diatoms were found to be the chief dietary constituents including such genera as *Bacteriastrum*, *Gyrosigma*, *Licomophora*, *Diploneis*, *Grammatophora*, *Mastogloia* and *Bacillaria*. Peridinians, silicoflagellates, foraminiferns, tininnids, annelid/crustacean bristles and detritus were also ingested. Captured particulate matter was found to have at least one dimension less than 15 μm, and no apparent limit as to the lower end of the acceptable size range. At 14°C, the average time taken for food to travel through an average gut size of 97 segments, with the width of fifth chaetiger of ~9 mm, was 7.7 h. Faecal matter leaves the anus in the form of a compact mass and is held together in an outer binding coat of a clear gelatinous mucous-like substance, giving the appearance of a cylindrical tube of uniform diameter. Faecal matter moves vertically toward the mouth of the tube via the ciliated faecal groove (the copragogue), located ventrally along the abdomen. This turns right at the posterior border of the thoracic region and passes dorsally, thereby avoiding the ventrally positioned mouth. Transportation of the faeces within the tubes is carried out primarily by the copragogic cilia, ~1.5 μm in diameter and ~26 μm in length, and aided by peristaltic body movement. Sometimes, these strings can be seen suspended between the palps and radioles, making their way slowly to the free edges of the branchial crown, whence they are removed by water flow.

During feeding and withdrawal, *Bispira volutacornis* executes rhythmic movements which continuously renew the water in contact with the body (i.e. irrigation). While withdrawn, the tube partly closes, leaving an opening at each side of the aperture that allows the passage of water. At regular intervals, 'piston-like' movements of the abdomen work against the confining walls of the tube. The simultaneous progression of swellings serially along the body; when the swelling reaches either the tail or the junction of thorax and abdomen, the irrigation process is reinitiated, with the pulse now travelling in the opposite direction. Polychaete behaviour in ambient water flow was observed over an 18 h-period (see Figure 3). When exposed, all crowns were actively rotating and tilting from side to side. Withdrawal of the crown into the tube can occur very quickly or comparatively slowly. Specimens, removed from their tubes could be kept alive for a number of weeks while those remaining in their natural tubes survived for an indefinite period. Specimens, within artificial tubes, were first observed to line the glass with a clear secretion that appeared to provide traction for the chaetae and body segments. Particulate matter was added to the mouth of the glass tube, increasing its length and allowing the partial closing of the new tube aperture.

Random colonization was registered for both the tube of *Bispira volutacornis* and the artificial settling surfaces at the study site, and involved several polychaetes, molluscs, barnacles, ascidians, tunicates and algae. Two species were found both within and on the tube, *Pisidia longicornis* (Linnaeus) and *Eupolymnia nebulosa* (Montagu).

DISCUSSION

The structure and organization of the branchial region of *Bispira volutacornis* is typical of the larger sabellids, with the crown's internal skeleton of large vacuolated cells resembling both that of *Sabella pavonina* (Nicol, 1930) and *Sabellastarte magnifica* (Shaw) (Fitzsimons, 1965).

Warner (1971) described sabellids as suspension feeders that use exogenous water movement to augment their own self-produced currents. In flowing water (1 to 3 cm s^{-1}), the apex of the crown in *Bispira volutacornis* is angled downstream, and this orientation of suspension feeding structures is known for a variety of animals (Warner, 1977). The path of natural particles and fluorescent dye streams around a sabellid crown in this orientation shows a downstream eddy into which the pinnules of the radioles project, enhancing particle capture potential (Warner, loc. cit.).

The authors found the gut contents of *B. volutacornis* to contain mainly detritus, benthic diatoms, peridinians, silicoflagellates, foraminiferans, together with annelid and crustacean bristles. Since an examination of gut contents could not be made for up to three hours after the specimens were collected, ingested protozoa, eggs and smaller larvae were by then rendered unidentifiable. While studying the foods of various benthic animals, Hunt (1925) examined the gut contents of *Sabella pavonina* and described the food as finely sorted plankton and detritus.

The average rate of food transport in the gut of *Sabella pavonina*, at 16°C, was 22.8 h for an average length of 234.7 segments (Nicol, 1930). By comparison, the average rate of transport in *Bispira volutacornis*, at 14°C, was 7.7 h for an average length of 97 segments. Since the average segmental width of *Sabella*, which can influence the size of the gut, was not considered, and given the temperature difference of 2°C, one cannot presume that *Sabella* has a faster rate of digestion than *B. volutacornis*.

In the present study the authors interpret the presence of *Pisidia longicornis* within the tube as one of refuge seeking. When *Eupolymnia nebulosa* (Montagu) was located within the tube, the feeding tentacles were not visible from the exterior. Although records show that *E. nebulosa* attaches to primary and secondary substrates (to the inclusion of biogenic materials), the authors could find no mention of any recurrent association with *B. volutacornis* or any other macrobenthic species for that matter. Rather than viewing it as an endoekete, the author sees the association as more of a commensal relationship. Within the *Bispira* tube, *E. nebulosa* would benefit from the irrigation current created by *B. volutacornis*, providing it with a convenient food source. The baffle effect of the branchial crown, precipitating suspended particles, and overspill from active food collection would also render both the internal and external tube surface of *B. volutacornis* highly attractive to an indirect deposit feeder such as *E. nebulosa*.

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