BIOLOGICAL CONTROL OF MARINE SEDIMENT STABILITY BY THE MUSSELS

Mytilus edulis L. AND *Modiolus modiolus* (L.)

Peter Shand B.Sc.

Being a thesis submitted for the degree of Doctor of Philosophy
in the University of Glasgow

April 1987

Department of Zoology,
University of Glasgow.

ACKNOWLEDGEMENTS

I would like to thank Mr. P. S. Meadows for his invaluable supervision and helpful criticism of the work reported in this thesis. I would also like to thank Professors K. Vickerman and R. S. Phillips in whose department the work was carried out.

I would like to thank the practical assistance and help given by the technical staff of the Zoology Department especially Mr. J. Baird, Mrs. E. Denton, Mrs. H. Hendry, Mr. A. McGregor, Mrs. C. McLagan, Mr. W. Orr and Mr. P. Rickus, and the staff at the Ship Testing Tank, Garscube.

I thank my wife Susan and our families for their perseverance and support during the study and all my friends in rooms G02 (Azra, Bobby, Iman, Mark and Mohammed) and G04 (Allan, Andy B., Andy G., Farage, Hadi, Ibrahim, Joe, Pat and Samira) for their contribution to a happy time. I also thank Peter and Jan for their kindness and advice on early 20th Century etchings etc.

TABLE OF CONTENTS

Page

LIST OF TABLES

Section 2

Page

Section 3

LIST OF FIGURES

LIST OF PLATES

GENERAL SUMMARY

Section 1: Scanning electron microscope study of the byssus complex for Mytlius edulis and Modiolus modiolus.

(1) The foot and byssus complex of Mytilus edulis and Modiolus modiolus were prepared for scanning electron microscopy.

(2) The external morphology of the foot and byssus complex of M. edulis was compared to that for Modiolus modiolus. The byssus complex of both species could be clearly divided into three main parts. These were the stem, threads and pad. There were obvious morphological differences between M. edulis and M. modiolus.

Section 2: Collection of animals and experiments with Mytilus edulis and Modiolus modiolus in different experimental sediments.

(1) Part 1. The collection of Mytilus edulis and Modiolus modiolus and sediment for analysis and experiments are described.

(2) The analysis of sediment from Arrochar (M. edulis site) and from Coilessan (M. modiolus site) is reported.

(3) Part 2. The rate of byssus thread production was determined for single Mytilus edulis and Modiolus modiolus in the laboratory.

(4) Animals were placed on sediment taken from the Mytilus site at Arrochar and left for up to 20 days (M. edulis and M. modiolus) or 100 days (M. modiolus only).

(5) The results showed that M. edulis thread production levelled off after about 8 days and that M. modiolus continued to produce threads up to the end of the experiment (100 days). A period of 12 days was chosen for all other experiments.

(6) Part 3. Single animals. Sediment collected from Arrochar was sieved into 7 particle size ranges. These were < 0.25mm, 0.25mm-0.5mm, 0.5mm-1.0mm, 1.0mm-2.0mm, 2.0mm-4.0mm, 4.0mm-8.0mm and 8.0mm-16.0mm. Four animals of each species were added to each

(9b). PART 3. GROUPS OF ANIMALS. Sediment collected from Arrochar was sieved into 5 particle size ranges. These were <0.25mm, 0.25-0.5mm, 0.5-1.0mm, 1.0-2.0mm and 2.0-4.0mm. 30-34 Mytilus edulis and 5 Modiolus modiolus were added to each particle seize range and left for 12 days.

(9c). M. edulis produced more threads in the particle size range 2.0-4.0mm than in the smaller particle size ranges. Animals in the size range 2.0-4.0mm also attached more threads to sediment and fewer threads to other animals than did animals in the smaller particle size ranges.

(9d). M. modiolus attached more threads to sediment of larger particle size ranges than to sediment of relatively smaller particle size ranges. This also applied to the total number of threads/animal.

(9e). M. edulis formed small clumps on the sediment after 1 day. These clumps continued to grow in size until 12 days (the termination of the experiment). Clumping was not related to particle size.

particle size range to determine how particle size affects thread production.

(7) The number of threads/animal, number of threads/stone, length of threads and size of byssus pads were obtained.

(8) M. edulis produced fewer threads in particle size ranges smaller than 2.0-4.0mm. M. modiolus attached more threads to sediment of particle size ranges 0.5-1.0mm, 1.0-2.0mm, 2.0-4.0mm and 4.0-8.0mm than in the particle size ranges <0.25mm, 0.25-0.5mm and 8.0-16.0mm. M. edulis produced fewer threads than M. modiolus in all the particle size ranges with the exceptions 1.0-2.0mm and 8.0-16mm.

(9) Longer byssus threads were produced in the particle size ranges <0.25mm (M. modiolus) and 0.25-0.5mm (both species) than in larger particle size ranges.

(10) Part 4: Field. The number and length of byssus threads, the number and weight of attached stones and the number of threads/stone were determined for M. edulis and M. modiolus collected from the field.

(11) There were differences in the number and the length of threads between animals (both species). M. modiolus attached more threads and longer threads to stones than did M. edulis.

(12) M. modiolus attached threads to a larger proportion of stones >1.0g than did M. edulis.

(13) Part 4: Laboratory experiments. Single animals. A set of 9 different experimental sediments were prepared with stone layers present or absent at different depths. Combinations of up to 4 stone layers were used at the depths 0-1cm (a layer), 3-4cm (b layer), 6-7cm (c layer) and 15-16cm (d layer). Two animals of each species were placed on the sediment surface and left for 12 days.

(14) The number of byssus threads at each depth attached to stones and

to sediment was noted.

(15) M. modiolus attached threads to stones in the a, b and c stone layers. Animals also attached a large number of threads to sediment. M. edulis, with few exceptions, readily attached threads to stones in the a layer, rarely to stones in the b layer and never to stones in the c layer. Very few threads were attached to sediment and only when a stone layer was absent at 0-1cm (a layer).

(16) M. modiolus produced more threads/stone at 6-7cm than at 0-1cm and 3-4cm.

(17) Thread length was not related to the presence or absence of stones at different depths in the sediment. There were differences in thread length within species. In addition, M. modiolus produced longer threads than did M. edulis.

(18) The vertical depth and plan view x and y co-ordinates of byssus pads were obtained for all animals.

(19) Plan, side and end views of thread vectors are shown for several animals.

(20) Field data are compared to data obtained from laboratory experiments.

(21) 2: Laboratory experiments. Groups of animals. A set of 3 different experimental sediments were prepared with stone layers a, b and c present (tank 1), with b and c present (tank 2) and with no stone layers present (tank 3, control).

(22) M. edulis attached more threads to stones (only in tank 1) and to other animals than they did to sediment. Animals in tank 1 (a layer present) attached fewer threads to other animals but more threads/animals than did animals in tanks 2 and 3 (no a layer present). M. modiolus in tank 1 (a stone layer present) produced

more threads than did animals in tanks 2 and 3 (no a layer present).

(23) Groups of M. edulis produced fewer threads than single animals when a stone layer was present at 0-1cm (a layer) and produce more threads than single animals when a stone layer was not present at 0-1cm.

Section 3 : The effects of mussels on sediment stability.

(1) An experimental Sea Water Flume was used to determine whether Mytilus edulis and Modiolus modiolus stabilise sediments.

(2) Experment 1. Single animals. Sediment was wet-sieved into 7 particle size ranges (<0.25mm, 0.25-0.5mm, 0.5-1.0mm, 1.0-2.0mm, 2.0-4.0mm, 4.0-8.0mm and 8.0-16.0mm). Each particle size range was added to one of 7 pneumatic troughs. Single M. edulis or M. modiolus were placed in tanks containing one of the 7 seven particle size ranges at various time intervals and the tanks placed in a 10°C aquarium. Control troughs containing sediment but no animals were also prepared. After 12 days each trough was placed in the flume, and the flume was then filled with sea-water to a depth of 25cm.

(3) The flume pump was switched on and the water current increased until critical erosion velocity was reached. Velocity profiles were obtained for sediment containing a single animal (both species) and control sediment at critical erosion velocity. The water current was increased at 3 minute intervals until the valve controlling water flow was completely open (maximum velocity). A video camera and recorder was used to film erosion around animals and over the sediment. Videos of tanks containing animals were compared to tanks containing no animals (controls).

(4) Experiment 2. Groups of animals. The same experiment was repeated for groups of animals in the 5 smallest particle size ranges

(<0.25mm, 0.25-0.5mm, 0.5-1.0mm, 1.0-2.0mm and 2.0-4.0mm).

(5) Experiments 1 and 2 showed that single animals and groups of both M. edulis and M. modiolus decreased the critical erosion velocity and critical bed shear stress in the three smallest particle size ranges of sediment (<0.25mm, 0.25-0.5mm and 0.5-1.0mm). M. modiolus, because of its size had a more destabilising effect than M. edulis.

(6) The same experiments were performed for groups of animals in 3 sets of tanks containing sediment with stones present or not present at different depths. Each tank contained sediment of particle size range <2.00mm with (i) stone layers a, b and c (0-1cm, 3-4cm and 6-7cm depth, respectively), (ii) stone layers b and or (iii) no stone layers (control).

(7) The experiments confirmed that both species have a destabilising effect on sediment but showed no difference between sediment with stones present at the surface and sediment with no stones present at the surface.

(8) In addition, sediment sorting occurred around animals in the sediment containing stones at different depths. Fine sediment was washed away and coarser sediment was left in grooves at the side of animals and built up behind groups of animals. This was more pronounced for sediment containing M. modiolus than for sediment containing M. edulis.

GENERAL INTRODUCTION

Estuaries can be defined as "semi-enclosed coastal bodies of water having free connection with the open sea and within which the sea water is measurably diluted with freshwater derived from land drainage" (Cameron and Pritchard, 1963; Groves and Hunt, 1980). In terms of chemical and physical fluctuations the estuarine environment is generally more extreme than the open sea or bodies of freshwater. The physico-chemical characteristics of deposits are determined by estuarine circulation and salinity differences and modified by the activity of benthic organisms (Postma, 1967).

Estuaries are often regarded as sediment sinks where sediment entering from rivers is laid down and transported by water currents (Postma, 1967; Guilcher, 1967; Davis, 1983). In brackish water deposition is supported by a process called flocculation. This is the coagulation of clay particles due to changes in the electrolytic potential which is caused by an increase in salinity. The larger particles fall faster than their smaller precursors (Postma, 1967; Mclusky, 1981). After deposition higher current velocities are required to resuspend sediment (Postma, 1967). Water circulation within estuaries depends on the shape of the estuary, the tidal range, vertical mixing between fresh and sea water and the bottom topography (Pritchard, 1967; Bowden, 1967, 1978; Davis, 1983).

Tidal currents are major agents of sediment transport in estuaries (Channon and Hamilton, 1976). Current velocities in estuaries vary between locations, sediment being eroded and deposited in specific areas (Green, 1968). The strong currents prevailing during spring tides will generally bring more material into suspension than neap tide currents (Postma, 1967). In intertidal regions the same area of shore may undergo sediment erosion and deposition at different times of the tidal cycle (Green, 1968). At slack water, fine suspended sediment settles out whereas throughout much of the flood and ebb cycle erosion is dominant over deposition (Davis, 1983). Despite this, estuarine mud flats are generally considered to be depositional environments (Anderson et al, 1981).

The resistance of sediment particles to movement by water currents is determined by the size and weight of particles. The velocity of a water current required to remove and transport a few sediment particles is called the entrainment, threshhold or critical erosion velocity (Briggs, 1977). Critical erosion velocity decreases with a decrease in the size of paricles down to about 0.3-0.6mm then increases again below 0.3mm (Hjulstrom, 1939). Coarser particles are heavier, requiring more lift to dislodge them from the bed. Finer particles tend to form compacted, cohesive beds and are more difficult to resuspend (Postma, 1967).

Many workers have shown that the activity of micro-organisms, plants and benthic and demersal animals modify the physical and chemical nature of marine sediments. These activities include movement into or over the bed, feeding, production of secretions which bind particles and production of faeces (Fagar, 1964; Webb, 1969; Neuman et al, 1970; Winston and Anderson, 1971; Rhoads, 1974). Thus marine organisms have a major influence on sediment stability. The effects of marine organisms on the structure of sediments and on sediment stability will be discussed in a later chapter to avoid repetition. The effects of organisms which produce root systems into the soil/sediment is however very pertinent to the thesis and worth noting at this stage. These include the protection given to soil by terrestial grasses on slopes (Branson and Owen, 1970), marram grass which stabilises sand dunes (Odum, 1959) and sea grasses, which produce a network of root systems into the sediment causing stabilisation (Frostic and McCave, 1979).

The work reported in this thesis is the results of a study to investigate the effects of two species of mussel, Mytilus edulis and Modiolus modiolus on estuarine sediments. I have considered three aspects which are important in a study of this kind. These are:

1. how animals modify the sedimentary environment
2. how the type of sediment affects the animal's behaviour.
3. how the physical presence of animals and/or the animals activities affect the stability of sediment in the surrounding sediment bed.

Several experiments were performed to consider these and the results compared with the existing body of knowledge. These are briefly described in the plan of the thesis at the end of this introduction.

The Clyde Estuary and Study Sites

The geology, hydrography and biology of the Clyde Estuary have been described by Deegan (1974), Collar (1974) and Smyth (1974) respectively. The estuary has two distinct parts which comprise a total area of over 2500km^{-2} contained in a series of glaciated sills; the first is an upper shallow drowned estuary, the second is the lower Firth of Clyde. In terms of water circulation it can generally be described as partially or well mixed. A recent symposium on the environment of the Estuary and Firth of Clyde, has been published by the Royal Society of Edinburgh (Ed. Allen et al, 1986). The publication gives an excellent series of papers on the marine environment of the Clyde Estuary and Firth.

The two study areas are both part of Loch long, a narrow loch about 10.5km in length from where it joins the rest of the estuary to the head of the loch. It is surrounded by hills along most of its

Plate 1. The sample site at Arrochar. The pale spots in the centre of the picture are Mytilus edulis

Plate 2. The sample area at Coilessan. Animals were collected from sediment at 10-15 metres depth (to the right of picture).

length. The first site (Arrochar; National grid reference NS 296 048) is an intertidal area of mud flats at the head of the loch adjacent to the small village of Arrochar (Plate 1). The second site (Coilessan; National Grid reference NS 267 016) is a subtidal site and is about 6km from Arrochar on the west side of the loch (Plate 2).

Description of animals

Mytilus edulis and *Modiolus modiolus* are filter-feeding bivalve molluscs. Both species belong to the Family Mytilidae.

Mytilus edulis

Mytilus edulis (Plate 3) is widely distributed in the boreal regions of the northern hemisphere where it is found most commonly in the mid intertidal region. Animals may also be subtidal in some areas. It is the most conspicuous bivalve on the intertidal shore around Britain. The length of shell is variable but normally grows up to a maximum of about 5cm. The shell is solid, equivalve and pointed at the anterior end (Plate 3). The umbo occurs at the anterior point of the shell.

M. edulis can survive in a wide range of environmental conditions (Seed, 1969). Loosanoff (1942) found that the gill cilia functioned at -1.0^{o}C and Kanwisher (1955) found that animals could survive temperatures as low as -15^{o}C, when 60% of the body may be frozen. *M. edulis* is euryhaline and can occur in nearly freshwater (White, 1937). Animals are found, although much reduced in size, in salinities of 4-5 ‰ in the Gulf of Finland (Segerstrale, 1957).

The reproduction of *M. edulis* has been studied by Chipperfield (1953), Bayne (1965), Seed and Brown (1975), Seed (1976), Pieters *et al* (1978), Lowe *et al* (1982), Sprung (1984), and Bayne *et al* (1978) and Thompson (1984). Animals mature at about 1 year old (Field, 1922; White, 1937; Seed, 1969). The sexes are separate and the gametes are shed into the sea where fertilization occurs.

Plate 3. Mytilus edulis

Plate 4. Modiolus modiolus

The frequency and seasonality of the reproductive cycle in *M. edulis* varies according to geographical distribution (Herlin-Houteville and Lubet, 1975). In Britain, populations living in the north spawn once a year (Spring) whereas populations in the south-west may spawn twice a year, in spring and late summer, due to milder winters and warmer summers (Seed and Brown, 1975; Seed, 1976). Ripening of the gonads takes place within a few weeks of the onset of spawning, generally commencing when the sea temperature rises above 7°C (Chipperfield, 1953).

The normal period for growth to metamorphosis in the plankton is about a month (Seed, 1976). In optimum conditions larval development may be completed in 20 days (Bayne, 1965; Sprung, 1984) but may also be delayed due to low temperatures or restricted food supply (Thorson, 1950; Bayne, 1965; Beaumont and Budd, 1982). In the absence of suitable settlement surfaces pediveligers can delay metamorphosis for up to 6 weeks (Bayne, 1965).

The larvae of *M. edulis* have a period of initial settlement on filamentous substrata and grow to 1-2mm in about 4 weeks (Seed and Brown, 1977). This initial settlement preferentially occurs on substrata such as bryozoans, hydroids and filiform algae (Colman, 1940; Blok and Geelen, 1958; Bayne, 1964; Seed, 1969). It is followed by a second period of dispersion when the animals detach themselves and enter the plankton again. Water currents are an important means of dispersal (Maas Geesteranus, 1942; Verwey, 1952; Rees, 1954; Dare, 1976; Sigurdson *et al*, 1976; Blok and Tan Mass, 1977). This dispersal occurs with the help of simple monofilament threads, distinct in form and function from the attachment threads (Sigurdson *et al*, 1976; Lane *et al*, 1985). The threads are used for suspension in the water column by virtue of the viscous forces acting on the thread. At settlement animals are gregarious and are attracted to adult beds. Niches, crevices and scarred or pitted surfaces are favoured (Blok and Geelen, 1958; Seed, 1969). This attraction is thought to occur by a thigmotactic response (Seed, 1968).

Animals produce byssus threads (thin collagenous threads with an attachment plaque) which they attach to hard substrates to form a firm anchorage. A detailed description of byssus threads is given in Section 1. M. edulis is found on rocky shores attached to rocks and large boulders and on mud flats where they attach to stones present in the sediment. At Arrochar the latter situation occurs. The majority of animals are found in clumps although single animals are not uncommon.

Aspects of the physiology and energetics of Mytilus edulis have been studied by Harger and Landenberger (1970), Widdows and Bayne (1971), Bayne (1975), Bayne et al (1976), Gabbot (1976), Hrs-Brenko (1977), Zurburg et al (1978), Davenport and Davenport (1984) and Gruffyed et al (1984).

Modiolus modiolus

Modiolus modiolus (Plate 4) has a wide distribution in the northern hemisphere where animals occur in rock pools on the lower shore down to depths of about 150 metres (Tebble, 1976; Wilson, 1977). M. modiolus is larger than M. edulis, animals growing up to about 20cm length. The shell is not as pointed at the anterior end as that of M. edulis, the umbo occuring above the anterior end.

In general, subtidal populations of M. modiolus appear to lack any cyclical reproductive activity. There is a slow but almost continuous release of gametes throughout much of the year (Seed and Brown, 1977; Comely, 1978). Small intertidal populations tend to exhibit a much more seasonal cycle (Seed and Brown, 1977). M. modiolus does not appear to become sexually mature until several years old and 40-50mm in length. A strategy of fast growth enhances survival because mortality in M. modiolus, particularly predation from crabs and starfish tends to be most acute in animals smaller than this size (Seed and Brown, 1977).

Larval development of M. modiolus is comparable to that of M. edulis, larvae remaining in the plankton for approximately a month (Schweinitz and Lutz, 1976). They settle out onto the periostracal spines of established M. modiolus and the byssus complex. Animals less than 40mm are seldom found away from animals (Comely, 1978). There is no evidence for a second planktonic dispersal as occurs in M. edulis.

Animals attach byssus threads to rocky substrates such as crevices in cliff faces, and to stones and gravel in sediment. In areas of sediment, animals are found with most of the shell below the sediment surface. At Coi lessan M. modiolus are found singly or in small clumps of 2-3 animals. In some areas they form larger groups (Comely, 1978) or large belts of animals up to 5 miles length and 3-4 miles width (Tebble, 1976).

Plan of thesis

The work reported in this thesis is divided into 3 main sections as follows.

Section 1. The external morphology of byssus threads produced by Mytilus edulis and Modiolus modiolus was studied by scanning electron microscopy.

Section 2. Several laboratory experiments were performed to determine how sediment with stones at different layers and of different particle size ranges affects byssus thread production. These experiments were:

(i) An initial experiment to determine the rate of byssus thread production.

(ii) The response of single animals and groups of animals to different particle size ranges of sediment.

(iii) The response of single animals and groups of animals to experimental sediments (particle size range <2.0cm) with stones present or not present at different depths.

Section 3. Experiments were performed to determine the effects of single animals and groups of animals on sediment stability. All experiments were performed under controlled conditions in an experimental sea water flume. These experiments were:

(i) the effects of single animals on sediment stability in different particle size ranges of sediment.

(ii) the effects of groups of animals on sediment stability in different particle size ranges of sediment.

(iii) the effects of groups of animals on sediment stability in sediment of particle size < 2.0mm, with stones present or not present at different depths.

SECTION 1

THE EXTERNAL MORPHOLOGY OF THE FOOT AND BYSSUS COMPLEX OF THE MUSSELS *Mytilus edulis* AND *Modiolus modiolus*

INTRODUCTION

This section compares the thread morphology of Mytilus edulis and Modiolus modiolus using scanning electron microscopy. These are interpreted in the light of work by other workers. It is prefaced by an introduction which reviews the structure, biochemistry and mechanical properties of byssus threads.

Structure of byssus threads

The production of byssus threads is one of several types of adhesion shown by marine organisms. Barnacles (Walker, 1981; Cook, 1970), oysters (Yonge, 1979), algae (Denny, 1980) and microorganisms (Marshall, 1976) all produce adhesives for attachment to hard substrates in the marine environment.

The detailed morphology of byssus threads has been elucidated for Mytilus galloprovincialis (Bairati and Vitellaro-Zuccarello, 1974a; 1974b; Vitellaro-Zuccarello, 1980) and Mytilus californianus (Tamarin and Keller, 1972; Tamarin et al, 1974; 1976; Tamarin, 1975). A less detailed description of Mytilus edulis is given in Allen et al (1976). These studies show that the byssus complex of the genus Mytilus have a similar morphology. Lane and Nott (1975) have studied the morphology and fine histochemistry of the foot for the pediveliger of Mytilus edulis. I do not know of any other morphological studies for M. edulis or of any for Modiolus modiolus. Biochemical studies have concentrated solely on Mytilus edulis.

Byssus threads form part of what is known as the byssus apparatus. The original function of the byssus apparatus was to secure the post-larva as it underwent metamorphosis to the adult (Yonge, 1962). In the Family Mytilidae and a few other groups this has been retained in the adult form. One point of interest is that post-larval mussels also produce simple monofilament threads distinct in form and function from the adult attachment threads (Lane et al, 1985). These allow the animal to drift in the water column before settling down on a suitable substrate.

The byssus apparatus consists of the root which is embedded in glandular and muscular tissue at the base of the animals foot, the byssus stem which is continuous with the root, and byssus threads. The proximal end of the thread forms a cuff around the distal part of the stem (Brown, 1952; Tamarin and Keller, 1972; Allen et al, 1976; Waite, 1983). Brown (1952) and subsequent authors divide the threads into four sections (figure 1):

(1) a ring of material, the cuff, which encloses the stem.

(2) the proximal region of the thread which comprises about one third of its length. This part of the thread is elastic and has a corrugated surface.

(3) the distal region of the thread which is cylindrical and smooth.

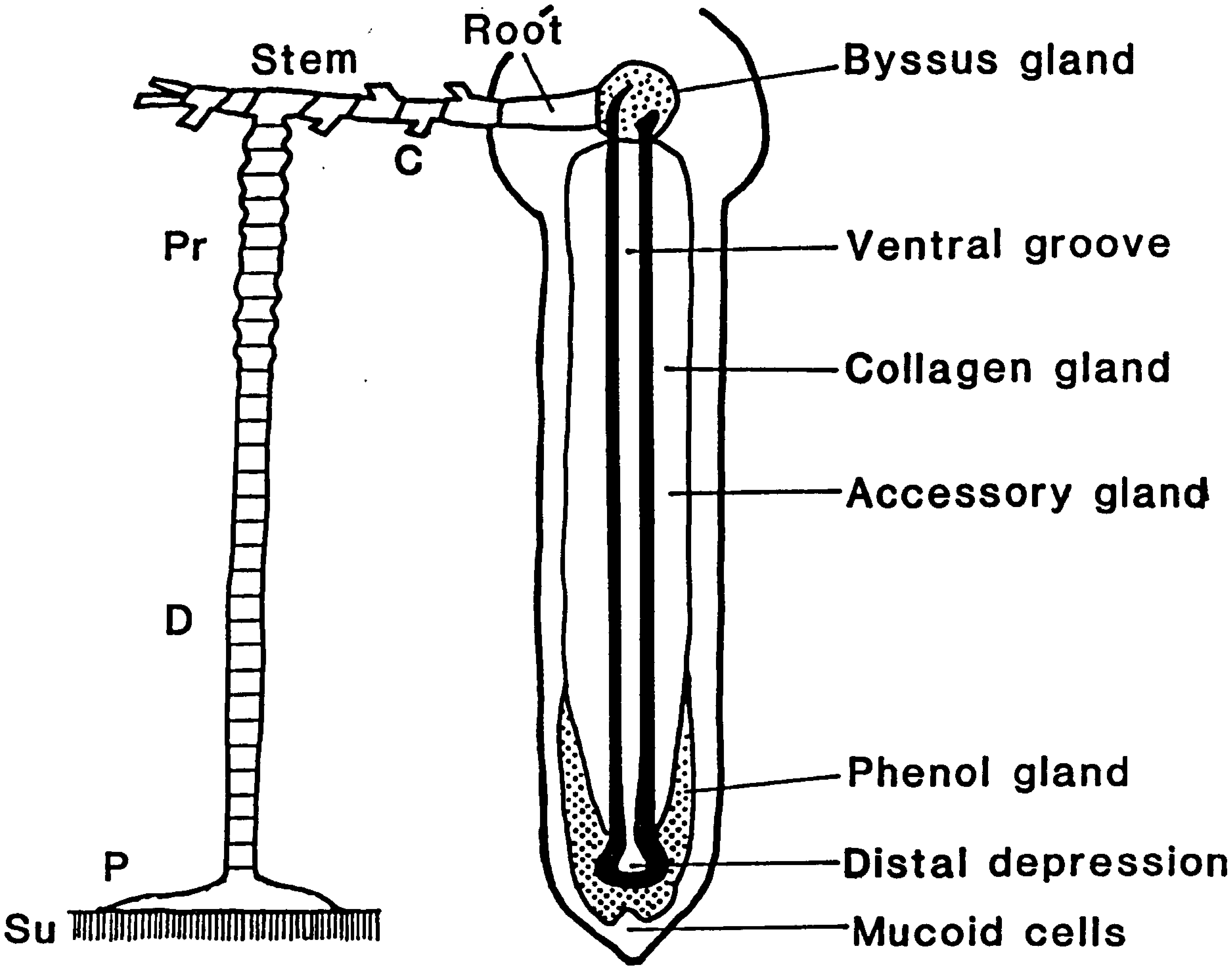
(4) the adhesive pad which is lanceolate in shape.

The ventral part of the animals foot contains a groove which runs almost the complete length terminating in a depression (the pedal or distal depression) at the distal end of the foot (Tamarin et al 1976). It is in this groove and depression that byssus threads are formed (figure 1).

At the base of the foot a complex system of exocrine glands (collectively termed the byssus gland) secretes collagen granules and other electron dense cylindroid granules (Tamarin, 1975). The secretions are mixed and the resultant matrix is propelled outward by the action of cilia. This matrix is the inner core of the byssus stem. The proximal part of threads are attached to the byssus stem by cuffs. The cuffs form the outer part of the byssus stem.

The threads consist of a central core of protein similar to

Figure 1. Diagrammatic view of the byssus secreting glands in the foot (ventral side) and of the byssus complex of *Mytilus*. C = cuff, Pr = proximal, corrugated part of thread, D = distal, smooth part of thread, P = pad and Su = substrate.



BYSSUS THREAD FOOT

collagen and an outer B type protein sheath (Bairati and Vitellaro-Zuccarello, 1974a; Smeathers and Vincent, 1979). The collagen is not as well structured and with less cross-linkages than the tendon collagen from the rat tail (Randall et al, 1952).

There is an interesting history in the study of the glands which produce threads. Brown (1952) suggested that the threads are formed from two secretions, the major central portion of the thread secreted from a gland called the white gland and the outer protein secreted from a gland called the purple gland (now commonly called the accessory gland). In addition she noted that a polyphenol oxidase was produced by tissues in the foot. Smyth (1954) argued that the purple gland produced the protein, and the ventral part of the purple gland (which he termed the enzyme gland) produced polyphenoloxidase. He also regarded the white gland as a developmental stage of the enzyme gland. This hypothesis was later supported by Gerzeli (1961) but Pujol (1967) and subsequent workers have supported and expanded upon the view put forward by Brown (1952), which is described below.

Figure 1 shows a diagrammatic view of the glands which form the byssus complex.

The thread core is produced by cells in the collagen/white gland (Brown, 1952; Mercer, 1952; Fitton-Jackson et al, 1953; Ruddal, 1955; Pujol, 1967; Tamarin and Keller, 1972; Vitellaro-Zuccarello, 1980). The collagen gland cells contain ellipsoid granules which appear to have fully formed collagen molecules (Pujol, 1970; Tamarin and Keller, 1972; Vitellaro Zuccarello, 1980). These are conducted to the groove by cellular processes and through longitudinal ducts to the distal depression. Vitellaro Zuccarello (1980) described a second type of granule present in the collagen gland. He suggests that these are used for the outer stem (cuffs) and proximal thread regions and the former used for the stiffer distal portion of the thread.

An outer sheath of B type protein which covers the inner collagen core is produced by the accessory gland which runs along either side of the ventral groove from the base of the foot to the pedal depression (Allen et al, 1976; Bairati and Vitellaro Zuccarello, 1974a). The cells in this gland contain granules of mottled appearance which are secreted directly into the groove. A substance called phenoloxidase is also produced from the gland (Brown, 1952; Smyth, 1954; Pikkarainen et al, 1968; Engel et al, 1971; Waite and Tanzer, 1981). Phenoloxidase is thought to act on an accessory protein to form a quinone which in turn cross-links with collagen secreted from the collagen gland (Brown, 1952; Pujol,1967; Tamarin et al, 1974). This process of cross-linking is called tanning (Wainright et al, 1976). Tanning takes place in the groove of the foot, which serves as a mould giving the thread its shape.

The protein which forms the pad is produced by a gland deep in the distal region of the foot called the phenol gland. Phenolic granules contain the protein and o-diphenols (Brown, 1952; Ravindranath and Ramalingan, 1972) The protein attaches the distal portion of the thread to the substrate. Mucous cells are located distal to the pedal depression and secrete a substance described as a sulphated polysaccharide (Pujol, 1967). The phenol granules and muco-polysaccharides are mixed and applied to the substrate by paddle shaped cilia (Tamarin et al, 1974, 1976). This application involves penetration of the substance into small indentations on the substrate surface (Bairati and Vitellaro-Zuccarello, 1974). Collagen from the collagen gland via longitudinal ducts forms the third component (Tamarin et al , 1976). The collagenous area of the plaque is continuous with the collagen of the thread. A B protein forms the upper covering of the attachment plaque (Tamarin et al, 1976; Waite, 1983). Tamarin *et al* (1976) argue that the geometry of the disc conforms to the theoretical requirements for efficient adhesion. Byssus threads are normally attached to microbial films and not directly onto the solid substrate (Waite, 1976).

The production of a byssus thread begins with the animal probing its foot on the surrounding substrate (across the surface or into the sediment if present, Engel *et al*). The foot can be extended to about three times its normal length (Cook, 1970). When a suitable substrate is found the animal presses the distal part of its foot firmly against the substrate. The secretion of the thread and adhesive pad can be seen if the animal attaches threads to clear glass. A milky secretion can then be observed in the pedal depression (Cook, 1970, Engel *et al*, 1971). The secretion hardens on contact with sea water. The complete secretion of a thread from finding a suitable substrate to removal of the animals foot may take less than 2 minutes (Cook, 1970). The thread and plaque of *Mytilus* is initially cream-coloured, but with time turns yellow, then brown.

Mechanical properties of byssus threads

The mechanical properties of a wide range of substances, from metals to calcareous shells have been determined by the use of tensile testing (Low, 1949; Wainwright *et al*, 1976). These techniques have been applied to the study of the mechanical properties of byssus threads.

Complete byssus apparatus

The attachment strength of the byssus for animals in the field have been tested by several workers (Glaus, 1967; Allen et. al., 1976; Smeathers and Vincent, 1976; Price 1980; 1981).

Septifer bifurcatus has the greatest attachment strength of a byssus producing bivalve so far tested (90 Newtons/animal, Harger (1970)). *Mytilus californianus* has a greater attachment strength than

Mytilus edulis (60 N and 36 N, respectively; Harger, 1970). The attachment strength of M. edulis varies throughout the year, being greatest in September (24 N) but only half that in May (Price, 1980). This probably accounts for the seemingly large discrepancies in results for different workers. Glaus (1968), found M. edulis had an attachment strength of 10-17 N whereas Harger (1970) found that the same species had an attachment strength of 36 N. The attachment strength of M. edulis also varies with height on the shore (Glaus, 1968).

Single threads

The measurements of length, break load, extension and cross-sectional area of the thread give the following standard mechanical properties:

$$\text{ultimate tensile stress } (\mathrm{N\ m^{-2}}) = \frac{\text{break load}}{\text{cross-sectional area of fracture surface}}$$

$$\text{ultimate tensile strain} = \frac{\text{increase in thread length prior to fracture}}{\text{original length}}$$

$$\text{Young's Modulus } (\mathrm{N\ m^{-2}}) = \frac{\text{ultimate tensile stress}}{\text{ultimate tensile strain}}$$

A high tensile strain means that the thread stretches before it breaks, that is, it has elastic properties. It can be likened to the properties of an elástic band. A low tensile strain means that there is only a small increase in length before breakage. It can be likened to the properties of metallic substances such as steel.

The study of mechanical properties for single threads has been confined to M. edulis (Allen et al, 1976; Smeathers and Vincent, 1979;

Price, 1980). Threads are well suited to absorbing the impact of waves and tides. The break load for whole wet threads is about 0.25 N (Smeathers and Vincent, 1979; Price, 1980). They have an ultimate tensile strain of 0.44N and Youngs Modulus of 8.5×10^7 Nm^{-2} (Smeathers and Vincent, 1976). The break load for whole dry threads is almost twice that of wet threads (0.55N) but the threads are less extendable. The proximal, corrugated portion of the thread is almost twice as extensible as the distal, smooth portion (tensile strain of 1.22 as opposed to 0.66; Smeathers and Vincent, 1979).

Byssus pads

Byssus pads attached to calcareous shells have an average breaking strength of 8×10^5 N m^{-2} and an average breaking strength of 4-5 x 10^5 Nm^{-2} to the periostracum (the proteinaceous cuticle covering the animals shell, Allen _et al_ (1976)). Larger forces are required to remove pads from polar surfaces such as slate and glass than non-polar surfaces such as paraffin wax and PTFE (Young and Crisp, 1982). However the field importance of this work is debatable since byssus pads are rarely if ever attached directly onto the solid substrate. Organic films less than 1um thick form within minutes of surface exposure to seawater (Characklis, 1981) and micro-organisms adhere to these organic films (Marshall, 1976). It is to the organic films that byssus threads are attached.

MATERIALS AND METHODS

I considered whether the procedure outlined below should be put in an appendix because S.E.M. procedures are fairly standard. However, I have decided to keep them in this materials and methods because it is the way I have prepared my specimens and observed them under the S.E.M..

Preparation of specimens

Byssus threads were prepared for Scanning electron microscopy using a standard technique which included fixing in glutaraldeyde, followed by fixing in osmium tetroxide, dehydrating the specimen in a graded series of acetone, critical point drying and gold coating. Glutaraldeyde and Osmium tetroxide are very toxic. They were therefore used in a fume cupboard and gloves were worn at all times. The following procedure was used.

1. Specimens were preserved in a 2.5% solution of glutaraldehyde in sea water for 1 hour.

2. The specimens were then rinsed several times in sea water for a total period of 1 hour.

3. An equal volume of 4% osmium tetroxide solution was added to the buffer. This gave a 2% solution of osmium tetroxide.

4. After a period of 1 hour the osmium tetroxide solution was gradually diluted with copious amounts of distilled water for one hour.

5. Specimens were then dehydrated using a series of acetone solutions of increasing concentrations (30%, 50%, 70%, 90%, 100% and 100% anhydrous). The specimens were given 10 minutes in each concentration.

6. Complete dehydration was achieved by critical point drying. Specimens were transferred to metal baskets, ensuring that the

specimens remained immersed in the anhydrous acetone. The metal baskets were placed inside the Critical Point Dryer and the chamber door sealed. The inlet valve was opened and the chamber filled with liquid carbon dioxide (CO_2). The CO_2 was re-flushed every 15 minutes for 1 hour. The chamber, filled with liquid CO_2 was heated to a pressure of 1200 lb/m^2 and a temperature of about 31^{o}C. This is the pressure and temperature (the critical point) at which carbon dioxide changes from a liquid to a gas. After 5 minutes the carbon dioxide gas was slowly vented from the chamber. Rapid venting could allow some gas to go back to liquid phase due to the local cooling effect produced by expansion of the gas. Ventilation time was therefore always in excess of 10 minutes. The baskets containing specimens were removed from the critical point drying apparatus after the pressure had returned to zero (1 atmosphere).

7. Aluminium stubs were covered with double-sided sellotape, leaving a margin around the edge. One to three specimens were mounted on each stub. These specimens were either byssus threads, stones with pads attached or the foot of an animal. Silver paint was applied to the margins of the stubs. The stubs were then gold coated as follows.

(a) they were placed in the gold coating machine.

(b) the argon cylinder was was opened to read 4 p.s.i. on the cylinder scale.

(c) the Operation switch was set to pump and the chamber was evacuated until the pirani gauge read 0.07 Tor.

(d) the leak valve was rotated one revolution anti-clockwise to introduce a small amount of argon gas. The pirani gauge dropped as gas was introduced. The pump automatically evacuated the chamber and when a reading of 0.07 Tor was reached the procedure was repeated.

(e) The H.T. position was selected on the Operation switch and the control (H.T.) rotated until the pointer indicated 1.2KV.

(f) The Operation switch was set to timer and an interval time of 2 minutes selected. The leak valve was rotated to read 40 amps on the current meter.

(g) at the end of 2 minutes the leak valve was turned to zero in a clockwise direction, the H.T. control switched to zero, the operation switch set to the off position and the argon gas supply at the cylinder switched off.

(h) air was admitted to the chamber by slowly lifting the air admittance valve on the top plate of the chamber. The stubs were then placed in the SEM for further study or stored.

SEM Procedure

Specimen insertion and removal

Specimen insertions and removals were carried out using the following procedure.

(a) the X-position and Y-position controls of the specimen carrier were set at 7, the tilt set to 33^{o} and the lever locked at this position.

(b) the MAGNIFICATION control was turned fully clockwise to the lowest magnification, the SED control switched off and the GAIN and BLACK levels were set to zero. The H.T was switched off by depressing the button to extinguish its light. Thirty seconds was allowed for filament cooling and then air was admitted by pressing the vacuum system AIR and OFF buttons in quick succession.

(c) after the noise of air entering had ceased the stage was pulled out using the two handles on the front of the stage.

(d) an Allen key was used to release the five specimen carrier.

(e) the five-specimen carrier was removed.

(f) the stubs were inserted into the holder and clamped using an Allen key. The stage was pushed back into the chamber ensuring a good seating of the sealing ring.

(g) the AIR and ON buttons of the vacuum system were pressed in close succession to evacuate the chamber to a working vacuum. When this is reached the H.V light extinguished.

(h) The stage was tilted to 10^{o} and locked in this position. An image of the specimen was obtained by following the general operating procedure described below.

General Operating Procedure

(a) The H.T button was switched to ON (button illuminates);

(b) the SPECIMEN POSITION control was switched to 3 and the DETECTOR to 2;

(c) the KV was switched to position 3 and the NUMBER OF LINES was switched to 250 lines;

(d) the 3X range was selected on the SED control;

(e) an image was obtained on the viewing monitor by increasing the GAIN and BLACK levels when the LINE TIME was switched to the IT position;

(f) specimens were examined at different magnifications and certain areas were selected for photography.

Photography

(a) After selecting an area of interest at an appropriate magnification and spot size the vacuum system was checked to ensure that the automatic vacuum system would not trigger. If the needle on the PVB meter approached 40 the ON button of the vacuum system was pressed. No further action was taken until the pump had ceased.

(b) the LINE NUMBER was set at 250 lines and the SCAN MODE button was pressed.

(c) the LINE TIME was switched to 1 msec and the image was focussed at one step higher magnification than desired for the photograph;

(d) astigmatism was corrected by moving the two SHIFT controls on the scan generator. The image was sharpened with one control and then with the other.

(e) the magnification was turned down one step and the line time set to the IT position.

(f) the SCAN MODE was switched back to FULL FRAME.

(g) 16 msecs was chosen on the LINE TIME control and 1000 lines on the scan generator. The signal profile on the videoscope was changed by altering the GAIN and BLACK levels. The signal ideally lies mid-way between the lines labelled "white" and "black" on the videoscreen;

(h) the 1X image button was pressed followed by the EXP button, to expose the film.

(i) at the end of the scan (1 minute) the EXP button went out automatically. The 1X button was released and the film then advanced.

(j) after obtaining the desired exposures the instructions for 'Specimen Insertion and Removal" were followed and the chamber left under vacuum.

RESULTS

Mytilus edulis

Scanning electron micrographs of the foot and the byssus apparatus are shown in Plates 5 to 12.

The foot is cylindrical in shape along most of its length and pointed at the tip (Plate 5). It has a corrugated surface. The groove in which threads are formed starts at the base of the foot and ends in a depression, the pedal depression, near the tip of the foot. The stem appears from an opening at the base of the foot (Plate 5). Threads are attached to the stem by cuffs (Plate 6). These cuffs have a smooth surface and are wrapped around the stem. Each new cuff partly overlaps the previous one.

Byssus threads are clearly divided into two parts. The proximal portion of the thread is flattened in shape and has a corrugated surface of variable morphology (Plates 7-8). Threads may show large corrugations over the whole surface (Plate 7) or small corrugations at the edge with larger corrugations in the centre of the thread (Plate 8). The distal portion of the thread is smoother and cylindrical in shape (Plate 9). The dorsal part of the distal portion is convex and the ventral part is slightly concave, although the latter is sometimes difficult to see. The surface has shallow longitudinal furrows. Threads become thinner towards the byssus pad. A torn thread is shown in Plate 10. The thread can be seen to consist of an inner rod-shaped core and an outer sheath which splits into strands when torn. The thread becomes laterally flattened as it joins the byssus pad.

The byssus pad is flattened and lanceolate in shape (Plates 11-12). It is thickest where the thread is connected and becomes thinner towards it's edges. The thread axis forms a sharp angle with the disc plane. In many threads a thin sail-like structure is formed on the dorsal side at the most distal part of the thread and along the

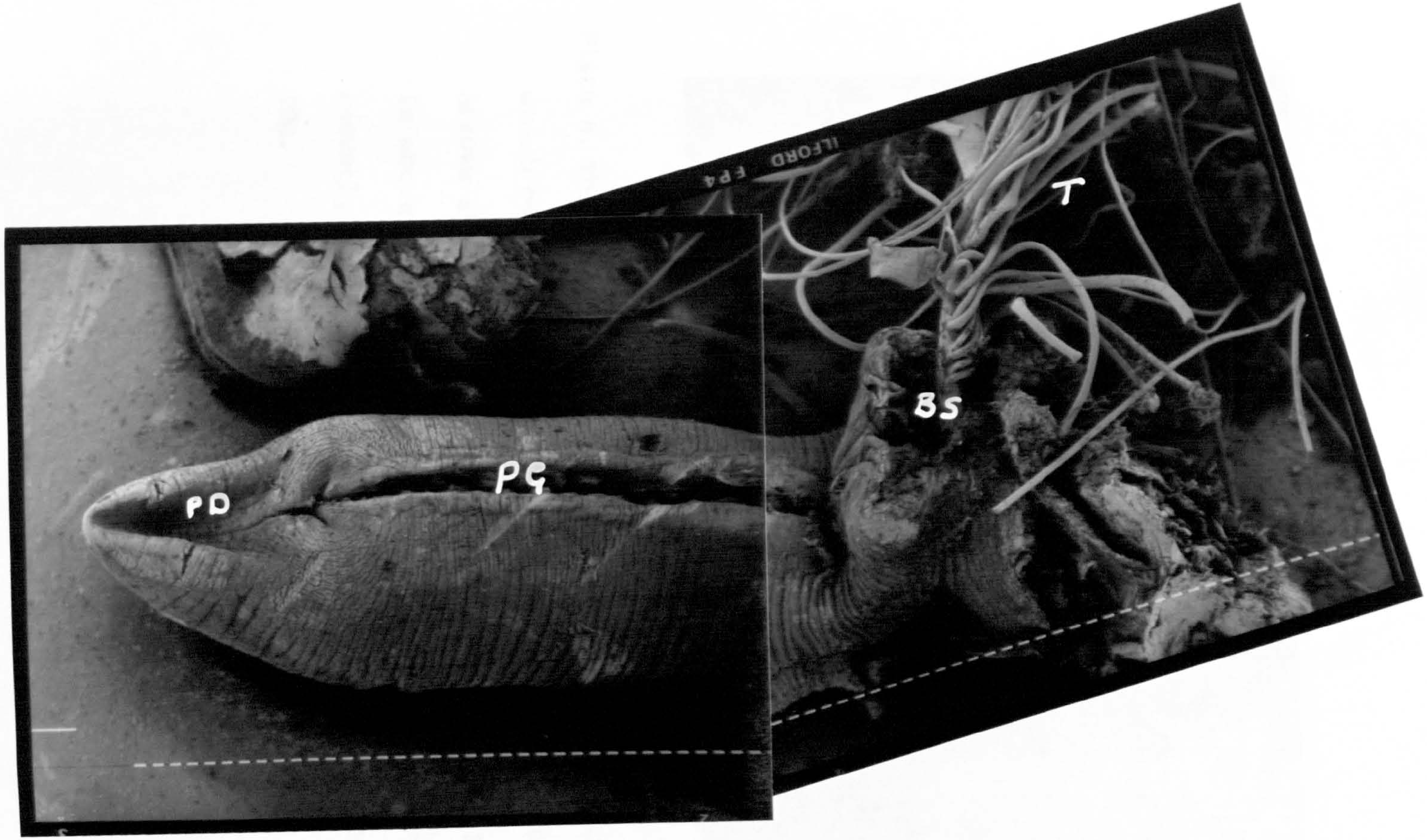


Plate 5. The foot and byssus stem of <u>Mytilus edulis</u> (x 20). PD = pedal depression, PG = pedal groove,BS= byssus stem and T = threads.Scale bars represent 100μ.

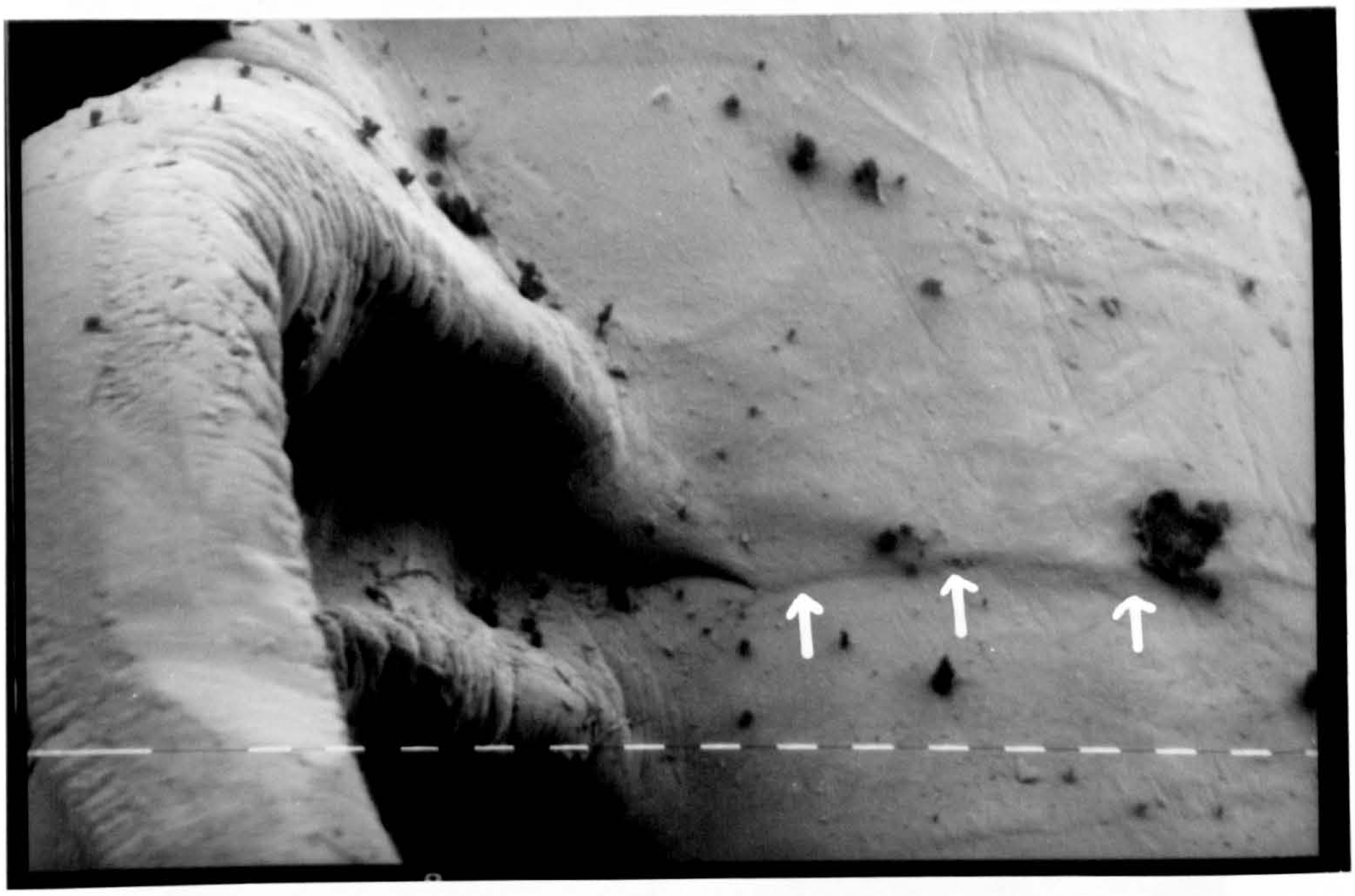


Plate 6. The byssus stem of Mytilus edulis showing two of the cuffs which overlap the central core of the stem and threads (x 440). Arrows show where the cuffs overlap. The proximal part of the stem is above the picture and the upper thread represents the most recently produced of the two threads shown. Scale bars represent 10μ.

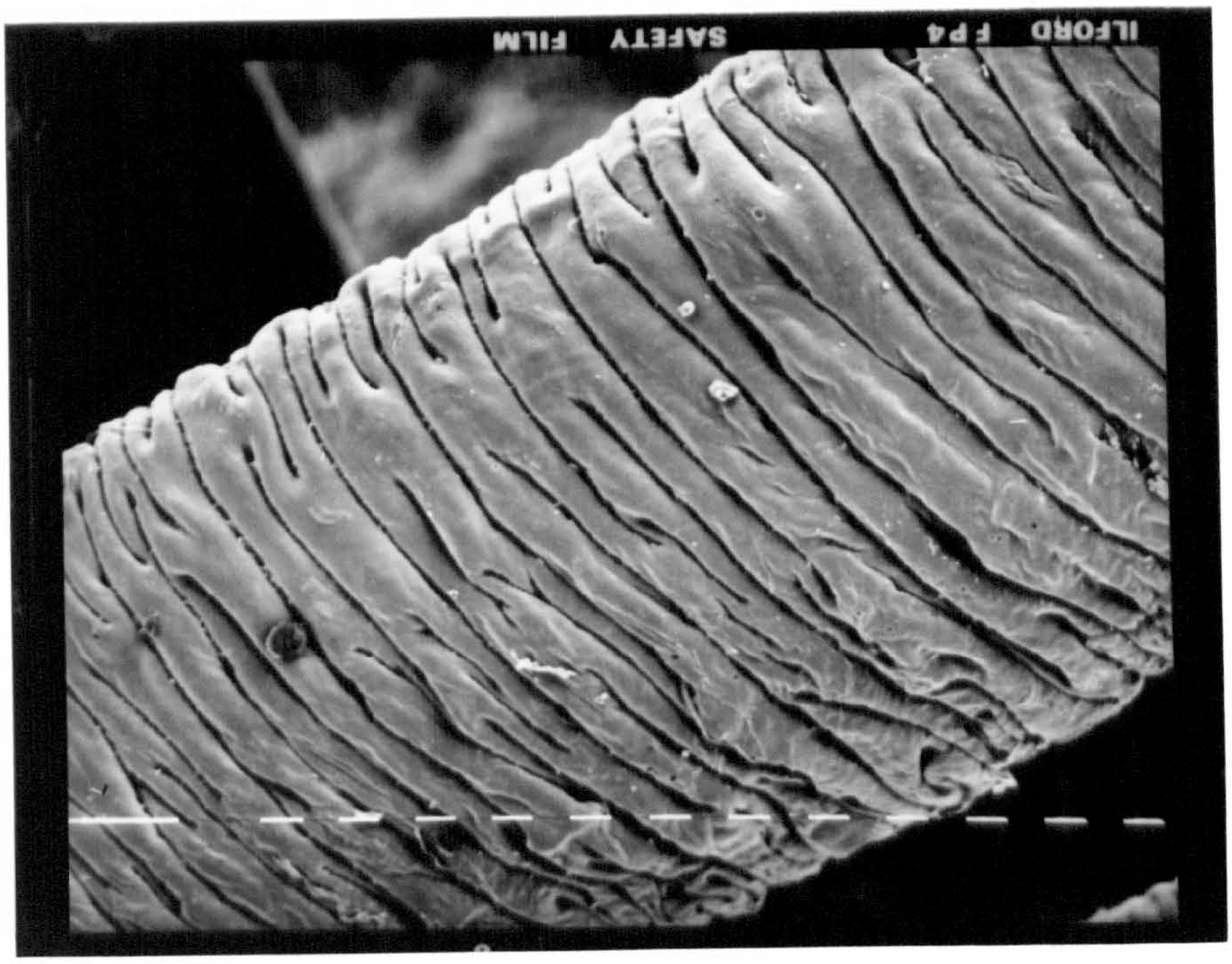


Plate 7. Mytilus edulis. The proximal corrugated part of the thread (x 115). Scale bars represent 10μ.

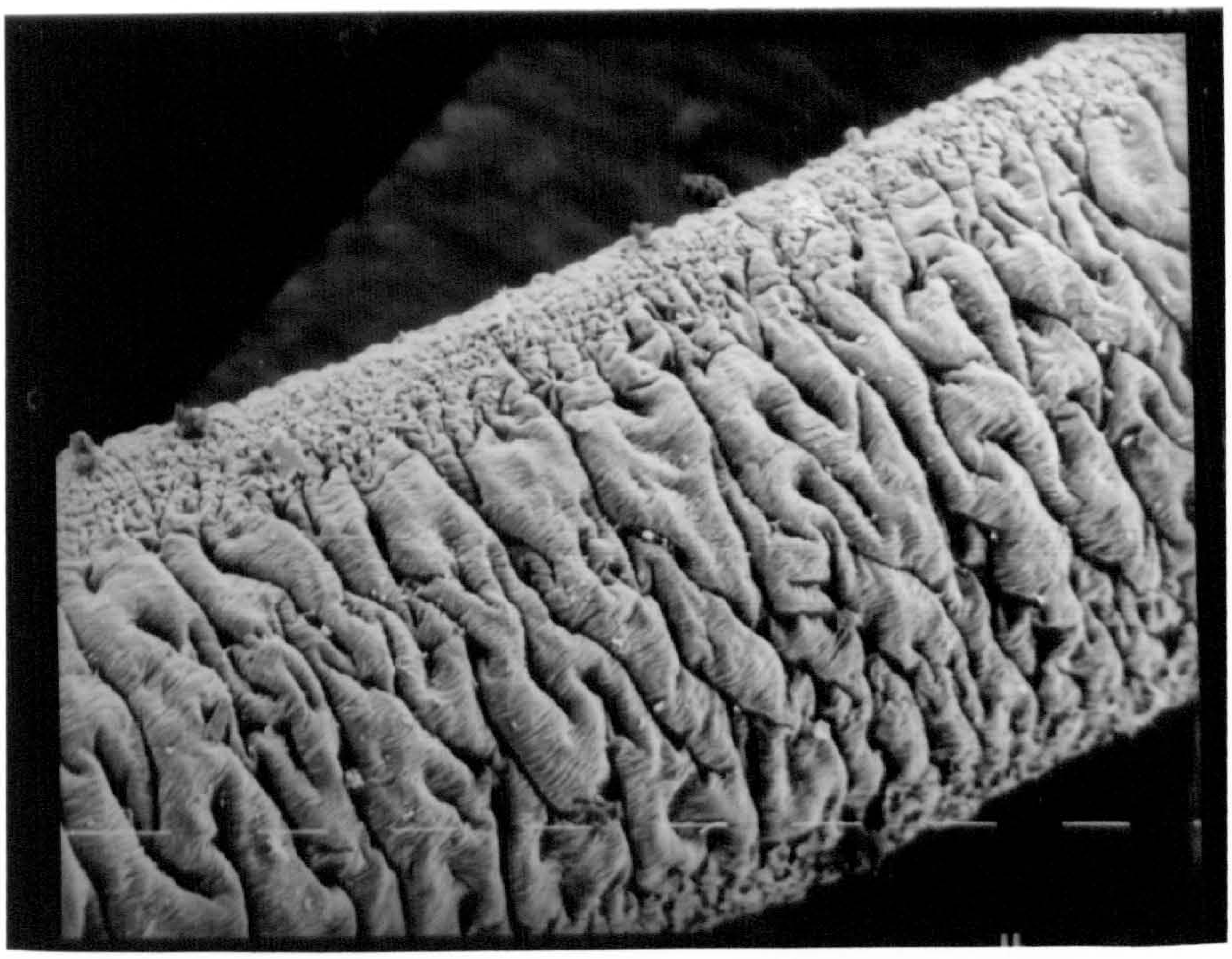


Plate 8. Mytilus edulis. The proximal corrugated part of the thread (x 730). Scale bars represent 10μ.

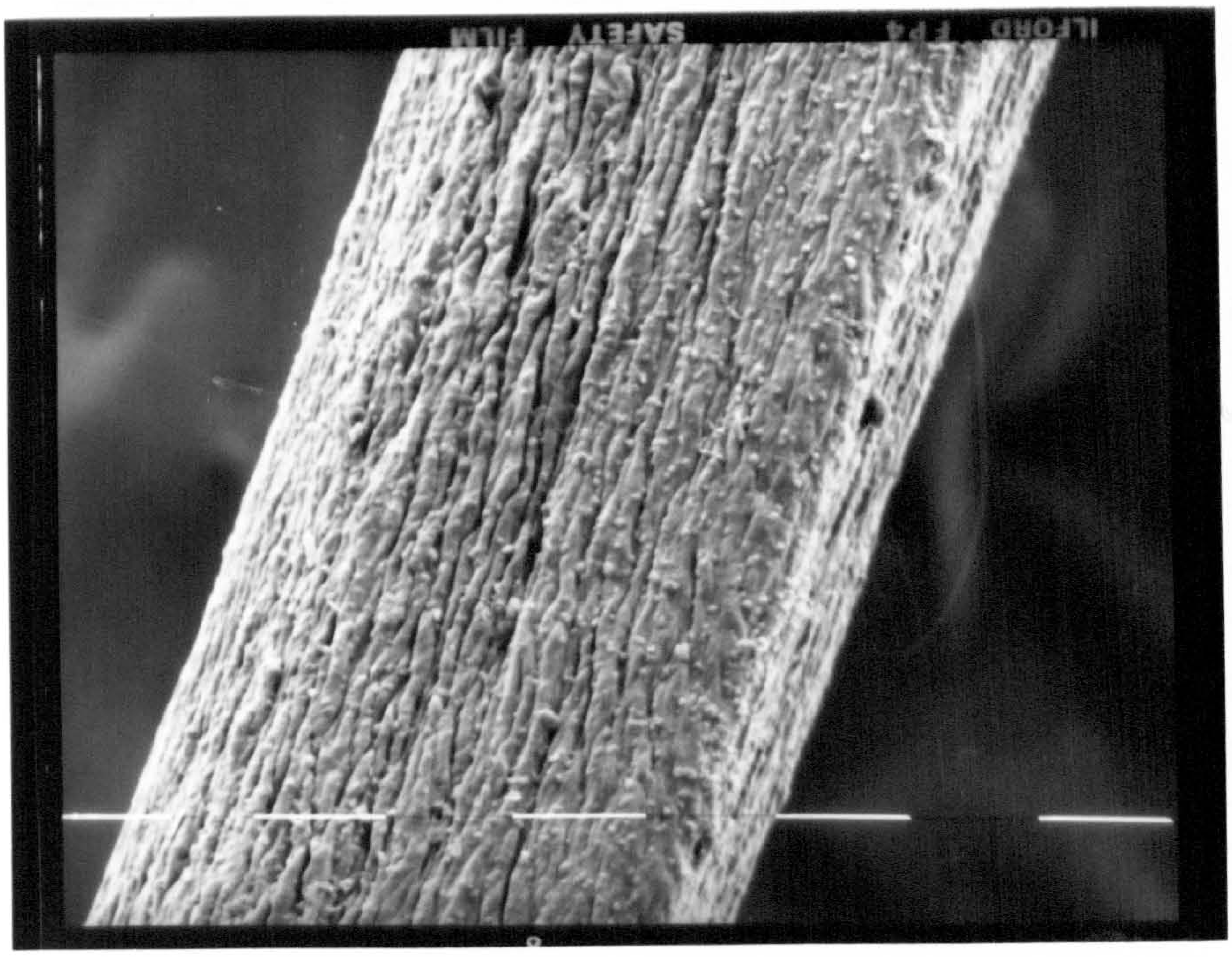


Plate 9. Mytilus edulis. The distal smooth part of the thread (x 1400). Scale bars represent 10µ.

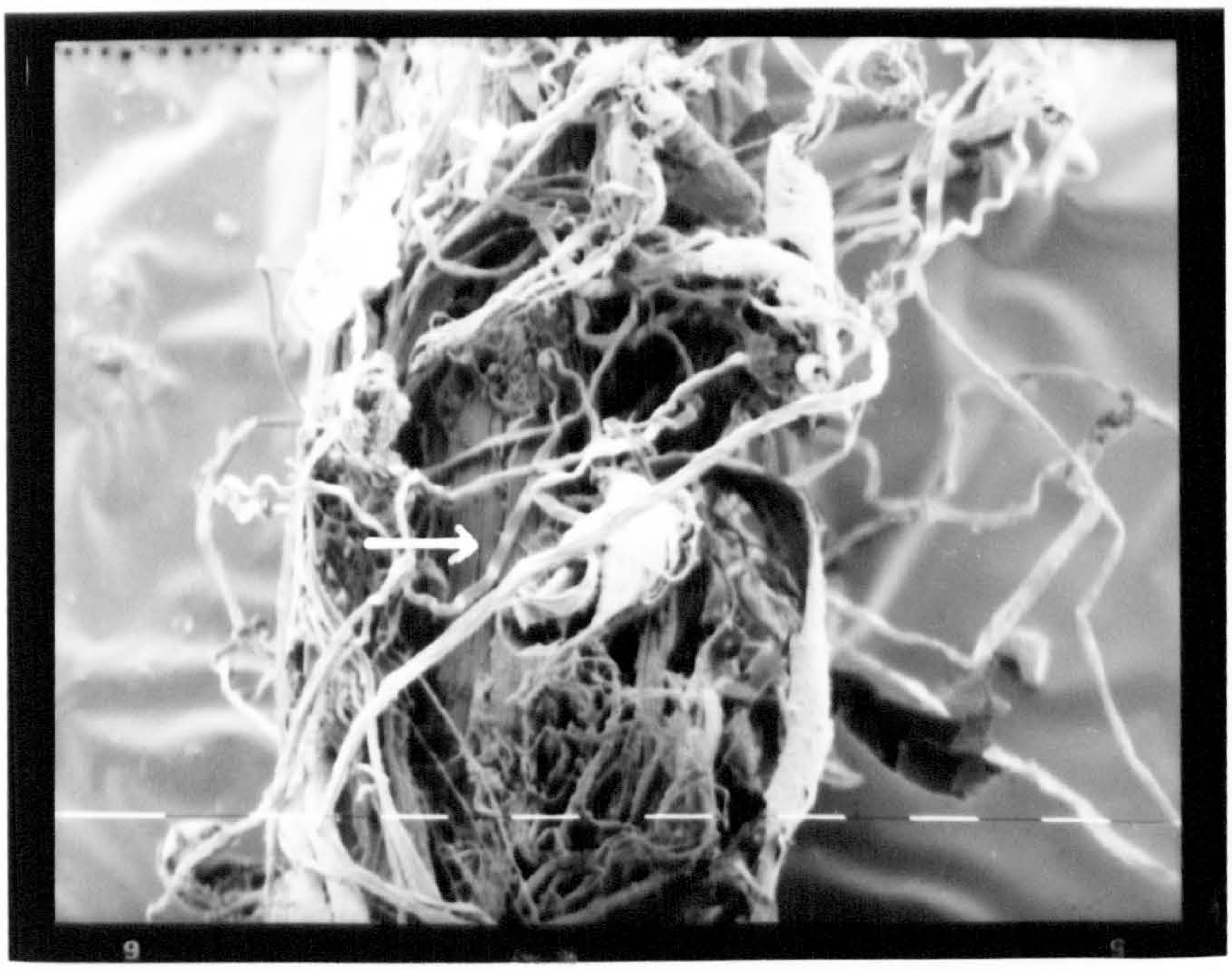


Plate 10. Mytilus edulis. Torn area part of distal part of the byssus thread (x 730). The central core of the thread is arrowed. Scale bars represent 10µ.

Plate 11. Byssus pad of Mytilus edulis attached to stone (x 28). Scale bar below plate represents 500µ.

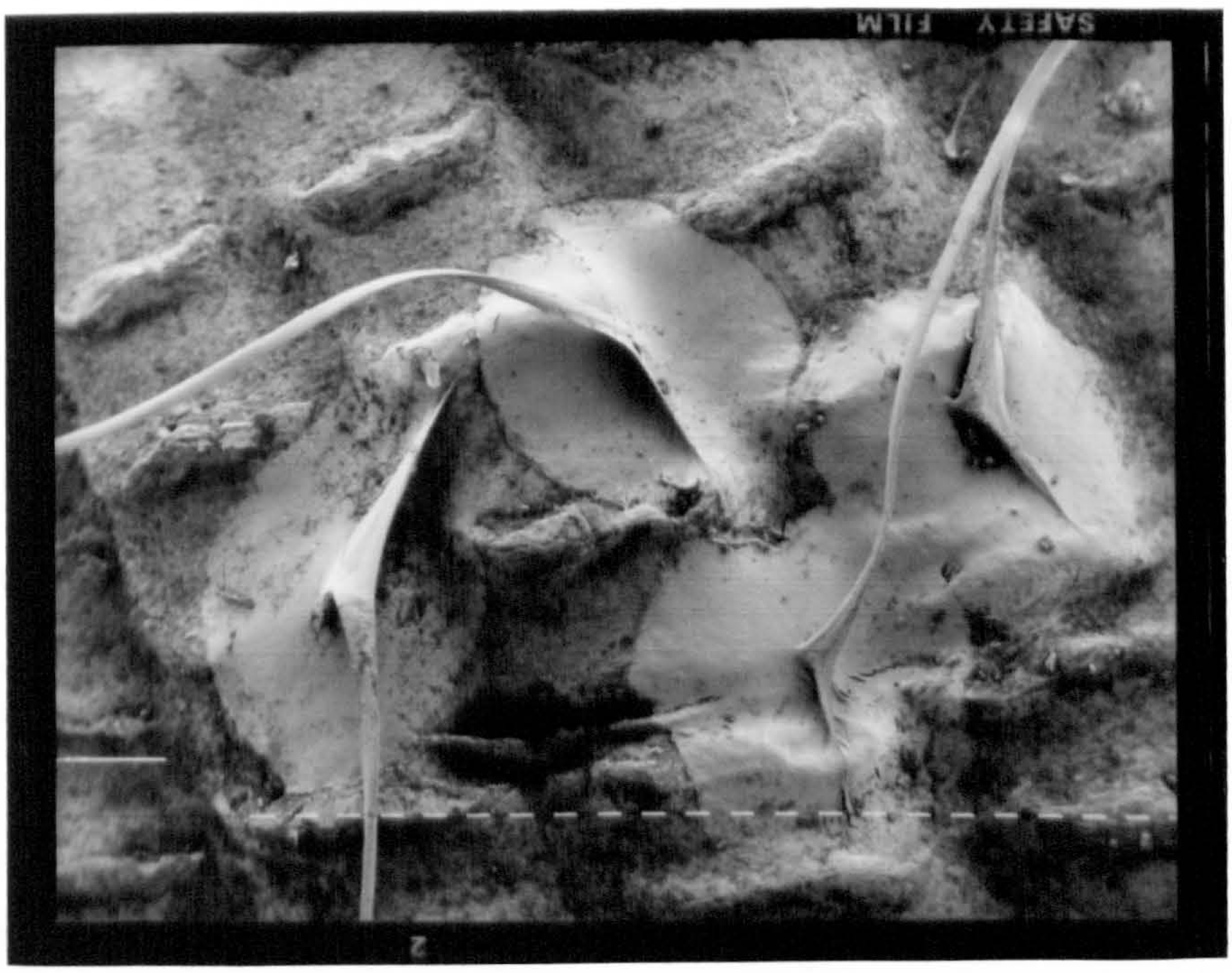


Plate 12. Four byssus pads of Mytilus edulis attached to the shell of a dead cockle Cerastoderma edule (x 23). Scale bars represent 100µ.

central axis of the pad to its tip (Plate 11). The angle between the ventral part of the thread and the pad is very sharp. In contrast, the angle between the dorsal part of the thread and the pad is shallow. The sail-like structure in other threads may be reduced to a thin line (Plate 12).

Modiolus modiolus

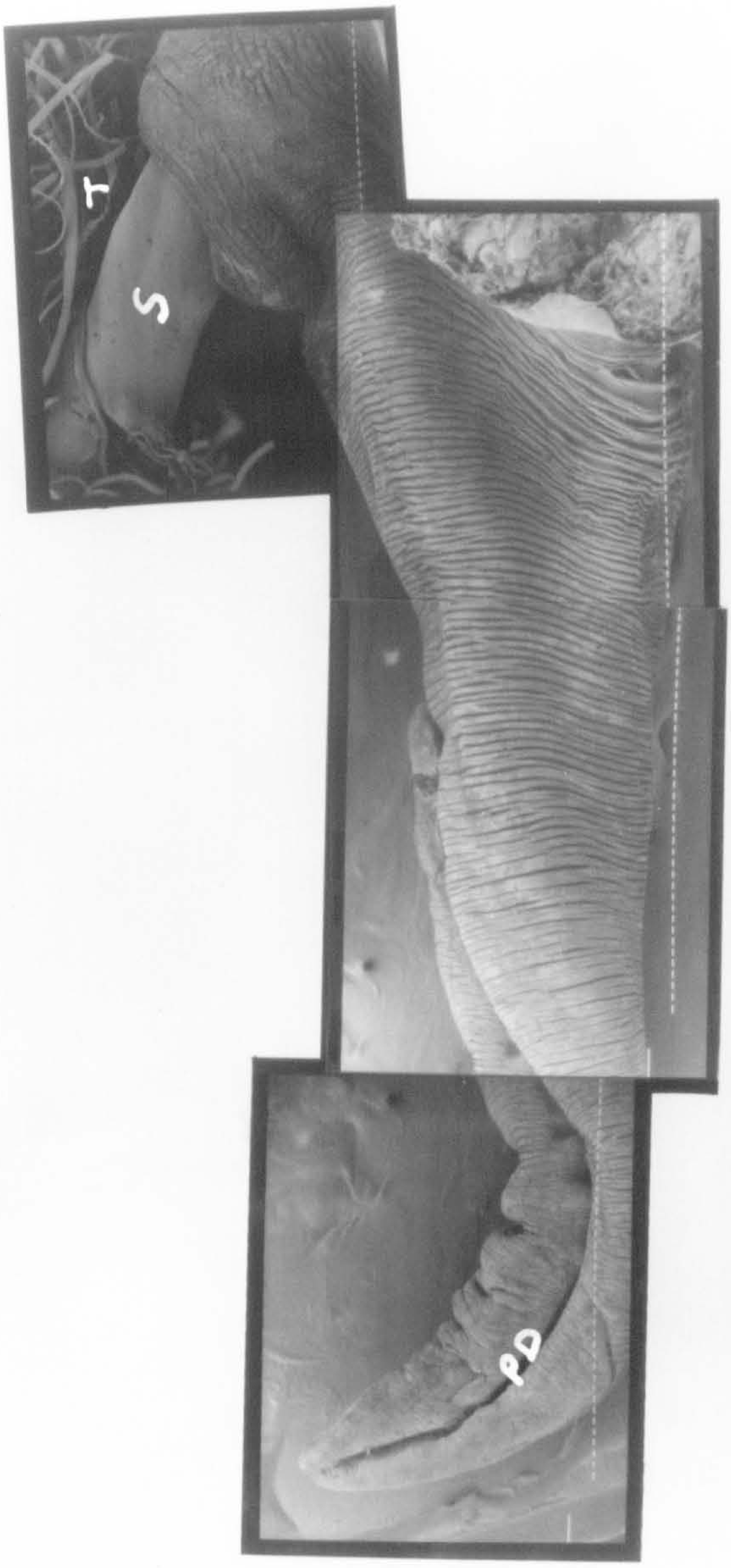
Scanning electron micrographs of the foot and the byssus apparatus are shown in Plates 13-19.

The foot of Modiolus modiolus (Plate 13) is, as would be expected, larger than the foot of M. edulis. It is cylindrical in shape, gradually becoming thinner and is pointed at the tip. The groove in which the threads are formed starts at the base of the foot and continues to the tip. There is no obvious pedal depression. The surface of the foot has a very corrugated structure. This is very pronounced at the base of the foot but less so at the end.

The byssus stem appears from a bulbous opening at the base of the foot (Plate 13). It has a very smooth surface. Several threads can be seen attached to the stem in Plates 13 and 14. The cuffs are much narrower as they become the proximal part of the threads. The most recent cuffs are formed near the proximal part of the stem. These almost completely overlie the older ones. In this way many threads protrude from a small area of stem. Approximately equal numbers of threads come from opposite sides of the stem.

The proximal part of the thread is flattened in shape (Plates 15-16). It has a corrugated surface which is very variable. The centre of the dorsal side may have a central ridge along parts of its length. The distal part of the thread is cylindrical on its dorsal side and slightly concave on its ventral side and has a smooth surface (Plate 17). Unlike the distal part of M. edulis threads, the surface does not have longitudinal furrows.

Plate 13. The foot and byssus stem of *Modiolus modiolus* (x 5). PD = pedal groove,
S = stem and T = threads. Scale bars represents 100μ.


T
S
PD

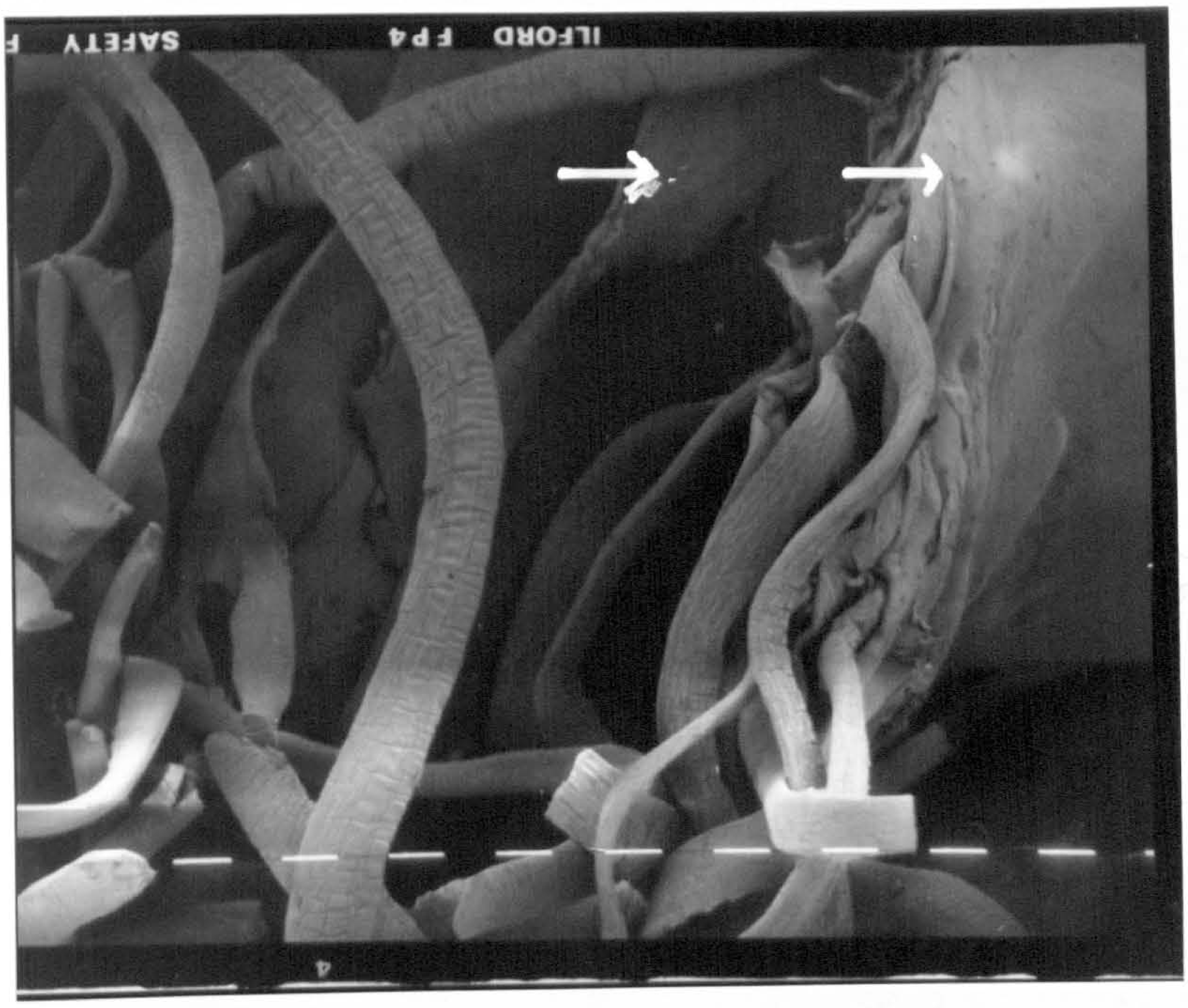


Plate 14. The byssus stem of Modiolus modiolus showing cuffs (arrowed) and threads (x 65). The proximal part of the stem is to the right of the picture. Scale bars represent 100μ.

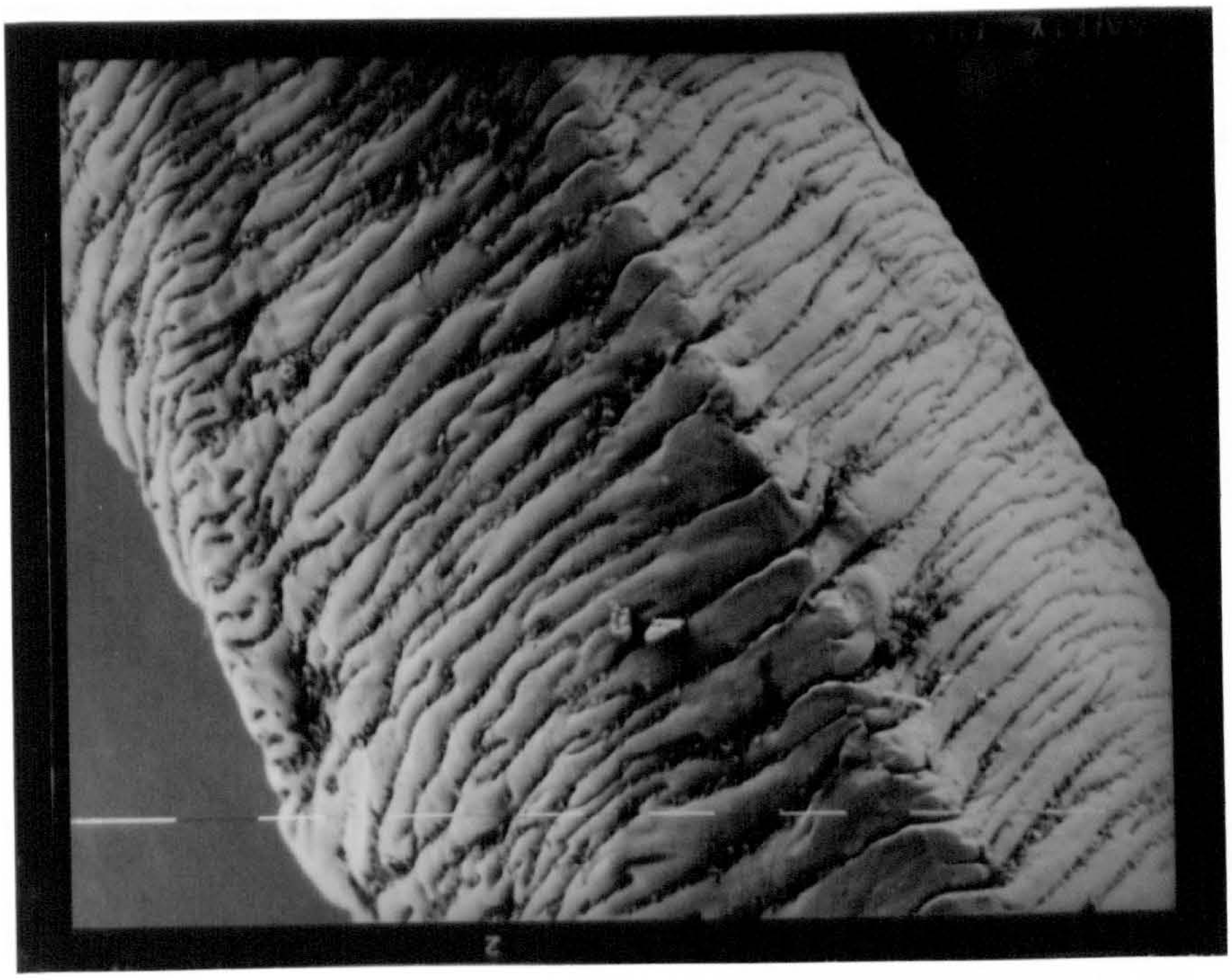


Plate 15. Modiolus modiolus. Proximal corrugated part of the thread (x 730). Scale bars represent 10μ.

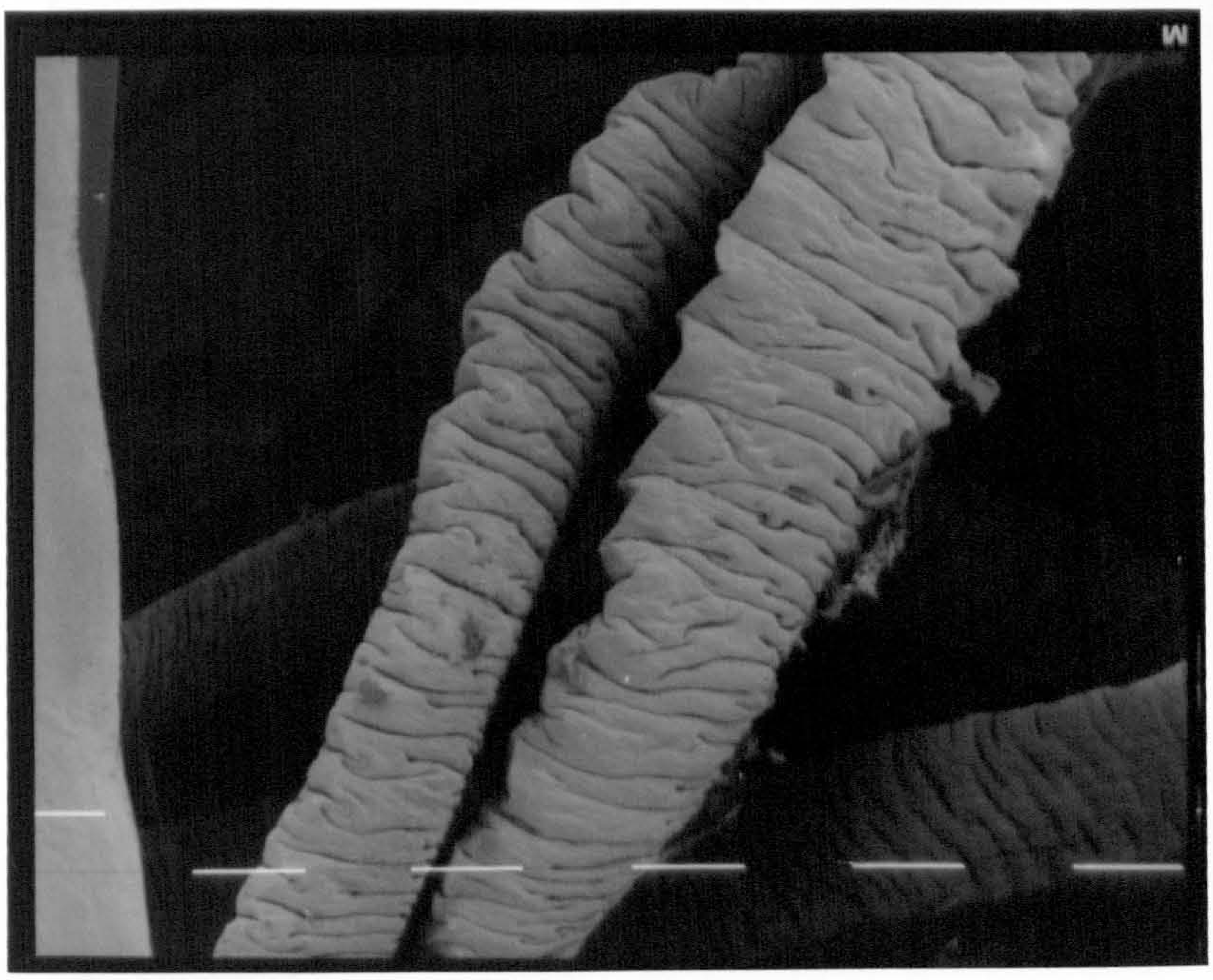


Plate 16. Modiolus modiolus. Proximal corrugated part of threads (x 115). Scale bars represent 10μ.

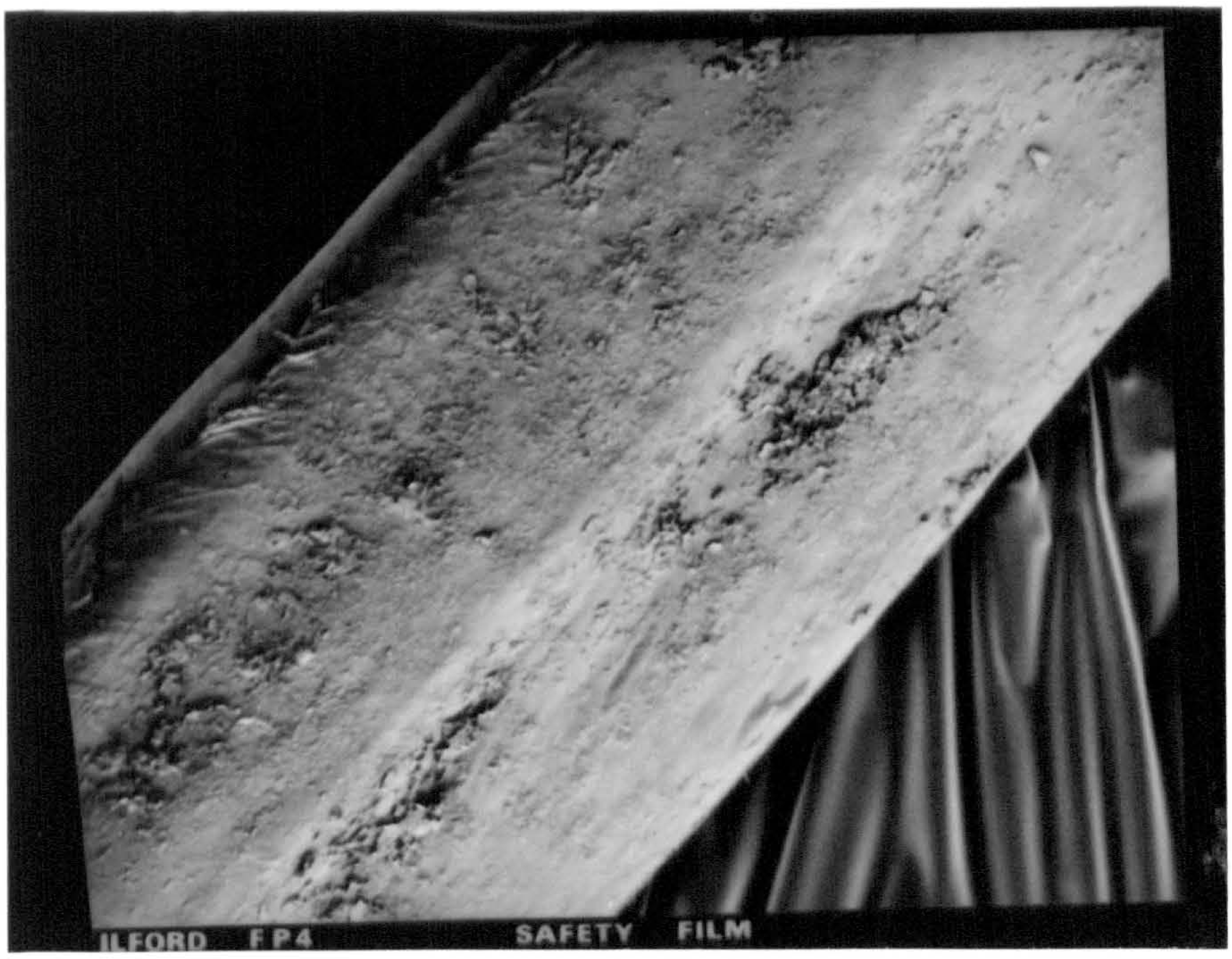


Plate 17. Modiolus modiolus. Distal smooth part of the thread (x 730). Scale bar below plate represents 50μ.

Plate 18. Byssus pads of Modiolus modiolus (x 28). Scale bars represent 100μ.

Pads are very variable in shape (Plates 18-20). They are not as flattened as the pads of M. edulis. They may also be triangular or long and thin (Plates 19-20), particularly when attached to small particles.

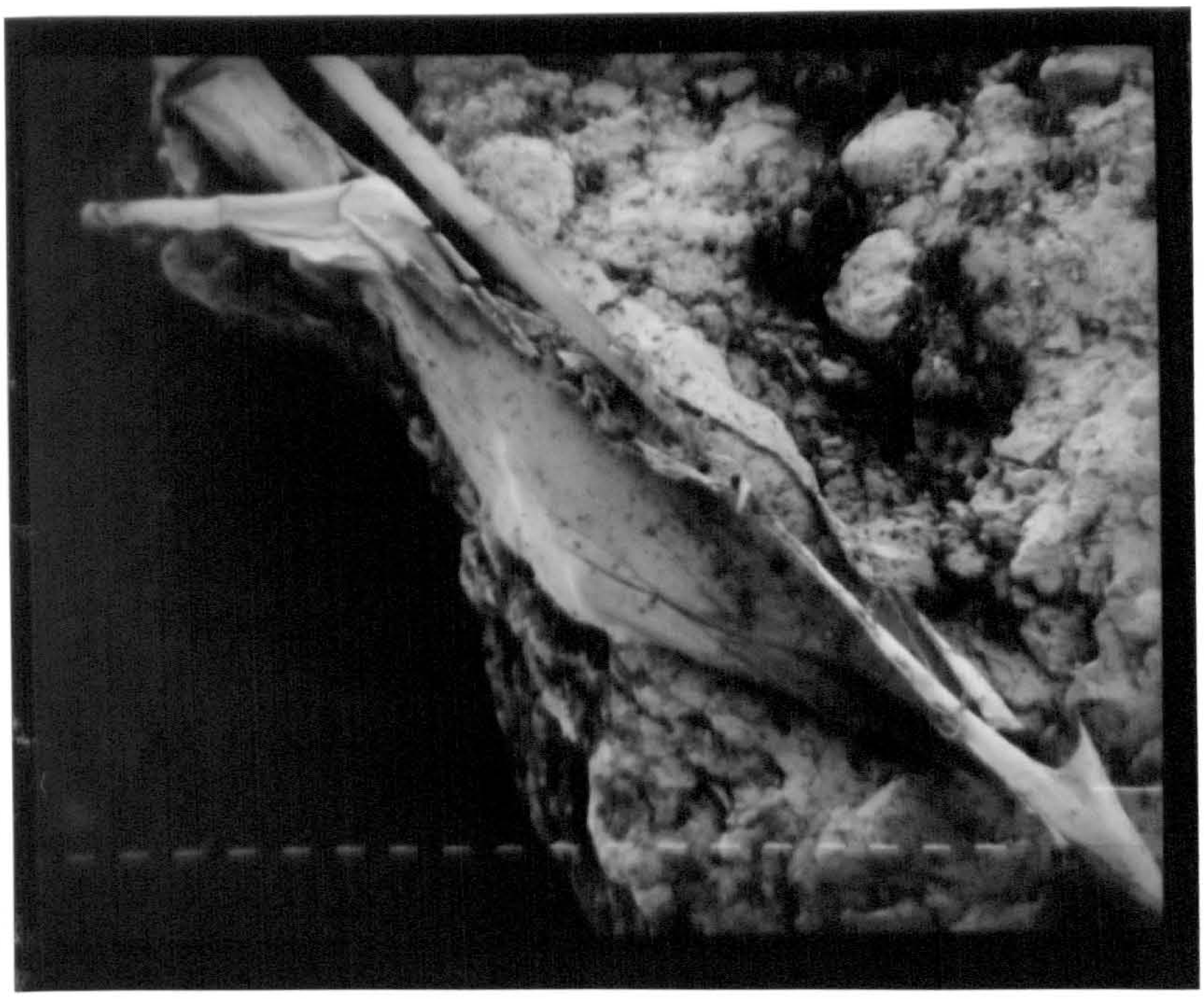


Plate 19. Byssus pad of <u>Modiolus</u> <u>modiolus</u> attached to side of stone (x 28). Scale bars represent 100µ.

Plate 20. Byssus pads of <u>Modiolus</u> <u>modiolus</u> attached to sediment particles (x 45). Scale bar below plate represents 500µ.

DISCUSSION

The only mussel species whose byssus complexes appear to have been studied by SEM methods are *Mytilus galloprovincialis* (Bairati and Vitellaro-Zuccarello, 1974a, 1974b; Vitellaro-Zuccarello, 1980), *Mytilus californianus* (Tamarin, 1975; Tamarin and Keller, 1972; Tamarin *et al*, 1974, 1976) and *Mytilus edulis* (Smeathers and Vincent, 1979). The papers by Bairati and Vitellaro Zuccarello and by Tamarin and his colleagues are detailed descriptions of the byssus complex for *M. galloprovincialis* and *M. californianus* respectively, but the paper by Smeathers and Vincent (1979) on *M. edulis* only shows the corrugated part of a single thread. I shall describe current knowledge of the byssus complex for *M. galloprovincialis* and *M. californianus* and then relate these to the structure of *Mytilus edulis* and *Modiolus modiolus*.

Mytilus galloprovincialis

The byssus stem is decribed by Bairati and Vitellaro-Zuccarello (1974b). It consisted of an inner laminated core which grows from the byssus gland. This continual growth ensures that the mussel is capable of forming new threads from the stem. The core is remarkably stretch resistant. The thread cuffs form the outer layers of the stem. These are rigid and ensure the threads firm connection to the inner part of the stem. The cuffs extend toward the root, sinking into the centre portion and eventually merge with the inner stem. They are thickest next to their own threads and thin out as they extend round the stem. The stem, therefore, consists of two structures: 1. a central cylindrical portion and 2. thread-connecting cuffs which enfold the central core and from which the threads extend.

The byssus threads are described by Bairati and Vitellaro-Zuccarello (1974a, 1974b). They state that the proximal portion of the thread duplicates the shape of the longitudinal groove of the foot and put forward the suggestion that the surface folds are due to two effects. The first is the pressure exerted as the muscles retract and the second is that when the thread material is pressed in a fluid state, it is moulded to the irregularities of the surface walls of the groove.

Threads consist of an inner rod shaped structure covered by an outer sheath. The proximal portion of the thread is corrugated. The corrugations disappear when the thread is pulled, but recover their shape as soon as pressure is released (Bairati and Vitellaro-Zuccarello, 1974b). It is unclear why there is a corrugated arrangement of the outer layers and a linear arrangement of the inner ones (Bairati and Vitellaro-Zuccarello, 1974b). One suggestion is that the inner core is resilient and causes the corrugated arrangement to retract after being pulled.

The smooth distal portion of threads are more rigid. Bairati and Vitellaro-Zuccarello (1974b) found that the outer and centre portions of the proximal part of the thread continue directly into the distal part of the thread. The centre portion retained its thickness whereas the outer portion became thinner towards the pad.

The byssus pad is a flattened plate with an essentially lanceolate shape. Its size varies considerably. The pad is thickest where the thread is connected to it and becomes increasingly thinner towards its edges. In most cases the thread axis forms a sharp angle with the disc plane. The main plane of the disc is aligned with the longitudinal axis of the thread. The ventral surface of the pad incorporates sediment and organic material (eg. diatoms) present on the substratum to which the pad is attached. This material appears more or less completely embedded in a granular matrix.

Mytilus californianus

The byssus stem protrudes from a cavity situated at the proximal end of the ventral groove of the animals foot (Tamarin, 1975). The byssus root consists of parallel sheets (lamellae) which interdigitate with an equal number of tissue septa. The lamellae are formed between these septa (Tamarin, 1975). As more root tissue is secreted between the septa, the lamellae are pushed outwards from the cavity. The root is then called the inner core of the stem. The outer part of the stem is formed by flattened rings (cuffs) which join threads to the stem (Tamarin, 1975). The cuffs are formed from the same substance and in the same manner as the threads themselves, that is by a secretion of collagen through longitudinal ducts in the foot into the pedal groove (Tamarin and Keller, 1972).

Tamarin and his colleagues (Tamarin, 1975; Tamarin and Keller, 1972; Tamarin et al, 1976) do not give a detailed morphology of M. californianus threads. Tamarin (1975, figure 3, Plate 1, p. 157) shows the stem and the proximal region of threads as they leave the cuffs. From this picture it appears that the proximal part of threads have small corrugations on the surface.

The pad is a flattened ovoid disc. The peripheral region is very thin and generally tapers towards the edge. Morphological evidence suggests that three different secretions are involved in the formation of the pads. These secretions have distinctive ultrastructural characteristics which are similar to the fine structure of granules from three different exocrine glands (Tamarin et al, 1974). The authors relate their findings to histochemical and biological studies on Mytilus edulis by other workers and characterised the three main secretions as forms of polyphenol, collagen and mucous (Brown, 1952; Pujol, 1967, Pujol et al, 1970; Pikkarainen et al, 1968). The distal depression of the foot is formed by a widening of the termination of the ventral groove (Tamarin et al, 1974). The surface of the depression is covered with epithelium having paddle-shaped cilia in contrast to cylindrical cilia on all other surfaces. Tamarin <u>et al</u> (1974) proposed that these cilia function as microscopic spatulas for the application of the adhesive pad.

<u>Mytilus edulis</u> and <u>Modiolus modiolus</u>

Brown (1952) described the gross morphology of the byssus complex for <u>Mytilus edulis</u>. Subsequent authors have used this description for the gross morphology of other <u>Mytilus</u> species (eg. Tamarin, 1975; Bairati and Vitellaro-Zuccarello, 1974a, 1974b). Smeathers and Vincent (1979) briefly describe the structure of <u>Mytilus</u> threads, mainly from the work of other authors and show two SEMs of the proximal corrugated region of a <u>M. edulis</u> thread. With this one exception I know of no other published accounts which show the morphology of the byssus complex for <u>M. edulis</u> or for <u>M. modiolus</u> using light microscopy or scanning electron microscopy.

The byssus apparatus of <u>Mytilus edulis</u> has an almost identical morphology to that of <u>Mytilus galloprovincialis</u> (Bairati and Vitellaro-Zuccarello, 1974b). The descriptions of byssus morphology can be interchanged for each species. The byssus apparatus of <u>Modiolus modiolus</u> is basically composed of the same parts as that of <u>M. edulis</u>, ie. it consists of a stem, cuffs and threads which terminate in an adhesive pad. Each thread consists of a proximal corrugated part a distal smooth part and the pad. There are however obvious differences. The structure of the thread cuffs are noticably different for <u>M. edulis</u> and <u>M. modiolus</u>. The cuffs of <u>M. modiolus</u> overlap much more and many more threads come from a corresponding area of stem than for <u>M. edulis</u>. In this way <u>M. modiolus</u> can produce many threads from a small area, thus economising on the size of stem and possibly producing a stronger attachment. The external morphology of the stem for <u>M. modiolus</u> (figures 10-11) and <u>M. californianus</u> (see figure 3, Plate 1, p157 in Tamarin, 1975) are similar in the respect that the cuffs and threads are packed closely together.

The pads of M. edulis and M. modiolus are very variable in shape so it is difficult to determine obvious differences. A detailed study of pads attached to the same substrate is required before real differences can be quantified.

Byssus pads are the attachment for each thread to the substrate. Few studies have shown the effects of pad size and substrate type on attachment strength. Allen et al (1976) found that the break load of M. edulis pads attached to other animals shells or periostracum was related to pad area. Young and Crisp (1982) found that larger forces were required to remove pads from polar surfaces than from non-polar surfaces. The size of pads and type of substrate may therefore appear to have important effects on how well mussels are attached to their substrate but Waite (1983) calculates that the threads are designed to break before the attachment pads. This does not, however include threads attached to small stones in sediments. In Section 2, I show that byssus pads produced by M. edulis and M. modiolus generally decrease in size with a corresponding decrease in particle size. Pads of both species vary in size and shape for the same particle size (Plates 11-12, M. edulis; Plates 18-20, M. modiolus). Experiments to determine the break load of byssus pads attached to different particle sizes and the position of breakage in threads could give interesting results. I have observed that M. edulis and M. modiolus which attached threads to small particles in experimental sediments could be pulled from the sediment, without breaking any threads. This was more difficult for M. modiolus because it produced many more threads, deeper in the sediment. A comparison of attachment strengths for pads attached to substrates with and without organic coatings on the surface could give important insights into marine fouling.

SECTION 2

COLLECTION OF ANIMALS AND SEDIMENT, AND EXPERIMENTS WITH ANIMALS IN DIFFERENT SEDIMENTS

INTRODUCTION

This introduction is divided into two parts. The first part describes particle size and particle size analysis. The second part introduces the distribution of benthic invertebrates.

Particle size

Theoretically most sediments have a log normal size distribution. If the sediment is divided into classes arranged on a log scale they show a normal distribution, with a high proportion of particles in the middle class and progressively less towards the extremes (Friedman and Sanders, 1978). However, it is rare to find a perfectly normal distribution for natural sediments. Most sediments show some degree of skewness (degree of asymmetry or non-normality of the size distribution) or kurtosis (peakedness of the size distribution).

Several scales have been used for particle size, the most commonly used one being the phi (ϕ) scale devised by Krumbein (1934). The phi scale was introduced as a log transformation to simplify the calculation of sediment characteristics such as the median, mean, sorting, skewness and kurtosis (Folk, 1966). Conversion from mm to phi is given by

$$\phi = -\log_2 \text{ particle diameter (mm)}$$

The phi scale enables sediments from different sampling areas to be compared easily in terms of their characteristics mentioned above.

Particle size analysis is usually conducted using the dry sieving method of Krumbein and Pettijohn (1938). There are two methods of calculating the mean, standard deviation, skewness and kurtosis of the size distribution for the data obtained from sieving. The first (Inman, 1952) is to draw a cumulative frequency curve on arithmetic probability paper. Size parameters can be calculated directly from the graph by the use of percentile values. A percentile value is the size value on the X-axis corresponding to a selected percentage on the Y-axis. The most commonly used values are the 5^{th}, 16^{th}, 25^{th}, 75^{th}, 84^{th} and 95^{th} percentiles (Friedman and Saunders, 1978). The size parameters are shown below along with their percentile values.

SIZE PARAMETER	PERCENTILE FORMULA
Median	$Md\phi = \phi 50$
	$= M\phi - (\sigma\phi \alpha\phi)$
Mean	$M\phi = 1/2\ (\phi 16 + \phi 84)$
	$= Md\phi + (\sigma\phi\alpha\phi)$
Sorting (standard deviation)	$\sigma\phi = 1/2\ (\phi 84 - \phi 16)$
Skewness	$\alpha 0 = \dfrac{(M\phi - Md\phi)}{\sigma\phi}$
Kurtosis	$BO = \dfrac{1/2\ (\phi 95 - \phi 5) - \sigma\phi}{\sigma\phi}$

The second method for calculating the mean, standard deviation, skewness and kurtosis is a mathematical one (Snedecor and Cochran (1980, pp. 78-81; Sokal and Rohlf, 1981, pp. 114-119). These are shown below.

Mean (x) $= \dfrac{(x_i + x_{ii} + x_{iii} \ldots\ldots xn)}{n}$

Sorting or standard deviation (σ) $= \sum \dfrac{(x_i - x)^2}{n-1}$

Coefficient of skewness $= \sum \left[\dfrac{(x_i - x)^3}{n-1} \times \dfrac{1}{\sigma^3} \right] -3$

Coefficient of kurtosis $= \sum \dfrac{(x_i - x)^4}{n-1} \times \dfrac{1}{\sigma^4}$

The median is an estimate of central tendency. It is the value which divides the distribution into two equal parts, that is, where 50% of the sediment is finer and 50% is coarser than the median.

The mean is another an estimate of central tendancy and locates a weighted central point to the curve. Unlike the median it is not based on the ranked values of the distribution but uses more of the available information. The mean, therefore is generally a more sensitive measure.

The standard deviation is a measure of the scatter about the mean and is an expression of sorting. The higher the standard deviation, the lower the sorting.

Skewness measures the degree of asymmetry or non-normality of the distribution. In a truly normal distribution the mean and median are identical. If the distribution deviates from normality the mean and median diverge. Skewness measures this departure from normality and describes the asymmetry near the centre of the curve. A positively skewed size distribution is one in which greater amounts of fine material occur than would be expected in a normal distribution. A negatively skewed size distribution is one in which greater amounts of relatively coarser material occurs (Inman, 1952, Folk, 1980).

Pictorial representations of positively and negatively skewed distributions and of their cumulative plots on probability paper are shown in Sokal and Rohlf (1981, p. 119).

Kurtosis measures the peakedness of the size distribution and is therefore related to sorting and skewness. If the coefficient of kurtosis given above is greater than zero, the distribution has a higher central peak falling rapidly on either side of the mean to longer tails, when compared to a normal distribution. This is called leptokurtosis. If the coefficient of kurtosis is less than zero, the distribution has a lower central peak, is flat topped, and tends to be convex with little or no tails at the extremes of the distribution, again when compared to a normal distribution. This is called platykurtosis. A normal distribution is called metokurtosis.

Factors which determine the distribution of benthic marine invertebrates

Several factors determine the distribution of sessile or semi-sessile marine invertebrates. Meadows and Campbell (1972a, 1972b) and Gray (1974) review the factors influencing habitat selection in benthic marine invertebrates.

LARVAE

The factors which influence substrate selection by larvae of epilithic animals include light, pressure, depth, temperature, water currents, contour and texture, the presence of microbial films and presence of the same species. A list of references for these are presented at the end of this introduction (List 1). The majority of studies relate to invertebrate species attached to rocky substrates but it is unlikely that different physiological responses occur for species which occur in sediments.

Several workers have shown that sediment dwelling invertebrates settle and metamorphose most readily in sand or mud from their normal habitat (Nelson, 1924; Wilson, 1932, 1948, 1951; Day and Wilson, 1934; Silen, 1954; Scheltema, 1956, 1961). Particle size, depth of sediment and the presence of organic films are important factors governing the distribution of invertebrates in sediment. Gray (1967) found that larvae of the archiannelid Protodrilus rubrophayngeus preferentially settled in sediment of 0.5-1.0mm diameter. Larval settlement in the polychaete Polydora ciliata is related to the optimal particle-size of sediment for tube-building (Kiseleva, 1967a; Dorsett, 1961). Other workers have shown grain size preferences for interstitial species

(Gray, 1966a, 1966b, 1967; Jansson, 1967). Some species show no preference for particular grain sizes of sediment (Scheltema, 1961; Kiseleva, 1966, 1967b; Lewis, 1968). In a series of experiments on the settlement of Ophelia bicornis larvae Wilson (1952, 1953a, 1953b, 1954, 1955) concluded that the presence of micro-organisms on sand grains plays an important role in making the sand attractive or repellent to the larvae. Later Wilson (1968) found that the strongest stimulus to settlement for the polychaete Sabellaria alveolata (L.) was contact with adult tubes of its own species or with tubes of recently settled young. In addition, greater numbers attached to the substrate in vigourously moving water than in stagnant water. After settling, a searching phase then commenced and if animals made contact with adult tubes metamorphosis occured.

ADULTS

Weiser (1959) investigated the distribution of interstitial organisms in Puget Sound and suggested that a high proportion of particles finer than 200μm diameter excluded many interstitial species. Boaden (1962) found that the rate of recolonisation of invertebrates into cleaned sediment was dependent on particle size. The amphipod Corophium volutator is not found in mud shallower than about 1cm. This has been confimed by laboratory experiments (Meadows, 1964b). C. volutator preferred sediment which has not been treated to remove micro-organisms (Meadows, 1964a) and also preferred fine sediment to course sediment (Meadows, 1964c). Gray (1966a, 1966b, 1967) has shown the importance of particle size and organic coating of sediment particles for the archiannelid Protodrilus symbioticus. Chapman and Newell (1949) concluded that the the main factors governing the distribution of Arenicola marina were particle size and depth of the substrate. Longbottom (1970) found that the abundance of

A. marina was correlated with particle size and amount of organic material in the sediment. Arenicola may not burrow or move horizontally through sediment if layers of ferric oxide, kaolin or clay occur (Reid, 1929). Other authors who relate the distribution of marine invertebrates to particle size include Cassie and Michael (1968) Biernbaum (1979), Bloom et al (1972), Penaz and Gonzalez (1983) and Sameot (1969).

Other factors which control the distibution of species include salinity (Boaden, 1963; McClusky, 1968; Shumway and Davenport, 1977; Gray, 1981), oxygen (Gray, 1966b; Gamble, 1971), sediment penetrability (Brown, 1982), sediment sorting (Bloom et al, 1972; Hulings and Gray, 1976), predation (Brown, 1982) and pollution (Gray, 1981).

MUSSELS

Initial settlement of Mytilus edulis occurs on filamentous structures such as bryozoans, hydroids and filiform algae (Colman, 1940; Blok and Geelen, 1958; Bayne, 1964; Seed, 1969). Secondary settlement occurs in niches and crevices in rocks or adult mussel beds (Blok and Geelen, 1958; Seed, 1969). Settlement of Modiolus modiolus occurs on the periostracal spines or byssus of adult animals (Comely, 1978).

Adult M. edulis are semi-sessile. Animals can shed their byssus complex and move to a new site (Price, 1981; pers. obs.). It is unlikely that adult M. modiolus move to new sites as readily as M. edulis since animals are much larger and heavier.

FACTORS WHICH AFFECT BYSSUS THREAD PRODUCTION

Several environmental and physical factors affect the production of byssus threads. These are listed at the end of this introduction (list 2). The majority of studies have been on intertidal species, mainly Mytilus edulis. Byssus production decreases with age (Glaus, 1968; van Winkle, 1970) and, in general, decreases at lower temperatures and salinities (Glaus, 1968; Allen _et al_, 1976; Stern and Achituv, 1978). Young (1985), however has shown that _M. edulis_ produce threads at a constant rate if they are gradually acclimated to lower temperatures and salinities. _M. edulis_ survives in the Gulf of Finland in salinities of 4 to 5 $^{0}/oo$ (Segerstrale, 1957). Moderate agitation and water velocities increase thread production by _M. edulis_ (van Winkle, 1970; Young, 1985). Exposure to air in intertidal mussels enhances thread production (van Winkle, 1970; Young and Crisp, 1982; Young, 1983, 1985). Prolonged exposure to air of _Modiolus modiolus_ results in the disruption of a regular heart beat (Coleman and Trueman, 1971). In addition animals are unable to retain water in the mantle cavity due to gaping and seepage through the byssal opening. The intertidal range of _M. modiolus_ is restricted to deep rock pools on the lower shore. Young (1985) has demonstrated the seasonality of thread production and corresponding seasonal variation in byssus strength for _M. edulis_ (Price, 1980; 1982).

Several chemicals/pollutants have been shown to reduce or inhibit byssus production. These are ammonia (Reddy and Menon, 1979), chlorine (Reish and Ayers, 1968), pesticides (Roberts, 1975) and petroleum hydrocarbons (Carr and Reish, 1978).

Martella (1974) found that animals involved in clumping activity formed more byssus threads than did isolated individuals.

Young (1983a) noted that _M. edulis_ attach more threads to large boulders than to stones and gravel in a muddy substratum. In laboratory experiments she found that animals attached pads to gravel but not to mud or silt less than 0.85mm in diameter. _M. edulis_ also attach more threads to polar surfaces such as slate and glass than they do to non-polar surfaces such as parafin wax (Young, 1983b).

The aim of the experiments reported in this section is to compare how thread production by M. edulis and M. modiolus is affected by different experimental sediments. The first experiment determines the rate of thread production for M. edulis and M. modiolus in sediment from Arrochar (Mytilus site) under laboratory conditions. A standard time period for leaving animals in sediment was then decided from the results. The second experiment determined the response of M. edulis and M. modiolus to sediment of different particle size ranges. The third experiment determined the response of M. edulis and M. modiolus to sediment with stones present or not present at different depths in the sediment.

The materials and methods and results in this section are reported in four main parts. The first part describes the materials and methods for the collection of animals and sediment for experiments and of the collection of sediment for particle size analysis. The results for the particle size analysis are then reported. The second to fourth parts describe the materials and methods, and results for the first to third experiments, respectively. The discussion at the end of this section relates to all three experiments.

The results were mainly analysed using two-way and one-way analyses of variance and student's t-tests. Probabilities of $P < 0.05$ (5%) were taken as significant except where stated. An asterisk rating system has been used to show the degree of significance for the t-tests. Except where stated the system is as follows:

Probability	Rating
$0.05 > P > 0.01$	*
$0.01 > P > 0.001$	**
$P < 0.001$	***

List 1. Factors which influence substrate selection by larvae of animals which attach to solid substrates.

Factor	Authors
Light	McDougal (1943), Thorson (1964), Kinzie (1973)
Pressure	Hardy and Bainbridge (1951), Rice (1964), Knight-Jones and Morgan (1966).
Temperature	Ryland (1962).
Watercurrents	Smith (1946), Pyefinch (1948), Knight-Jones and Crisp (1953), Crisp (1955), Crisp and Stubbings (1957)
Contour and texture	Crisp and Barnes (1954), McDougal (1943)
Prescence of micro-organisms	Scheer (1945), Zobell and Allen (1935)
Presence of same species	Knight-Jones (1953), Wisely (1960)

List 2. Physical and environmental factors which affect the production of byssus threads.

Factor	Author	Species
Age (size of animal)	Glaus (1968)	M. edulis
	Harger (1970)	M. edulis & Mytilus californianus
	van Winkle (1970)	M. edulis & M. demissus
Temperature	Glaus (1968)	Mytilus edulis
	Allen et al (1976)	M. edulis
	Stern andAchituv (1978)	Brachidontes variabilis
	Young (1985)	M. edulis
Salinity	Glaus (1968)	M. edulis
	van Winle (1970)	M. edulis and Modiolus demissus
	Allen et al (1976)	M. edulis
	Stern and Achituv (1978)	B. variabilis
	Young (1985)	M. edulis
Calcium and magnesium in water	van Winkle (1970)	M. edulis & M. demissus
Water velocity	Maheo (1970)	M. edulis
	vanWinkle(1970)	M.edulis& M. demissus
Agitation	van Winkle (1970)	M. edulis & M. demissus
	Young (1985)	M. edulis
Exposure to air (tidal regime)	van Winkle (1970)	M.edulis& M. demissus
	Price (1980)	M. edulis
	Young (1983)	M. edulis
	Young (1985)	M. edulis

List of physical and environmental factors which affect the production of byssus threads (cont.)

Factor	Author	Species
Seasonality	Price (1982; 1985)	*M. edulis*
	Young (1985)	*M. edulis*
Clumping	Martella (1974)	*M. edulis*
Type of substrate	Young (1983a; 1983b)	*M. edulis*

PART 1. COLLECTION OF ANIMALS AND SEDIMENT FOR EXPERIMENTS AND SEDIMENT FOR PARTICLE SIZE ANALYSIS

MATERIALS AND METHODS

Mytilus edulis and Modiolus modiolus were collected from Loch Long, a sheltered Sea Loch forming part of the Clyde Sea Area. Mytilus edulis was collected from mussel beds at the head of Loch Long, beside Arrochar (National Grid Reference N.S. 296 048, Plate 1,). Modiolus modiolus was collected from a subtidal site at Collessan, on the west side of Loch Long (National Grid Reference N.S. 267 016, Plate 2).

SITE DESCRIPTIONS

Mytilus edulis

The intertidal mudflats at Arrochar are composed of sediment which is very firm, allowing easy access to the sampling site. Animals were most concentrated in the central area of the mudflats between mid and low tide level. A stream in which fewer animals are found carries freshwater through the centre of the mudflats. Animals were collected on the sediment bank to the west side of the stream flow at mid-low tide level.

I chose animals which were unattached to other animals and of length 3.5cm to 4.49cm. The animals were removed by digging with my fingers beneath the byssus threads and attached stones. Care was taken lifting the animal and stones into plastic bags. In the laboratory threads were cut at the point of insertion between the shell valves. The threads with attached stones were fixed in a 5% solution of glutaraldehyde in sea-water for one hour and then stored in sea-water.

Modiolus modiolus was collected by SCUBA diving. The shoreline is typical of many boulder shores (Lewis, 1964; Chapman, 1974). The most obvious biological features on the shore are the zonation of seaweeds, and the presence of barnacles and gastropod molluscs. Pelvetia canaliculata is present on rocks on the upper shore, Ascophylum nodosum and Fucus serratus on the middle shore, Fucus serratus on the lower shore and Laminaria digitata on the extreme lower shore to about 7-8 metres. Littorina saxatalis, Littorina obtusata, Littorina littorea, Nucella lapillus and Patella vulgata are all common on and under boulders. Laminaria saccharina is found subtidally down to about 15 metres. At about 7-8 metres depth the substrate changes to a gentle sediment slope. The sediment bed slopes gradually down to 20 metres, the deepest I have dived at this site. Large numbers of the tube dwelling sea anemone Cerianthus lloydii were present in the sediment.

Modiolus modiolus is found subtidally, in crevices between rocks or with byssus threads attached to stones in sediment. Animals were only collected from sediment. They were present as single animals or in small clumps, buried in the sediment with a quarter to half of the shell exposed above the sediment surface. Individuals of size range 11.5cm to 13.49cm were collected by two divers from a depth of 10-15 metres. The following technique was used to remove each mussel. The animal was held by one diver as the other diver waved his hand close to the sediment surface. The resultant current washed away unattached sediment leaving a crater with the byssus threads and attached stones. Animals were carefully placed in collecting bags. In the laboratory threads with attached stones were removed, fixed and stored in the same manner as for Mytilus edulis.

Sediment was collected from the mussel beds in the low intertidal region at Arrochar. The surface sediment down to a depth of about 15 cm was removed with a spade and placed in large plastic bags. Sledges were used to take the bags of sediment to the roadside. Sediment from the subtidal Modiolus site was not collected for the experiments because it was difficult to obtain in large quantities.

Collection of sediment for particle size analysis

Sediment cores were collected from the sample sites at Arrochar and Coilessan for particle size analysis. The collection of sediment from Arrochar was relatively straightforward. Plastic cores of 10cm diameter were pushed into the sediment to a depth of about 15cm. A spade was used to dig the core out from the sediment. The core was taken back to the laboratory for analysis. Sediment cores from Coilessan were collected by SCUBA divers. Sediment samples were obtained at a depth of about 15 metres. The cores were pushed into the sediment to a depth of about 15cm and dug from the sediment by hand. The cores were then placed in plastic bags and taken to the surface, placed in more plastic bags and taken back to the laboratory for analysis.

Sediment from each site was dried in an oven at 60°C for 1 week. Any aggregations present after drying were broken down gently by hand to avoid crushing individual sediment particles. The sediment was then mixed thoroughly. Four samples of sediment from each site, approximately 100g in weight were sieved. An Endecott sieve shaker
+1 0
using British standard sieves of mesh size 2.00mm, 1.40mm, 1.00mm,
−1 355µm, 250µm − 2 − 3
710µm, 500µm, 180µm, 125µm, 90µm, 63µm, 45µm, 38µm and a base was used. The sieves were stacked on the shaker in decreasing mesh size from the top and the sediment sample placed on the top (2.00mm) sieve. Shaking was carried out for 1 hour. Sediment from each sieve was checked to determine whether aggregates were still present. If the percentage of aggregates was greater than 5% of the total number of particles present the sample was sieved again for 1 hour. Sieving was repeated until less than 5% of the particles were still in the form of aggregates.

After shaking, the sediment in each sieve was brushed into separate pre-weighed plastic containers and weighed. Sediment size parameters including mean, median, sorting, skewness and kurtosis were then calculated.

RESULTS

The results of the particle size analysis for Arrochar and Coilessan sediments using the dry sieving method are shown both as percentage weight curves (figure 1) and cumulative percentage weight curves (figure 2). Both sediments contain a large weight % of particles greater than 2.00mm (-1 ø). Sediment from Arrochar contains a larger amount of coarser material than sediment from Coilessan.

The mean, sorting, skewness and kurtosis could not be calculated from the cumulative percentage curve because the percentile values ø5 and ø16 could not be obtained. The median was calculated from the cumulative percentage curve and the remaining sediment characteristics were calculated mathematically. These are shown in Table 1. Each measure is described below.

<u>Mean and median particle diameter</u>

The median particle size of sediment was higher (lower ø value) for sediment from Arrochar than for sediment from Coilessan. The mean particle size was also higher (smaller ø value) for sediment from Arrochar than from Coilessan.

<u>Sorting (standard deviation)</u>

The higher the standard deviation, the poorer the sorting. Sediment from both sites were poorly sorted.

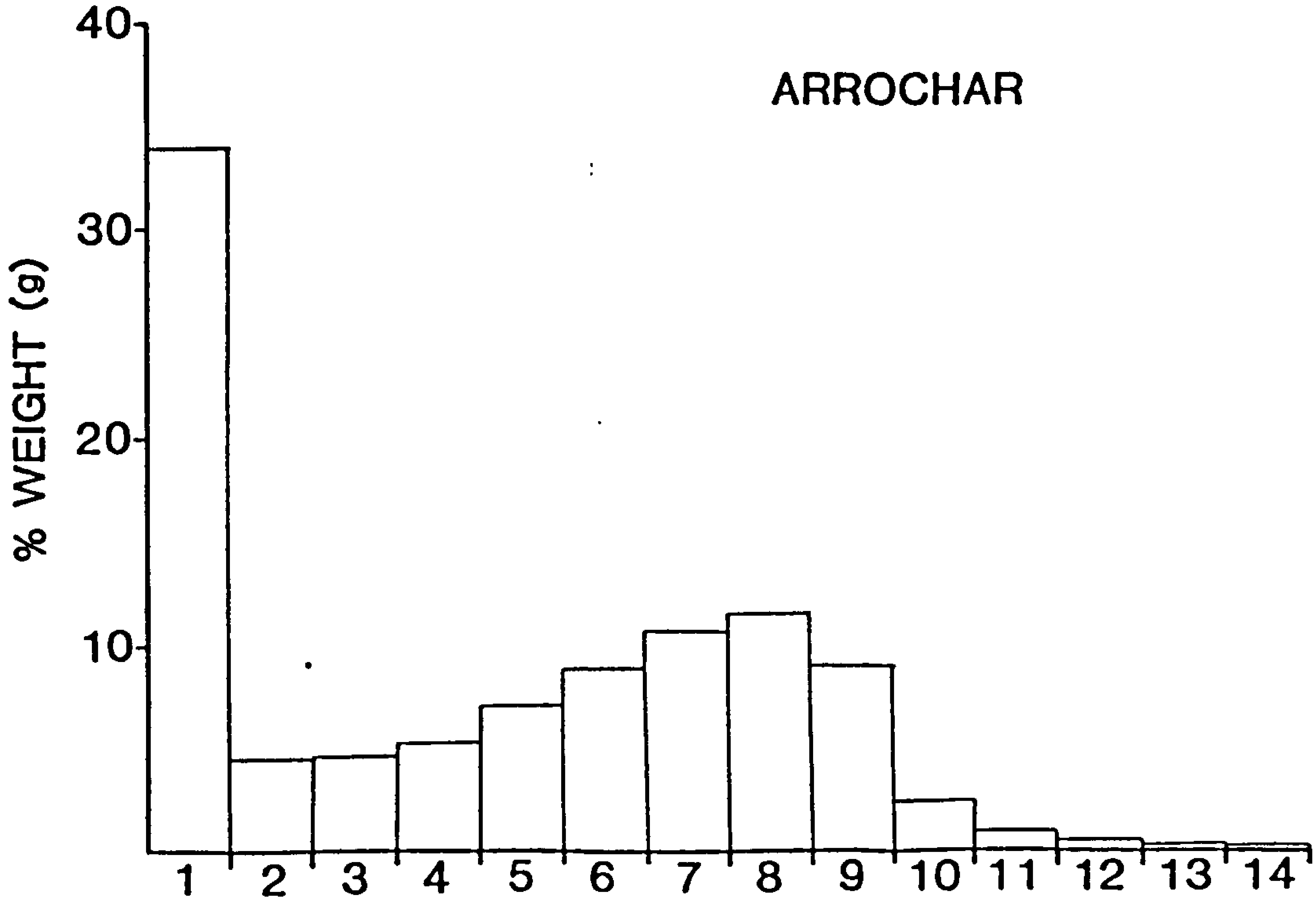
<u>Skewness</u>

The size distribution of sediment from Arrochar was positively skewed. This means that more fine material occurred than would be expected in a normal distribution. The size distribution of sediment from Coilessan was near symmetrical.

<u>Kurtosis</u>

Sediment from both sides were very platykurtic, that is, the distribution was very flat.

Figure 1. Particle size. Percentage weight (g) against particle diameter (phi units) for sediment from Arrochar and Coilessan. Particle size class 1 = < -1.0 ø (phi), 2 = -1.0 to -0.5 ø, 3 = -0.5 to 0 ø, 4 = 0 to 0.5 ø, 5 = 0.5 to 1.0 ø, 6 = 1.0 to 1.5 ø, 7 = 1.5 to 2.0 ø, 8 = 2.0 to 2.5 ø, 9 = 2.5 to 3.0 ø, 10 = 3.0 to 3.5 ø, 11 = 3.5 to 4.0 ø, 12 = 4.0 to 4.5 ø, 13 = 4.5 to 5.0 ø and 14 = 5.0 to 5.5 ø.


ARROCHAR
% WEIGHT (g)
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14

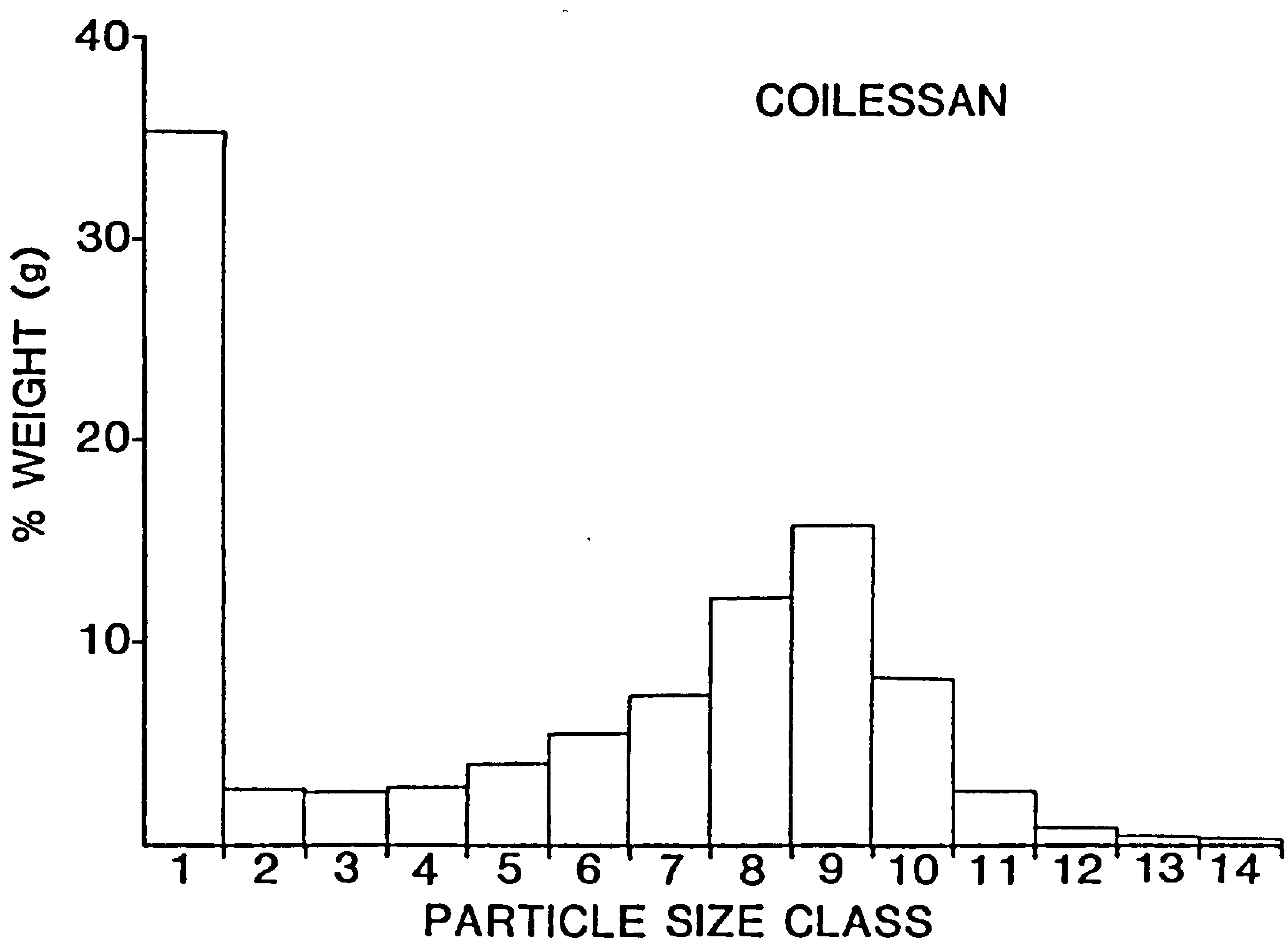
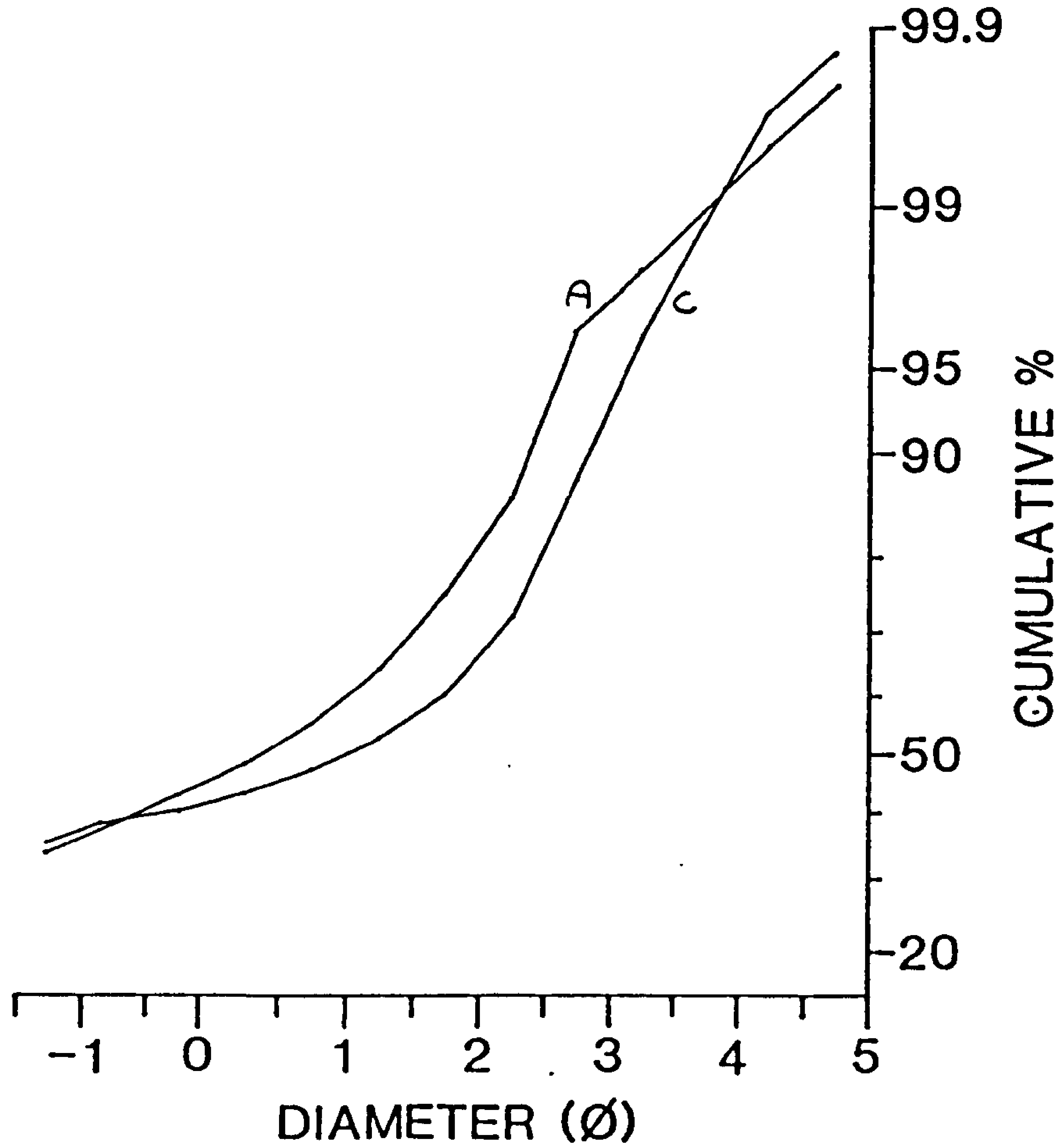

COILESSAN
% WEIGHT (g)
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14
PARTICLE SIZE CLASS

Figure 2. Size-cumulative frequency curves for sediment from Arrochar and Coilessan.


A
C
99.9
99
95
90
50
20
CUMULATIVE %
-1
0
1
2
3
4
5
DIAMETER (Ø)

Nomenclature	Arrochar		Coillessan	
	phi (ϕ)	Verbal	phi (ϕ)	Verbal
Median	0.38		1.00	
Mean	0.5640		0.8894	
Sorting	1.6193	(Poorly sorted)	1.8406	(Poorly sorted)
Skewness	0.1182	(Fine skewed)	-0.0014	(Near symmetrical)
Kurtosis	-1.2359	(Very Platykurtic)	-1.5834	(Very Platykurtic)

Table 1. Characteristics of sediment from sample sites at Arrochar and Coilessan. Verbal descriptions are from Folk (1980).

PART 2. RATE OF BYSSUS THREAD PRODUCTION BY THE MUSSELS *Mytilus edulis* AND *Modiolus modiolus*

MATERIALS AND METHODS

Mytilus edulis and Modiolus modiolus were collected from Arrochar and Colliesan respectively and sediment from Arrochar as described on pages 64-65. Thirty animals of each species were collected for the twenty day experiment and fifteen Modiolus modiolus for the one hundred day experiment.

Sediment was carefully sorted by hand to remove animals and stones with attached byssus threads. Sorted sediment was placed in tanks to a depth of 7.5cm in a 10°C aquarium and covered with sea-water. The tanks were connected to a recirculating filtered sea-water system. Three days after collection the animals were placed on the sediment surface in several rows at least 6cm apart. Animals were numbered 1 to n (n = total number of animals) from left to right along each row. Three animals were removed at each of the following times;

20 day experiment; 3 hours, 6 hours, 12 hours, 18 hours, 1 day, 2 days, 4 days, 8 days, 12 days, and 20 days.

100 day experiment; 20 days, 40 days, 60 days, 80 days, and 100 days.

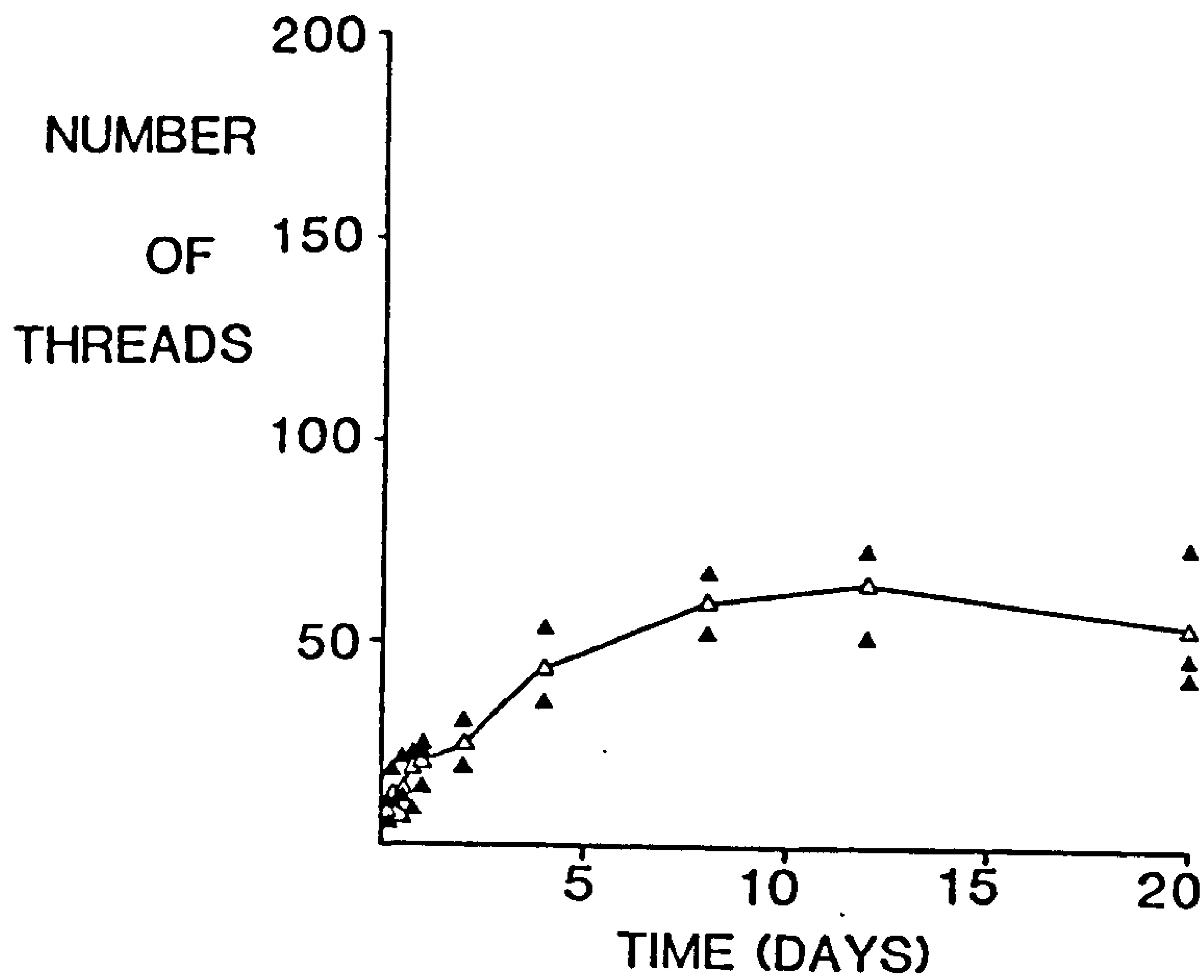
Each animal was chosen with the aid of random number tables. The number of threads produced by each animal was recorded.

RESULTS

The number of byssus threads produced by *Mytilus edulis* and *Modiolus modiolus* are shown in Figures 3 and 4. The number of threads produced by *M. edulis* increased to a mean of 60.33 after 8 days (Figure 3). Between 8 and 20 days the mean number of threads did not increase. In contrast, the mean number of threads produced by *M. modiolus* increased steadily to 192.6 at the end of the 20 day experiment (figure 3). The mean number of threads increased to 556 after 80 days (figure 4). The large difference in the mean values of 60 and 100 days (figure 4) is because of one animal at 80 days produced 832 threads, thus increasing the mean value. Without this animal the curve would show a small but steady increase in the number of threads from 20 to 100 days.

Figure 3. The number of byssus threads produced by Mytilus edulis and Modiolus modiolus in a muddy sediment with stones. Closed triangles represent the number of threads produced by individual animals and open triangles represent the mean number of threads/animal.

MYTILUS EDULIS



MODIOLUS MODIOLUS

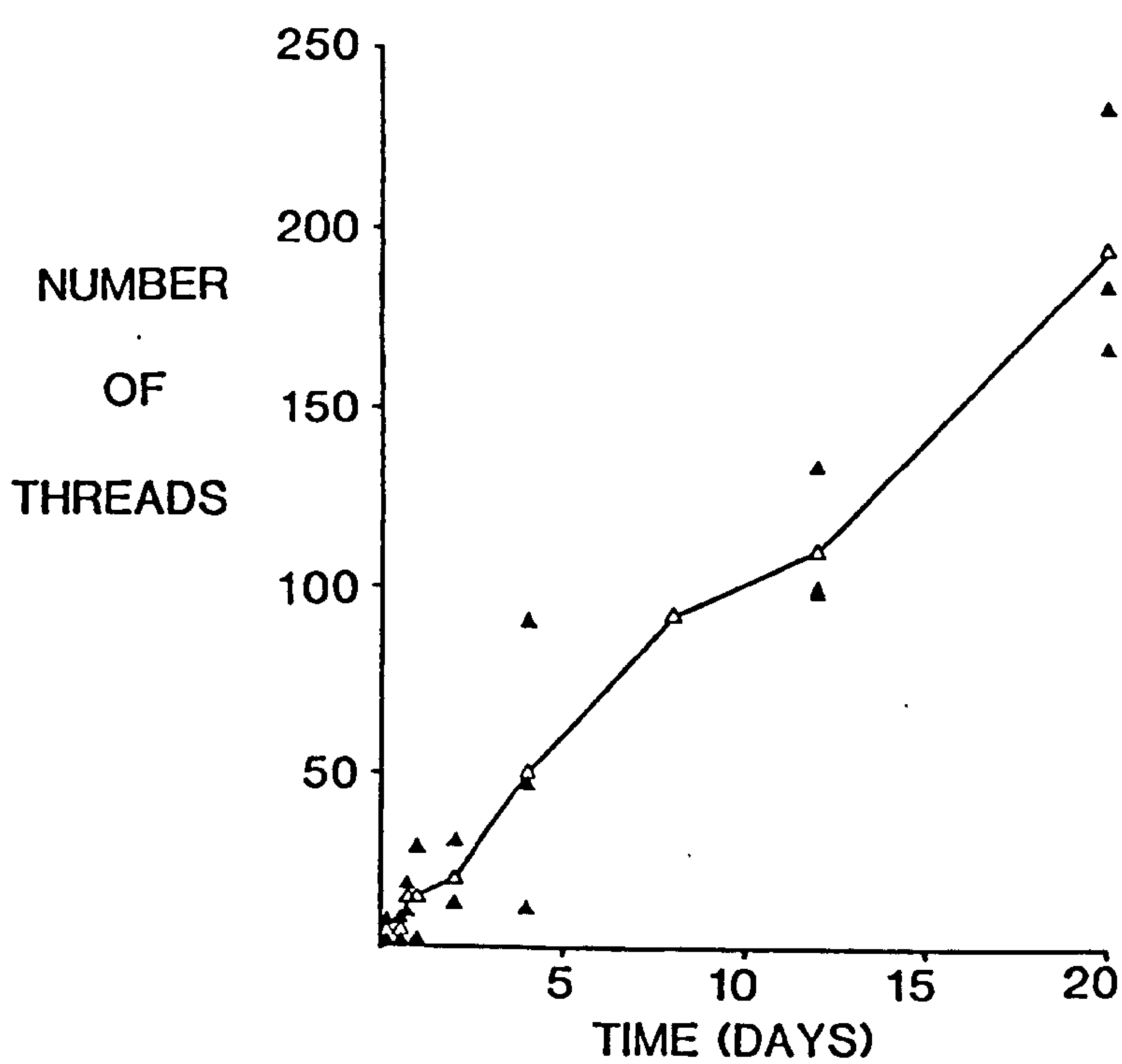
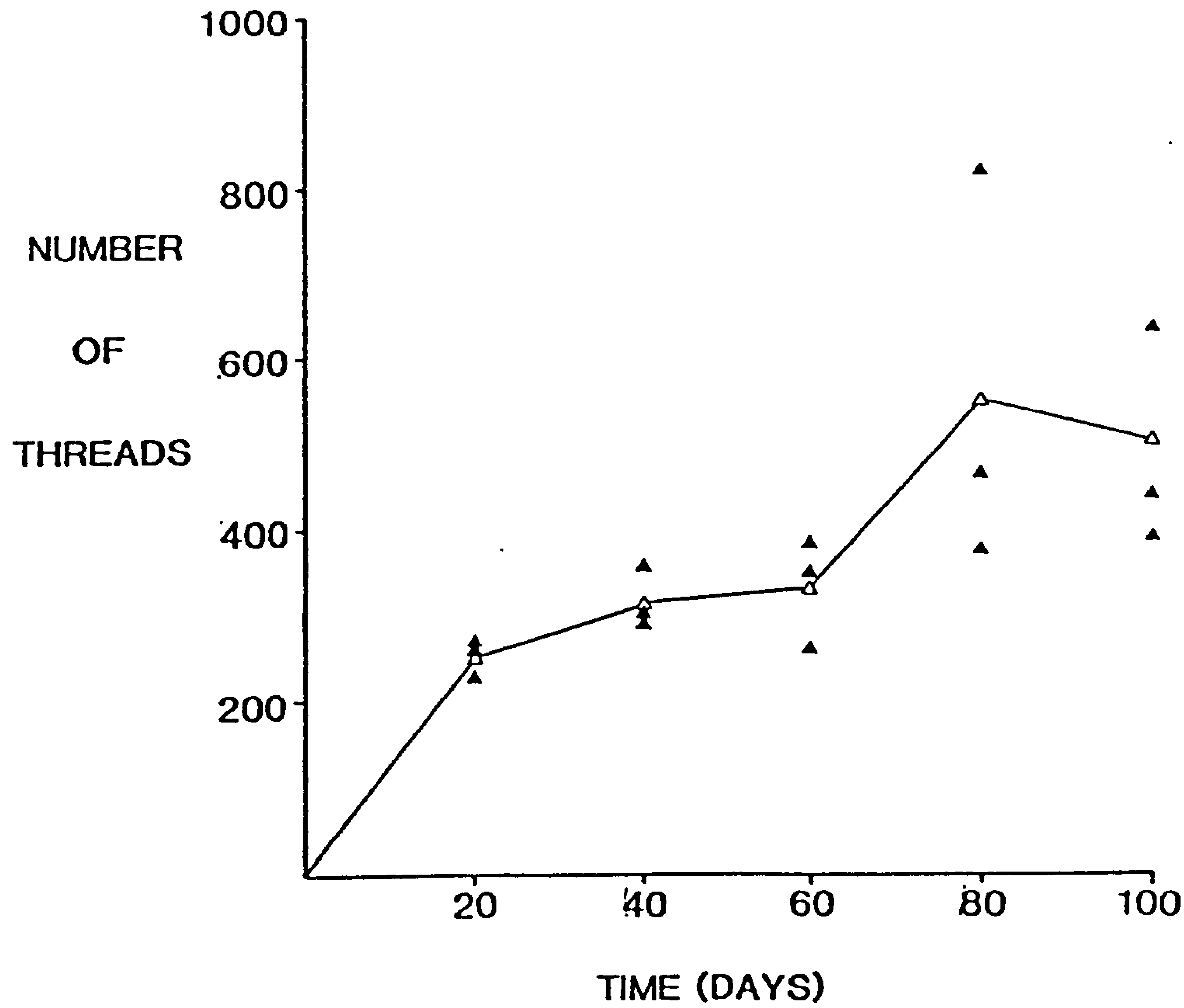


Figure 4. The number of byssus threads produced by Modiolus modiolus in a muddy sediment with stones. Closed triangles represent the number of threads produced by individual animals and open triangles represent the mean number of threads/animal.


1000
800
600
400
200
NUMBER
OF
THREADS
20
40
60
80
100
TIME (DAYS)

PART 3. THE EFFECTS OF DIFFERENT PARTICLE SIZE RANGES OF SEDIMENT ON BYSSUS THREAD PRODUCTION BY *Mytilus edulis* AND *Modiolus modiolus*

MATERIALS AND METHODS

Mytilus edulis and Modiolus modiolus were collected from Arrochar and Coliessan respectively and sediment from Arrochar, as described on pages 64-65. In the laboratory threads were cut at the point of insertion between the shell valves.

This part of the materials and methods is divided into two parts. The first part describes the experiment for single animals and the second describes the experiment for groups of animals.

SINGLE ANIMALS

Sediment was wet-sieved through a series of sieves in large bins containing seawater. The sieve sizes were 16mm, 8mm, 4mm, 2mm, 1mm, 0.5mm and 0.25mm (Table 2). The two sieves of greatest sieve diameter (16mm and 8mm) were used to obtain sediment of particle size range 8mm to 15.99mm. The 16mm sieve was placed on top of the 8mm sieve and sediment samples added until all the sediment was sieved into the bucket. Sediment of particle diameter 8.0mm to 15.99mm was retained between the two sieves and the remaining sediment smaller than 8.0mm went through the sieves into the bucket. Water was drained from the bin and the particle size range obtained by following the same procedure with sieves of size 8mm and 4mm. This was repeated for successively smaller sieves until the following particle size ranges were obtained.

8.0mm to 15.99mm, 4.0mm to 7.99mm, 2.0mm to 3.99mm, 1.0mm to 1.99mm 0.5mm to 0.99mm, 0.25mm to 0.49mm, and < 0.25mm. These shall be refered to as 8-16mm, 4-8mm, 2-4mm, 1-2mm, 0.5-1mm, 0.25-0.5mm and < 0.25mm in future for clarity.

Sediment of each particle size range was added to 2 of 14 tanks (30 x 20 x 20cm). This gave 2 tanks for each of the 7 particle size ranges. One of each pair of tanks was used for Mytilus edulis and one

Sieve size(mm)	Phi scale	Particle size range obtained
16mm	-4	
		8mm to 15.99mm
8mm	-3	
		4mm to 7.99mm
4mm	-2	
		2mm to 3.99mm
2mm	-1	
		1mm to 1.99mm
1mm	0	
		0.5mm to 0.99mm
0.5mm	+1	
		0.25mm to 0.49mm
0.25mm	+2	
		< 0.25mm

Table 2. The diameter of sieves used in experiment 3 and particle size ranges obtained. Phi scale (ϕ) = $-\log_2$ of the particle diameter in millimetres (Holme and McIntyre, 1971).

for <u>Modiolus modiolus</u>. The tanks were placed in larger tanks containing running sea water in a 10^{o}C aquarium. Three days after collection, four animals of each species were added to each of the 14 tanks containing sediment. This gave 7 tanks for <u>Mytilus edulis</u> and 7 tanks for <u>Modiolus modiolus</u> each tank containing four animals of one species and one of the 7 particle size ranges.

Animals were removed from the tanks after 12 days. The following measurements were made on each animal;

1. Number of threads.
2. Length of each thread.
3. Number of threads/stone.

I later decided to measure the size of byssus pads for each particle size range. The threads from each animal had mistakenly been pooled for storage. Measurements of pads were therefore for each particle size as opposed to each animal. The length and width of thirty byssus pads from each particle size range were measured for each species. The length and width of each byssus pad were summed and divided by 2 to give an estimate for pad size,

$$\text{i.e.} \quad \text{pad size} = \frac{\text{length of pad + width of pad}}{2}$$

The length/width ratio was determined for each byssus pad to give a rough estimate of overall shape.

<u>GROUPS OF ANIMALS</u>

Sediment was sieved into five particle size ranges in the same manner as sediment for the single animal experiment. The particle size ranges obtained were 2-4mm, 1-2mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm. Sediment of each particle size range were added to 2 of 10 pneumatic troughs of 30cm diameter and 16cm depth). The troughs were added to tanks which contained a continuous supply of sea-water at 10^{o}C. Three days after collection 30-34 <u>M. edulis</u> or 5 <u>M. modiolus</u> were placed on the sediment in each pneumatic trough at one animal's width apart. This gave 5 troughs for M. edulis and 5 for M. modiolus, each trough containing animals of one species and one of five particle size ranges. Animals were placed at one of eight orientations on the sediment surface. These orientations were numbered from 1 (0^{o}, ie facing forwards) to 8 (315^{o}) at 45^{o} intervals. The orientation of each animal was chosen with the aid of random number tables. Sea-water was drained to expose the upper surface of animals at periods of 1,2,4,8 and 12 days. A clear perspex grid was placed on the animals and the outlines of the trough and animals drawn. A record of the movements for each animal was thus obtained. After 12 days the trough was placed in an experimental sea-water flume to determine whether groups of animals stabilise or destabilise sediments. The flume experiments are described in Section 3.

The number of threads attached to sediment, other animals and the animals own shell were recorded immediately after the flume experiment.

RESULTS

SINGLE ANIMALS

Number of byssus threads produced. Comparison between sediment of different particle size ranges and between species.

The number of byssus threads *Mytilus edulis* and *Modiolus modiolus* attached to sediment of different particle size ranges is shown in Figure 5.

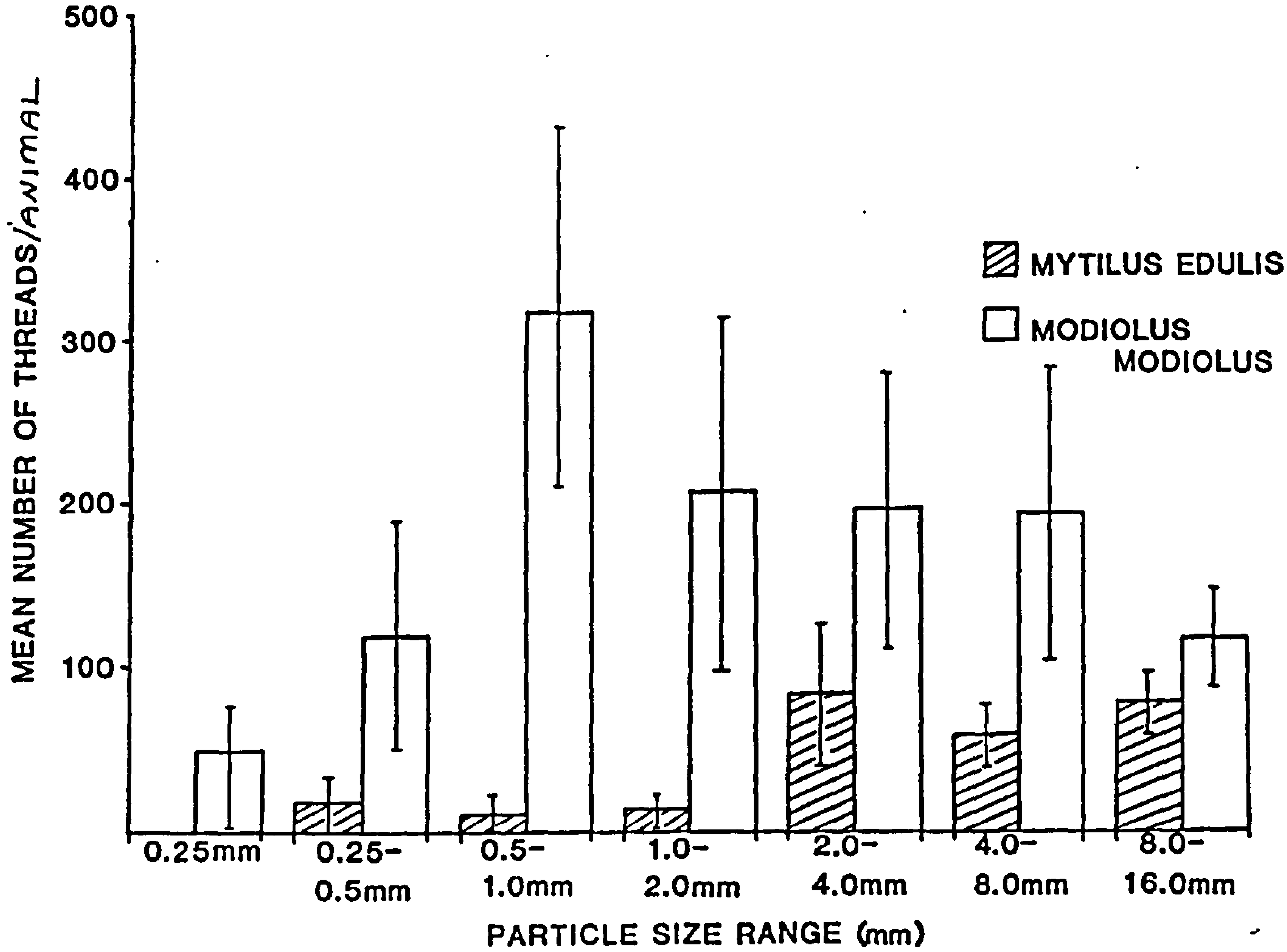
The data for number of threads was found to have a non-normal distribution (using the rankit method to determine normality). Three transformations were used to assess which would be the best for normalising the data ($\log_{10}(x)$, square-root and arcsin). The best transformation was found to be the square-root and all statistical analyses were therefore performed on square-root transformed data.

One-way analyses of variance were performed on the data to test differences in the number of threads between particle size ranges. These anovars showed that there were significant differences in the number of byssus threads between particle size ranges for both species (*Mytilus edulis* $P < 0.001$; *Modiolus modiolus* $0.005 > P > 0.001$, Table 3). The particle size range < 0.25mm was not used for *Mytilus edulis* because animals did not attach byssus threads to sediment.

T-tests were then performed on the data to compare differences between pairs of particle size ranges for *M. edulis* and for *M. modiolus*. The following results were obtained.

Mytilus edulis; The results are shown in tables 3 (anovars) and 4 (t-tests). Significantly fewer threads were attached to sediment of the particle size ranges 0.25-0.5mm, 0.5-1.0mm and 1.0-2.0mm than were attached to sediment of the size ranges 2.0-4.0mm, 4.0-8.0mm and 8.0-16.0mm. No other comparisons were significant.

Figure 5. The mean number of threads produced by *Mytilus edulis* and *Modiolus modiolus* in different particle size ranges of sediment. Means were calculated for 4 animals except *M. edulis* in the particle size range 0.25-0.5mm (2 animals) and *M. modiolus* in 0.5-1.0mm (3 animals).



MEAN NUMBER OF THREADS/ANIMAL
500
400
300
200
100
MYTILUS EDULIS
MODIOLUS MODIOLUS
0.25mm
0.25-0.5mm
0.5-1.0mm
1.0-2.0mm
2.0-4.0mm
4.0-8.0mm
8.0-16.0mm
PARTICLE SIZE RANGE (mm)

Modiolus modiolus; The results are shown in Tables 3 (anovars) and 5 (t-tests). Significantly fewer threads were attached to sediment of the particle size range < 0.25mm than to sediment of particle size ranges greater than 0.25-0.5mm. In addition, significantly more threads were attached to sediment of the particle size range 0.5-1.0mm than to the particle size ranges 0.25-0.5mm and 8.0-16.0mm.

T-tests were performed on the data to compare differences between species at each particle size range. These are shown in Table 6. M. modiolus attached significantly more threads to sediment of the particle size ranges 0.25-0.5mm, 0.5-1.0mm, 1.0-2.0mm, and 4.0-8.0mm than did M. edulis. There were no significant differences between species in the particle size ranges 2.0-4.0mm and 8.0-16.0mm. No test was performed for the particle size range <0.25mm because M. edulis did not attach byssus threads to sediment.

	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Sizerange	5	202.28	40.46	11.75	P<0.001
	Error	18	61.99	3.44		
	Total	23	264.27			
Modiolus modiolus	Size range	6	308.82	51.47	5.59	0.005> P> 0.001
	Error	20	184.02	9.20		
	Total	26	492.85			

Table 3. One-way analysis of variance comparing the number of byssus threads attached to sediment of different particle size ranges (square-root transformed data) for *Mytilus edulis* and *Modiolus modiolus*. The size ranges compared were 8-16mm, 4-8mm, 2-4mm, 1-2mm, 0.5-1.0mm and 0.25-0.5mm for *M. edulis* and 8-16mm, 4-8mm, 2-4mm, 1-2mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm for *M. modiolus*. d.f. = degrees of freedom, F = variance ratio and P = probability.

Comparison	t	d.f.	P
0.25-0.5mm to 0.5-1.0mm	0.536	6	0.90> P> 0.50
0.25-0.5mm to 1.0-2.0mm	0.888	6	0.50> P> 0.40
0.25-0.5mm to 2.0-4.0mm	3.980	6	0.01> P> 0.001**
0.25-0.5mm to 4.0-8.0mm	3.871	6	0.01> P> 0.001**
0.25-0.5mm to 8.0-16.0mm	4.880	6	0.01> P> 0.001**
0.5-1.0mm to 1.0-2.0mm	0.419	6	0.90> P> 0.50
0.5-1.0mm to 2.0-4.0mm	4.107	6	0.01> P> 0.001**
0.5-1.0mm to 4.0-8.0mm	4.263	6	0.01> P> 0.001**
0.5-1.0mm to 8.0-16.0mm	5.672	6	0.01> P> 0.001**
1.0-2.0mm to 2.0-4.0mm	3.932	6	0.01> P> 0.001**
1.0-2.0mm to 4.0-8.0mm	4.119	6	0.01> P> 0.001**
1.0-2.0mm to 8.0-16.0mm	5.668	6	0.01> P> 0.001**
2.0-4.0mm to 4.0-8.0mm	1.027	6	0.40> P> 0.20
2.0-4.0mm to 8.0-16.0mm	0.135	6	0.90> P> 0.50
4.0-8.0mm to 8.0-16.0mm	1.417	6	0.40> P> 0.20

Table 4. Mytilus edulis. Students t-tests comparing the number of byssus threads animals attached to sediment of different particle size ranges (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Comparison	t	d.f.	P
<0.25mm to 0.25-0.5mm	2.163	6	0.10> P> 0.05
<0.25mm to 0.5-1.0mm	5.225	5	0.01> P> 0.001**
<0.25mm to 1.0-2.0mm	3.496	6	0.02> P> 0.01*
<0.25mm to 2.0-4.0mm	3.687	6	0.02> P> 0.01*
<0.25mm to 4.0-8.0mm	3.584	6	0.02> P> 0.01*
<0.25mm to 8.0-16.0mm	3.066	6	0.05> P> 0.02*
0.25-0.5mm to 0.5-1.0mm	2.942	5	0.05> P> 0.02*
0.25-0.5mm to 1.0-2.0mm	1.426	6	0.20> P> 0.10
0.25-0.5mm to 2.0-4.0mm	1.417	6	0.40> P> 0.20
0.25-0.5mm to 4.0-8.0mm	1.345	6	0.40> P> 0.20
0.25-0.5mm to 8.0-16.0mm	0.025	6	P> 0.90
0.5-1.0mm to 1.0-2.0mm	1.370	5	0.40> P> 0.20
0.5-1.0mm to 2.0-4.0mm	1.640	5	0.20> P> 0.10
0.5-1.0mm to 4.0-8.0mm	1.672	5	0.20> P> 0.10
0.5-1.0mm to 8.0-16.0mm	4.416	5	0.01> P> 0.001**
1.0-2.0mm to 2.0-4.0mm	0.121	6	P> 0.90
1.0-2.0mm to 4.0-8.0mm	0.173	6	0.90> P> 0.50
1.0-2.0mm to 8.0-16.0mm	1.801	6	0.20> P> 0.10
2.0-4.0mm to 4.0-8.0mm	0.058	6	P> 0.90
2.0-4.0mm to 8.0-16.0mm	1.897	6	0.20> P> 0.10
4.0-8.0mm to 8.0-16.0mm	1.784	6	0.20> P> 0.10

Table 5. *Modiolus modiolus*. Students t-tests comparing the number of byssus threads animals attached to sediment of different particle size ranges (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Comparison	t	d.f.	P
0.25–0.5mm	4.117	6	$0.01 > P > 0.001^{**}$
0.5–1.0mm	8.196	5	$P < 0.001^{***}$
1.0–2.0mm	5.317	6	$0.01 > P > 0.001^{**}$
2.0–4.0mm	2.420	6	$0.10 > P > 0.05$
4.0–8.0cm	3.466	6	$0.02 > P > 0.01^{*}$
8.0–16.0 mm	2.324	6	$0.10 > P > 0.05$

Table 6. Students t-tests comparing the number of byssus threads *Mytilus edulis* and *Modiolus modiolus* attached to sediment of different particle size ranges (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Length of byssus threads. Comparison between sediments of different particle size range and between species.

The mean length of byssus threads animals produced in different particle size ranges are shown in Tables 7 (Mytilus edulis) and 8 (Modiolus modiolus).

One-way analyses of variance were performed on the data to test differences between animals in each particle size range. These showed (Tables 9-10) that there were significant differences between animals for both species, except M. edulis in the particle size ranges 0.5-1.0mm and 2.0-4.0mm.

The data for the animals in each particle size range were pooled to compare differences between particle size ranges. The pooled data are shown in Tables 7 (M. edulis) and 8 (M. modiolus) and figure 6.

One-way analyses of variance were performed on the pooled data to test differences in the length of byssus threads between particle size ranges. The results for pooled data were interpreted very carefully because significant differences were found between animals. Because of this I have taken the significant probability level as 0.01 (1%) rather than 0.05 (5%). The results are shown in Table 11. There were significant differences in thread length between particle size ranges for both species (Mytilus edulis $P<0.001$; Modiolus modiolus $P<0.001$, Table 11).

T-tests were then performed on the data to compare differences between pairs of particle size ranges for M. edulis and M. modiolus using the same conservative criterion. The following results were obtained (Table 12, M. edulis; Table 13, M. modiolus). In each table significant values are denoted an asterisk (*).

M. edulis: The general picture of results (Tables 11 and 12) is that longer byssus threads were produced in the smallest particle size

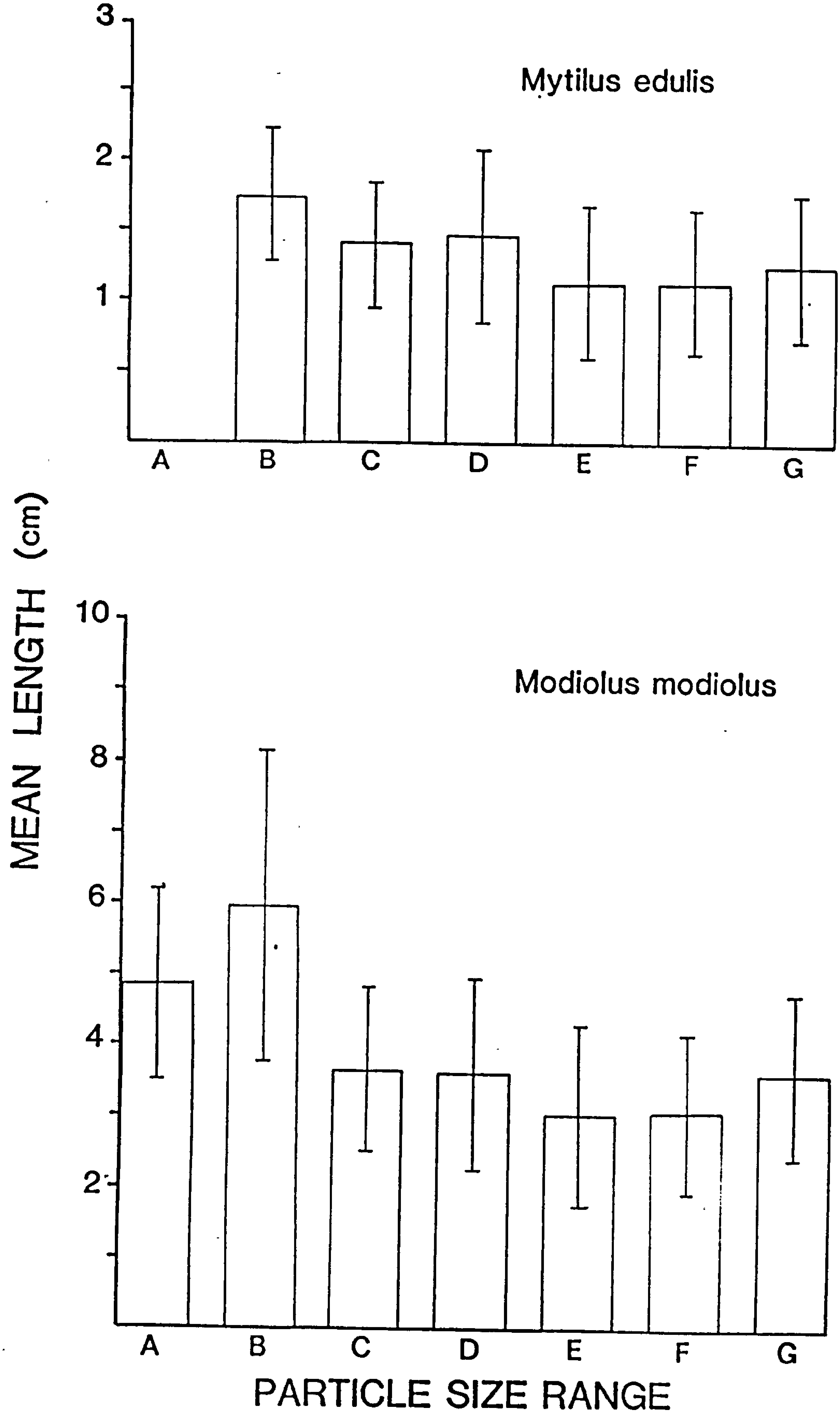
Particle size range	Individual animals			Pooled animals	
	Animal	N	Length of threads mean std dev	N	Length of threads mean std dev
0.25–0.5mm	1	28	1.803 ± 0.472	35	1.749 ± 0.472
	2	7	1.532 ± 0.243		
0.5–1.0mm	1	6	1.404 ± 0.533	41	1.390 ± 0.445
	2	29	1.403 ± 0.469		
	3	2	1.353 ± 0.222		
	4	4	1.296 ± 0.294		
1.0–2.0mm	1	4	0.840 ± 0.297	51	1.464 ± 0.614
	2	26	1.704 ± 0.651		
	3	4	0.836 ± 0.196		
	4	17	1.392 ± 0.446		
2.0–4.0mm	1	77	1.134 ± 0.570	335	1.137 ± 0.538
	2	35	1.005 ± 0.691		
	3	85	1.097 ± 0.585		
	4	138	1.196 ± 0.435		
4.0–8.0mm	1	70	1.158 ± 0.470	231	1.141 ± 0.510
	2	75	1.070 ± 0.449		
	3	53	1.315 ± 0.546		
	4	33	0.986 ± 0.594		
8.0–16.0mm	1	87	0.918 ± 0.370	308	1.239 ± 0.509
	2	49	1.074 ± 0.311		
	3	88	1.397 ± 0.474		
	4	84	1.501 ± 0.554		

Table 7. *Mytilus edulis*. The mean length of byssus threads (± std dev) animals produced in different particle size ranges of sediment. Columns 2-4 represent individual animals, and columns 5-6 represent pooled animals in each particle size range. N = number of threads.

	Individual animals			Pooled animals	
Particle size range	Animal	N	Length of threads mean std dev	N	Length of threads mean std dev
<0.25mm	1	19	4.82 ± 1.85	160	4.85 ± 1.35
	2	89	5.44 ± 0.91		
	3	43	4.00 ± 1.18		
	4	9	3.17 ± 0.91		
0.25-0.5mm	1	91	6.49 ± 1.88	511	5.95 ± 2.18
	2	246	7.04 ± 1.57		
	3	130	4.57 ± 1.83		
	4	44	2.84 ± 1.31		
0.5-1.0mm	1	212	4.54 ± 0.82	959	3.65 ± 1.12
	2	431	3.71 ± 0.93		
	3	316	2.97 ± 1.09		
1.0-2.0mm	1	139	5.05 ± 1.59	832	3.61 ± 1.35
	2	110	1.87 ± 0.49		
	3	234	3.28 ± 0.84		
	4	349	3.80 ± 0.96		
2.0-4.0mm	1	168	3.53 ± 1.07	792	3.04 ± 1.28
	2	244	3.79 ± 1.24		
	3	98	1.39 ± 0.72		
	4	282	2.68 ± 0.82		
4.0-8.0mm	1	249	3.20 ± 1.07	772	3.07 ± 1.12
	2	289	3.48 ± 1.04		
	3	115	1.88 ± 0.75		
	4	119	2.97 ± 0.93		
8.0-16.0mm	1	105	3.91 ± 1.05	468	3.62 ± 1.18
	2	84	4.25 ± 0.87		
	3	157	3.37 ± 1.17		
	4	122	3.25 ± 1.14		

Table 8. *Modiolus modiolus*. The mean length of byssus threads (± std dev) animals produced in sediment of different particle size ranges. Columns 2-4 represent individual animals and columns 5-6 represent pooled animals. N = number of byssus threads.

Figure 6. The length of byssus threads produced by Mytilus edulis and Modiolus modiolus in different particle size ranges of sediment (data for each particle size range pooled). The data for four animals was pooled except M. edulis in the particle size range 0.25–0.5mm (data for 2 animals pooled) and M. modiolus in 0.5–1.0mm (data for 3 animals pooled). A = <0.25mm, B = 0.25-0.5mm, C = 0.5-1.0mm, D = 1.0-2.0mm, E = 2.0-4.0mm, F = 4.0-8.0mm, G = 8.0-16.0mm.



Mytilus edulis
Modiolus modiolus
MEAN LENGTH (cm)
3
2
1
10
8
6
4
2
A
B
C
D
E
F
G
PARTICLE SIZE RANGE

Particle size range	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
	Animals	1	0.411	0.411	1.89	0.1> P>
0.25-0.5mm	Error	33	7.175	0.217		0.05
	Total	34	7.586			
	Size range	3	0.044	0.015	0.07	P> 0.75
0.5-1.0mm	Error	37	7.884	0.213		
	Total	40	7.927			
	Size range	3	4.725	1.575	5.24	0.005> P
1.0-2.0mm	Error	47	14.140	0.301		0.001
	Total	50	18.864			
	Size range	3	1.212	0.404	1.40	0.25>
2.0-4.0mm	Error	331	95.565	0.289		P> 0.10
	Total	334	96.777			
	Size range	3	2.795	0.932	3.71	0.05>
4.0-8.0mm	Error	227	56.945	0.251		P> 0.025
	Total	230	59.739			
	Size range	3	18.261	6.087	30.13	P< 0.001
8.0-16.0mm	Error	304	61.419	0.202		
	Total	307	79.680			

Table 9. Mytilus edulis. One-way analyses of variance comparing the length of byssus threads animals produced in different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

Particle size range	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
	Animals	3	89.14	29.71	21.15	P< 0.001
<0.25mm	Error	163	228.98	1.40		
	Total	166	318.11			
	Animals	3	992.30	330.77	117.84	P< 0.001
0.25-0.5mm	Error	507	1423.10	2.81		
	Total	510	2415.41			
	Size range	2	314.439	157.219	169.219	P< 0.001
0.5-1.0mm	Error	956	887.318	0.928		
	Total	958	1201.757			
	Size range	3	659.675	219.89	211.28	P< 0.001
1.0-2.0mm	Error	828	861.740	1.04		
	Total	831	1521.410			
	Size range	3	480.78	160.26	158.21	P< 0.001
2.0-4.0mm	Error	788	798.22	1.01		
	Total	791	1279.00			
	Size range	3	214.672	71.557	72.557	P<0.001
4.0-8.0mm	Error	768	759.127	0.988		
	Total	771	973.799			
	Size range	3	68.75	22.92	18.15	P< 0.001
8.0-16.0mm	Error	464	585.88	1.26		
	Total	467	654.63			

Table 10. *Modiolus modiolus*. One-way analyses of variance comparing the length of byssus threads produced by animals in different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Size range	5	17.908	3.582	13.17	P<0.001
	Error	995	270.573	0.272		
	Total	1000	288.481			
Modiolus modiolus	Size range	6	3454.26	575.71	309.68	P<0.001
	Error	4487	8341.61	1.86		
	Total	4493	11795.87			

Table 11. One-way analyses of variance comparing the length of byssus threads produced in different particle size ranges of sediment for *M. edulis* (pooled data). d.f. = degrees of freedom, F = variance ratio and P = probability. Probabilities of P< 0.01 are regarded as significant.

Comparison	t	d.f.	P
0.25-0.5mm to 0.5-1.0mm	3.407	74	0.01> P> 0.001*
0.25-0.5mm to 1.0-2.0mm	2.311	84	0.05> P> 0.02
0.25-0.5mm to 2.0-4.0mm	6.473	368	P< 0.001*
0.25-0.5mm to 4.0-8.0mm	6.641	264	P< 0.001*
0.25-0.5mm to 8.0-16.0mm	5.653	341	P< 0.001*
0.5-1.0mm to 1.0-2.0mm	0.650	90	0.9> P> 0.5
0.5-1.0mm to 2.0-4.0mm	2.894	374	0.01> P> 0.001*
0.5-1.0mm to 4.0-8.0mm	2.939	270	0.01> P> 0.001*
0.5-1.0mm to 8.0-16.0mm	1.809	347	0.9> P> 0.05
1.0-2.0mm to 2.0-4.0mm	3.973	384	P< 0.001*
1.0-2.0mm to 4.0-8.0mm	3.948	280	P< 0.001*
1.0-2.0mm to 8.0-16.0mm	2.839	357	0.01> P> 0.001*
2.0-4.0mm to 4.0-8.0mm	0.090	564	P> 0.90
2.0-4.0mm to 8.0-16.0mm	2.468	641	0.02> P> 0.01
4.0-8.0mm to 8.0-16.0mm	2.214	537	0.05> P> 0.02

Table 12. *Mytilus edulis*. Students t-tests comparing the length of byssus threads produced in different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probability values of P< 0.01 are regarded as significant and are denoted an asterisk (*).

ranges. Significantly longer threads were produced in the particle size range 0.25-0.5mm than in the particle size ranges 0.5-1.0mm, 2.0-4.0mm, 4.0-8.0mm and 8.0-16.0mm. Significantly longer threads were produced in the particle size ranges 0.5-1.0mm and 1.0-2.0mm than in the particle size ranges 2.0-4.0mm and 4.0-8.0mm. In addition, significantly longer threads were produced in the particle size range 1.0-2.0mm than in the particle size range 8.0-16.0mm.

M modiolus (table 13): The general picture of results is that longer threads were produced in the two smallest particle size ranges. Significantly longer threads were produced in the particle size ranges < 0.25mm and 0.25 - 0.5mm than in larger particle size ranges. In addition, significantly longer threads were produced in the particle size range 0.25-0.5mm than in <0.25mm. Significantly longer threads were produced in the particle size ranges 1.0-2.0mm and 8.0-16.0mm than in the particle size ranges 2.0-4.0mm and 4.0-8.0mm.

Comparison	t	d.f.	P
< 0.25mm to 0.25–0.5mm	6.024	669	P< 0.001*
< 0.25mm to 0.5–1.0mm	12.216	1117	P< 0.001*
< 0.25mm to 1.0–2.0mm	10.696	990	P< 0.001*
< 0.25mm to 2.0–4.0mm	16.218	950	P< 0.001*
< 0.25mm to 4.0–8.0mm	17.608	930	P< 0.001*
< 0.25mm to 8.0–16.0mm	11.016	626	P< 0.001*
0.25–0.5mm to 0.5–1.0mm	26.775	1468	P< 0.001*
0.25–0.5mm to 1.0–2.0mm	24.355	1341	P< 0.001*
0.25–0.5mm to 2.0–4.0mm	30.370	1301	P< 0.001*
0.25–0.5mm to 4.0–8.0mm	31.035	1281	P< 0.001*
0.25–0.5mm to 8.0–16.0mm	20.589	977	P< 0.001*
0.5–1.0mm to 1.0–2.0mm	0.744	1789	0.5> P> 0.1
0.5–1.0mm to 2.0–4.0mm	10.563	1749	P< 0.001*
0.5–1.0mm to 4.0–8.0mm	10.637	1729	P< 0.001*
0.5–1.0mm to 8.0–16.0mm	0.518	1425	0.9> P> 0.5
1.0–2.0mm to 2.0–4.0mm	8.595	1622	P< 0.001*
1.0–2.0mm to 4.0–8.0mm	5.554	1602	P< 0.001*
1.0–2.0mm to 8.0–16.0mm	0.136	1298	0.9> P> 0.5
2.0–4.0mm to 4.0–8.0mm	0.459	1562	0.9> P> 0.5
2.0–4.0mm to 8.0–16.0mm	7.892	1258	P< 0.001*
4.0–8.0mm to 8.0–16.0mm	8.091	1238	P< 0.001*

Table 13. *Modiolus modiolus*. Students t-tests compariing the length of byssus threads produced in different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Number of threads/stone. Comparison between sediments of different particle size range and between species.

The number of threads/stone for animals in different particle size ranges are shown in Tables 14 (Mytilus edulis) and 15 (Modiolus modiolus).

One-way analyses of variance were performed on the data to test differences between animals in each particle size range. These showed that there were significant differences between animals for M. edulis in the particle size ranges 0.25-0.5mm, 0.5-1.0mm and 8.0-16.0mm (Table 16) and M. modiolus in the particle size ranges <0.25mm, 0.25-0.5mm and 1.0-2.0mm for M. modiolus (Table 17).

The data for M. edulis and for M. modiolus in each particle size range was pooled to test differences between particle size ranges. These are shown in Tables 14 (M. edulis) and 15 (M. modiolus).

One-way analyses of variance were performed on the pooled data to test differences in the number of threads/stone between particle size ranges. As for the length of byssus threads the results of pooled data were interpreted very carefully because significant differences were found between animals in several particle size ranges which had then been pooled. The same conservative criterion of $P < 0.01$ was therefore used to assess significance. The results showed that there were significant differences between particle size ranges for both species (Mytilus edulis $P < 0.001$; Modiolus modiolus $P < 0.001$, Table 18).

T-tests were then performed to compare differences between pairs of particle size ranges for M. edulis and for M. modiolus. These showed (Tables 19-20) that there was a significantly greater number of threads/stone in the larger of any particle sizes compared ($P < 0.001$ for all comparisons).

	Individual animals			Pooled animals	
Particle size range	Animal	N	Number of threads/stone mean s.d.	N	Number of threads/stone mean s.d.
0.25-0.5mm	1	151	0.181 ± 0.103	163	0.21 ± 0.15
	2	12	0.583 ± 0.195		
0.5-1.0mm	1	8	0.750 ± 0.267	67	0.61 ± 0.25
	2	51	0.560 ± 0.239		
	3	4	0.500 ± 0.000		
	4	4	1.000 ± 0.000		
1.0-2.0mm	1	4	1.000 ± 0.000	61	0.93 ± 0.23
	2	36	0.889 ± 0.211		
	3	4	1.000 ± 0.000		
	4	17	1.000 ± 0.306		
2.0-4.0mm	1	68	1.132 ± 0.411	298	1.12 ± 0.39
	2	32	1.094 ± 0.296		
	3	73	1.164 ± 0.441		
	4	125	1.104 ± 0.377		
4.0-8.0mm	1	45	1.556 ± 0.813	167	1.38 ± 0.83
	2	58	1.293 ± 0.773		
	3	40	1.325 ± 0.944		
	4	24	1.375 ± 0.824		
8.0-16.0mm	1	15	5.80 ± 6.16	98	3.15 ± 3.38
	2	17	2.94 ± 2.77		
	3	31	2.84 ± 2.34		
	4	35	2.40 ± 2.22		

Table 14. *Mytilus edulis*. The number of threads/stone (mean ± std dev) for animals in different particle size ranges of sediment. Columns 2-4 represent individual animals and columns 5-6 represent pooled animals for each particle size range. N = number of threads.

	Individual animals			Pooled animals	
Particle size range	Animal	N	Number of threads/stone mean s.d.	N	Number of threads/stone mean s.d.
< 0.25mm	1	162	0.117 ± 0.090	2073	0.078 ± 0.047
	2	1267	0.073 ± 0.043		
	3	559	0.077 ± 0.036		
	4	85	0.082 ± 0.012		
0.25-0.5mm	1	649	0.140 ± 0.058	3157	0.137 ± 0.062
	2	1222	0.141 ± 0.065		
	3	925	0.137 ± 0.066		
	4	361	0.121 ± 0.045		
0.5-1.0mm	1	633	0.334 ± 0.181	2363	0.367 ± 0.196
	2	941	0.386 ± 0.205		
	3	789	0.368 ± 0.193		
1.0-2.0mm	1	187	0.732 ± 0.376	1222	0.675 ± 0.381
	2	221	0.492 ± 0.291		
	3	330	0.697 ± 0.351		
	4	484	0.721 ± 0.416		
2.0-4.0mm	1	167	1.006 ± 0.681	808	0.971 ± 0.511
	2	265	0.921 ± 0.421		
	3	93	0.989 ± 0.590		
	4	283	0.993 ± 0.437		
4.0-8.0mm	1	118	2.11 ± 1.53	394	1.959 ± 1.49
	2	141	2.05 ± 1.64		
	3	70	1.64 ± 1.25		
	4	659	1.83 ± 1.29		
8.0-16.0mm	1	45	2.36 ± 1.69	182	2.751 ± 2.00
	2	29	2.90 ± 2.34		
	3	64	2.45 ± 1.73		
	4	44	2.75 ± 2.39		

Table 15. Modiolus modiolus. The number of threads/stone (mean ± std dev) for animals in different particle size ranges of sediment. Columns 2-4 represent individual animals and columns 5-6 represent pooled animals for each particle size range. N = number of threads.

Particle size range	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
	Animals	1	1.795	1.795	143.52	P< 0.001
0.25-0.5mm	Error	161	2.014	0.013		
	Total	162	3.809			
	Size range	3	0.904	0.301	5.65	0.005>
0.5-1.0mm	Error	63	3.362	0.053		P> 0.001
	Total	66	4.266			
	Size range	3	0.182	0.061	1.13	0.50> P>
1.0-2.0mm	Error	57	3.056	0.054		0.25
	Total	60	3.238			
	Size range	3	0.203	0.068	0.44	0.75> P>
2.0-4.0mm	Error	294	45.703	0.155		0.50
	Total	297	45.906			
	Size range	3	1.945	0.648	0.93	0.50> P>
4.0-8.0mm	Error	163	113.528	0.696		0.25
	Total	166	115.473			
	Size range	3	128.80	42.90	4.11	0.01> P>
8.0-16.0mm	Error	94	981.90	10.40		0.001
	Total	97	1110.70			

Table 16. *Mytilus edulis.* One-way analyses of variance comparing the number of threads/stone for animals in different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

Particle size range	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
	Animals	3	0.283	0.094	44.99	P< 0.001
<0.25mm	Error	2069	4.336	0.002		
	Total	2072	4.619			
	Animals	3	0.117	0.090	10.18	P< 0.001
0.25-0.5mm	Error	3153	12.124	0.003		
	Total	3156	12.242			
	Size range	2	0.185	0.093	28.87	P< 0.001
0.5-1.0mm	Error	2360	7.568	0.003		
	Total	2362	7.754			
	Size range	3	9.157	3.052	22.01	P< 0.001
1.0-2.0mm	Error	1218	168.898	0.139		
	Total	1221	178.055			
	Size range	3	1.041	0.347	1.33	0.50> P>
2.0-4.0mm	Error	804	209.496	0.261		0.25
	Total	807	210.537			
	Size range	3	11.92	3.97	1.79	0.25> P>
4.0-8.0mm	Error	390	865.43	2.22		0.20
	Total	393	877.35			
	Size range	3	7.46	2.49	0.62	0.75> P>
8.0-16.0mm	Error	178	713.11	4.01		0.50
	Total	181	720.57			

Table17. *Modiolus modiolus*. One-way analyses of variance comparing the number of threads/stone for animals in different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Size range	5	567.59	113.52	75.01	P< 0.001
	Error	848	1283.38	1.51		
	Total	853	1850.98			
Modiolus modiolus	Size range	6	2602.434	433.739	2111.50	P< 0.001
	Error	10192	2093.618	0.205		
	Total	10198	4696.051			

Table 18. One-way analyses of variance comparing the number of threads/stone in different particle size ranges of sediment (pooled data) d.f. = degrees of freedom, F = variance ratio and P = probability. Probabilities of P< 0.01 are regarded as significant.

Comparison	t	d.f.	P
0.25-0.5mm to 0.5-1.0mm	14.675	228	P< 0.001*
0.25-0.5mm to 1.0-2.0mm	27.019	222	P< 0.001*
0.25-0.5mm to 2.0-4.0mm	28.469	459	P< 0.001*
0.25-0.5mm to 4.0-8.0mm	17.649	328	P< 0.001*
0.25-0.5mm to 8.0-16.0mm	11.094	259	P< 0.001*
0.5-1.0mm to 1.0-2.0mm	7.479	126	P< 0.001*
0.5-1.0mm to 2.0-4.0mm	10.193	363	P< 0.001*
0.5-1.0mm to 4.0-8.0mm	7.425	232	P< 0.001*
0.5-1.0mm to 8.0-16.0mm	6.129	163	P< 0.001*
1.0-2.0mm to 2.0-4.0mm	3.639	357	P< 0.001*
1.0-2.0mm to 4.0-8.0mm	4.139	226	P< 0.001*
1.0-2.0mm to 8.0-16.0mm	5.107	157	P< 0.001*
2.0-4.0mm to 4.0-8.0mm	4.540	463	P< 0.001*
2.0-4.0mm to 8.0-16.0mm	10.169	394	P< 0.001*
4.0-8.0mm to 8.0-16.0mm	6.441	263	P< 0.001*

Table 19. Mytilus edulis. Students t-tests comparing the number of threads/stone for animals in different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Comparison	t	d.f.	P
< 0.25mm to 0.25-0.5mm	36.970	5228	$P < 0.001^*$
< 0.25mm to 0.5-1.0mm	65.459	4434	$P < 0.001^*$
< 0.25mm to 1.0-2.0mm	70.352	3293	$P < 0.001^*$
< 0.25mm to 2.0-4.0mm	78.809	2879	$P < 0.001^*$
< 0.25mm to 4.0-8.0mm	57.228	2465	$P < 0.001^*$
< 0.25mm to 8.0-16.0mm	56.847	2253	$P < 0.001^*$
0.25-0.5mm to 0.5-1.0mm	65.459	4434	$P < 0.001^*$
0.25-0.5mm to 1.0-2.0mm	76.609	4377	$P < 0.001^*$
0.25-0.5mm to 2.0-4.0mm	89.237	3963	$P < 0.001^*$
0.25-0.5mm to 4.0-8.0mm	68.110	3549	$P < 0.001^*$
0.25-0.5mm to 8.0-16.0mm	68.135	3337	$P < 0.001^*$
0.5-1.0mm to 1.0-2.0mm	31.976	3583	$P < 0.001^*$
0.5-1.0mm to 2.0-4.0mm	48.141	3169	$P < 0.001^*$
0.5-1.0mm to 4.0-8.0mm	49.376	2755	$P < 0.001^*$
0.5-1.0mm to 8.0-16.0mm	50.744	2543	$P < 0.001^*$
1.0-2.0mm to 2.0-4.0mm	14.994	2028	$P < 0.001^*$
1.0-2.0mm to 4.0-8.0mm	27.419	1614	$P < 0.001^*$
1.0-2.0mm to 8.0-16.0mm	29.818	1402	$P < 0.001^*$
2.0-4.0mm to 4.0-8.0mm	16.885	1200	$P < 0.001^*$
2.0-4.0mm to 8.0-16.0mm	20.086	988	$P < 0.001^*$
4.0-8.0mm to 8.0-16.0mm	4.093	574	$P < 0.001^*$

Table 20. Modiolus modiolus. Students t-tests comparing the number of threads/stone for animals in different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probabilities of $P < 0.01$ are regarded as significant and are denoted by an asterisk (*).

Size of byssus pads attached to sediment. Comparison between sediment of different particle size ranges and between species.

The size (pad size = (length + width)/2) and shape (length/width) of thirty byssus pads/that animals attached to different particle size ranges of sediment are shown in Tables 21 and 22. Figures 7 and 8 show byssus pads of Mytilus edulis and Modiolus modiolus attached to different particle size ranges of sediment.

Size of byssus pads

One-way analyses of variance were performed on the data to test differences between pad size in different particle size ranges for pooled animals of Mytilus edulis and of Modiolus modiolus. The data, as stated in the materials and methods were accidentally pooled. I have therefore interpreted the results very carefully and have taken the significant probability level as 0.01 (1%) rather than 5%. The anovars showed that there were significant differences in pad size between different particle size ranges for both species (Mytilus edulis $P<0.001$; Modiolus modiolus $P<0.001$, Table 23).

T-tests were then performed on data to compare differences between pairs of particle size ranges for M. edulis and M. modiolus. I have again taken the significant probability level as 0.01 (1%) rather than 0.05 (5%). The results are shown in Tables 24 (M. edulis) and 25 (M. modiolus). In each table significant results are denoted by an asterisk (*).

M. edulis: The results are shown in Table 24. In general smaller byssus pads were produced in particle size ranges less than 1.0mm. Significantly smaller pads were produced in the particle size ranges <0.25mm and 0.25-0.5mm than in other particle size ranges. Significantly smaller pads were produced in the particle size range 1.0-2.0mm than 4.0-8.0mm, in 2.0-4.0mm than 4.0-8.0mm and in 4.0-8.0mm than 8.0-16.0mm.

Particle size Range	*Mytilus edulis* Mean	*Mytilus edulis* std dev	*Modiolus modiolus* Mean	*Modiolus modiolus* std dev
8-16mm	0.904	0.228	1.390	0.341
4-8mm	1.105	0.171	1.163	0.192
2-4mm	0.982	0.173	1.378	0.269
1-2mm	0.975	0.152	1.055	0.192
0.5-1mm	0.585	0.154	0.679	0.205
0.25-0.5mm	0.490	0.092	0.684	0.153
<0.25mm	-	-	0.847	0.215

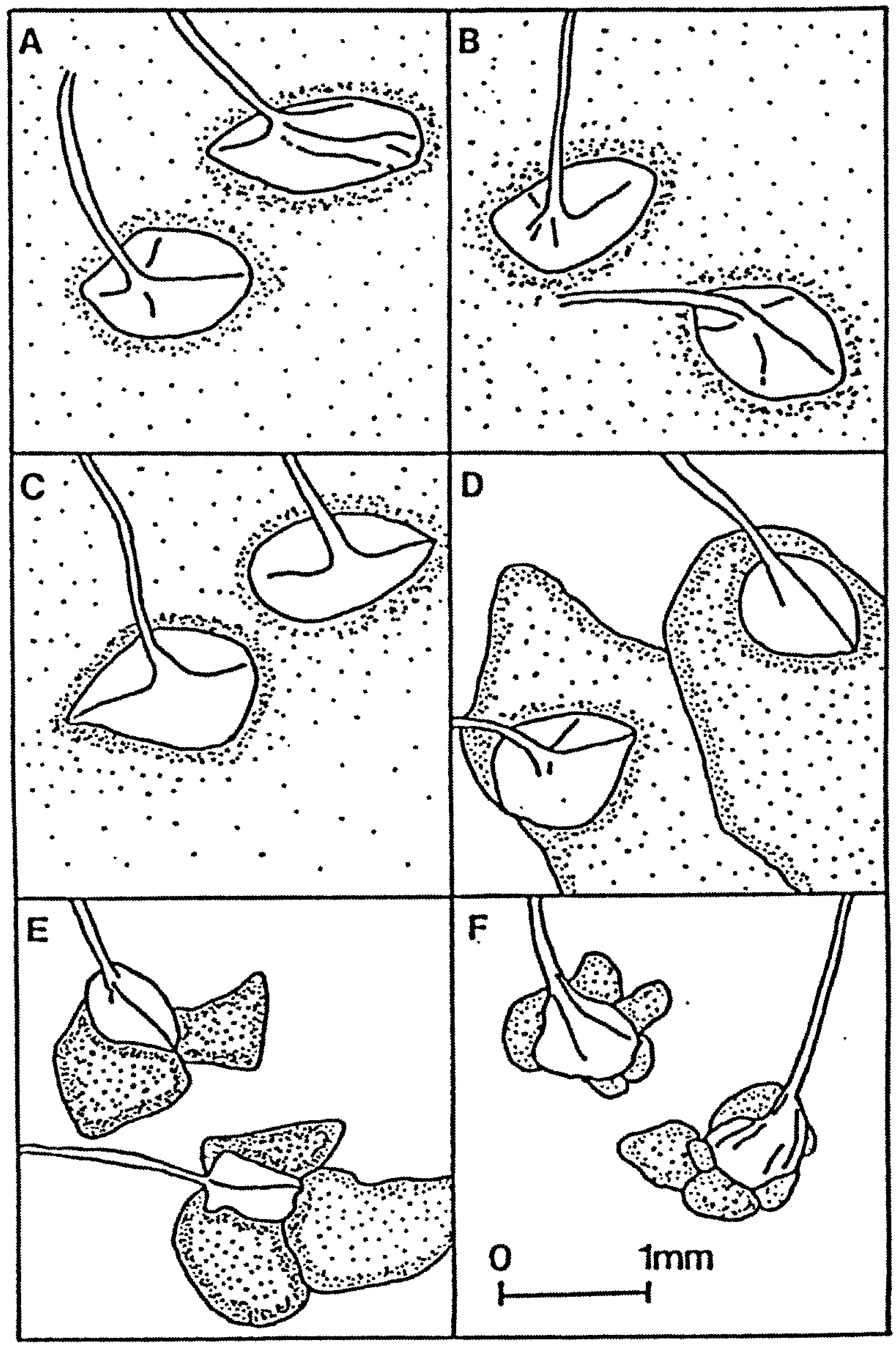
Table 21. The size of byssus pads *Mytilus edulis* and *Modiolus modiolus* attached to sediment of different particle size ranges. Size = (length + width)/2.

Particle size Range	*Mytilus edulis* Mean	*Mytilus edulis* std dev	*Modiolus modiolus* Mean	*Modiolus modiolus* std dev
8-16mm	1.813	0.638	1.828	0.908
4-8mm	1.532	0.321	1.577	0.505
2-4mm	1.514	0.369	2.035	0.655
1-2mm	1.627	0.349	2.088	0.653
0.5-1mm	1.655	0.433	2.680	1.207
0.25-0.5mm	1.498	0.229	2.077	1.143
<0.25mm	-	-	2.080	0.804

Table 22. The shape factor of byssus pads *Mytilus edulis* and *Modiolus modiolus* attached to sediment of different particle size ranges. Shape factor = length/width.

Figure 7. Byssus pads produced by *Mytilus edulis* in different particle size ranges of sediment. A to F represent different particle size ranges.

MYTILUS EDULIS



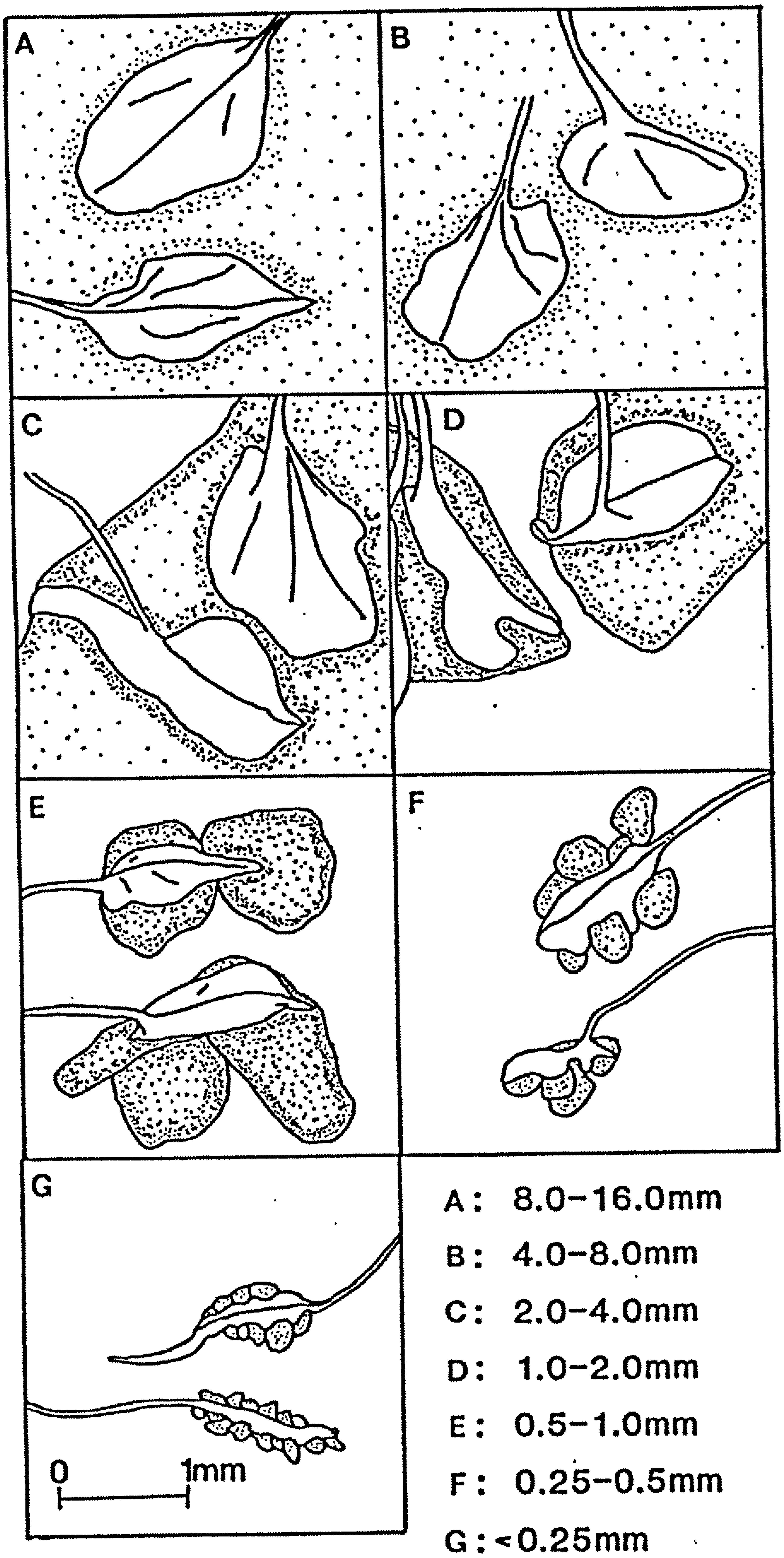
A: 8.0–16.0mm B: 4.0–8.0mm

C: 2.0–4.0mm D: 1.0–2.0mm

E: 0.5–1.0mm F 0.25–0.5mm

Figure 8. Byssus pads produced by *Modiolus modiolus* in different particle size ranges of sediment. A to F represent different particle size ranges.

MODIOLUS MODIOLUS



A: 8.0–16.0mm
B: 4.0–8.0mm
C: 2.0–4.0mm
D: 1.0–2.0mm
E: 0.5–1.0mm
F: 0.25–0.5mm
G: <0.25mm

Species	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus	Size range	5	5.8716	1.1743	38.83	P< 0.001
edulis	Error	174	5.2627	0.0302		
	Total	179	11.1343			
Modiolus	Size range	6	21.2518	3.5420	69.57	P< 0.001
modiolus	Error	203	10.3348	0.0509		
	Total	209	31.5866			

Table 23. One-way analyses of variance comparing the size of byssus pads attached to different particle size ranges of sediment (pooled data). d.f. = degrees of freedom, F = variance ratio and P = probability.

Comparison	t	d.f.	P
0.25-0.5mm to 0.5-1.0mm	2.502	58	0.02> P> 0.01
0.25-0.5mm to 1.0-2.0mm	7.379	58	P< 0.001*
0.25-0.5mm to 2.0-4.0mm	7.054	58	P< 0.001*
0.25-0.5mm to 4.0-8.0mm	10.030	58	P< 0.001*
0.25-0.5mm to 8.0-16.0mm	4.395	58	P< 0.001*
0.5-1.0mm to 1.0-2.0mm	9.872	58	P< 0.001*
0.5-1.0mm to 2.0-4.0mm	9.368	58	P< 0.001*
0.5-1.0mm to 4.0-8.0mm	12.368	58	P< 0.001*
0.5-1.0mm to 8.0-16.0mm	6.365	58	P< 0.001*
1.0-2.0mm to 2.0-4.0mm	0.159	58	0.9> P> 0.5
1.0-2.0mm to 4.0-8.0mm	3.103	58	0.01> P> 0.001*
1.0-2.0mm to 8.0-16.0mm	1.413	58	0.2> P> 0.1
2.0-4.0mm to 4.0-8.0mm	2.770	58	0.01> P> 0.001*
2.0-4.0mm to 8.0-16.0mm	1.481	58	0.2> P> 0.1
4.0-8.0mm to 8.0-16.0mm	3.852	58	P< 0.001*

Table 24. M. edulis. Students t-tests on the size of byssus pads attached to sediment of different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

M. modiolus: The results are shown in Table 25. In general, smaller pads were produced in particle size ranges less than 2.0-4.0mm. There were no significant differences in pad size between the particle size ranges 1.0-2.0mm and 4.0-8.0mm and between 2.0-4.0mm and 8.0-16.0mm. In all other comparisons, pads produced in the smaller particle size range were significantly smaller than pads produced in the larger particle size range.

T-tests were performed on data to compare differences between species at each particle size range. In the particle size ranges 0.25-0.5mm, 2.0-4.0mm and 8.0-16.0mm M. modiolus attached significantly larger byssus pads to sediment particles than did M. edulis (Table 26).

Shape of byssus pads

If a byssus pad is much longer than broad, it will have a large shape factor. Conversely, if it is not much longer than it is broad, it will have a small shape factor.

One-way analyses of variance were performed on the data to test differences between pads in different particle size ranges for Mytilus edulis and for Modiolus modiolus. The same conservative criterion of probability, that is, $P<0.01$ was used to assess significance. The results showed that there was a significant difference in pad shape between particle size ranges for M. modiolus ($P< 0.001$) but no significant difference between size ranges for M. edulis ($0.05> P> 0.025$, Table 27).

T-tests were then performed on data to compare differences between pairs of particle size ranges for M. edulis (Table 28) and M. modiolus (Table 29). In each table, significant values ($P< 0.01$ are denoted by an asterisk(*).

M. edulis (Table 28): In general, byssus pads were longer than broad. For all comparisons, there were no significant differences

Comparison	t	d.f.	P
0-0.25mm to 0.25-0.5mm	8.368	58	P< 0.001*
0-0.25mm to 0.5-1.0mm	4.629	58	P< 0.001*
0-0.25mm to 1.0-2.0mm	14.535	58	P< 0.001*
0-0.25mm to 2.0-4.0mm	17.260	58	P< 0.001*
0-0.25mm to 4.0-8.0mm	17.366	58	P< 0.001*
0-0.25mm to 8.0-16.0mm	13.958	58	P< 0.001*
0.25-0.5mm to 0.5-1.0mm	4.629	58	P< 0.001*
0.25-0.5mm to 1.0-2.0mm	3.966	58	P< 0.001*
0.25-0.5mm to 2.0-4.0mm	8.476	58	P< 0.001*
0.25-0.5mm to 4.0-8.0mm	6.014	58	P< 0.001*
0.25-0.5mm to 8.0-16.0mm	7.386	58	P< 0.001*
0.5-1.0mm to 1.0-2.0mm	7.339	58	P< 0.001*
0.5-1.0mm to 2.0-4.0mm	11.372	58	P< 0.001*
0.5-1.0mm to 4.0-8.0mm	9.447	58	P< 0.001*
0.5-1.0mm to 8.0-16.0mm	9.790	58	P< 0.001*
1.0-2.0mm to 2.0-4.0mm	5.344	58	P< 0.001*
1.0-2.0mm to 4.0-8.0mm	2.166	58	0.05> P> 0.02
1.0-2.0mm to 8.0-16.0mm	4.685	58	P< 0.001*
2.0-4.0mm to 4.0-8.0mm	3.554	58	P< 0.001*
2.0-4.0mm to 8.0-16.0mm	0.194	58	0.9> P> 0.5
4.0-8.0mm to 8.0-16.0mm	3.382	58	0.01> P> 0.001*

Table 25. M. modilus. Students t-tests on the size of byssus pads attached to sediment of different particle size ranges (pooled data). t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Comparison	t	d.f.	P
0.25–0.5mm	3.382	58	0.01> P> 0.001*
0.5–1.0mm	2.082	58	0.05> P> 0.02
1.0–2.0mm	1.796	58	0.1> P> 0.05
2.0–4.0mm	6.800	58	P< 0.001*
4.0–8.0cm	1.234	58	0.4> P> 0.2
8.0–16.0 mm	6.488	58	P< 0.001*

Table 26. Comparison between species. Students t-tests comparing the size of byssus pads _Mytilus edulis_ and _Modiolus modiolus_ attached to sediment of different particle size ranges. t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Species	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus	Size range	5	2.142	0.428	2.55	0.05> P>
edulis	Error	174	29.180	0.168		0.025
	Total	179	31.323			
Modiolus	Size range	6	20.177	3.363	4.40	P< 0.001
modiolus	Error	203	155.063	0.764		
	Total	209	175.240			

Table 27. One-way analyses of variance comparing the shape of byssus pads attached to sediments of different particle size range. Shape = length of pad/width of pad, d.f. = degrees of freedom, F = variance ratio and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Comparison	t	d.f.	P
0.25-0.5mm to 0.5-1.0mm	1.761	58	0.1> P> 0.05
0.25-0.5mm to 1.0-2.0mm	1.699	58	0.1> P> 0.05
0.25-0.5mm to 2.0-4.0mm	0.206	58	0.9> P> 0.5
0.25-0.5mm to 4.0-8.0mm	0.479	58	0.9> P> 0.5
0.25-0.5mm to 8.0-16.0mm	2.555	58	0.02> P> 0.01
0.5-1.0mm to 1.0-2.0mm	0.275	58	0.9> P> 0.5
0.5-1.0mm to 2.0-4.0mm	1.359	58	0.2> P> 0.1
0.5-1.0mm to 4.0-8.0mm	1.250	58	0.4> P> 0.2
0.5-1.0mm to 8.0-16.0mm	1.124	58	0.4> P> 0.2
1.0-2.0mm to 2.0-4.0mm	1.220	58	0.4> P> 0.2
1.0-2.0mm to 4.0-8.0mm	1.098	58	0.4> P> 0.2
1.0-2.0mm to 8.0-16.0mm	1.403	58	0.2> P> 0.1
2.0-4.0mm to 4.0-8.0mm	0.203	58	0.9> P> 0.5
2.0-4.0mm to 8.0-16.0mm	2.227	58	0.05> P> 0.02
4.0-8.0mm to 8.0-16.0mm	2.159	58	0.05> P> 0.02

Table 28. _M. edulis_. Students t-tests on the shape of byssus pads animals attached to sediment of different particle size ranges (pooled data). Shape = length of pad/width of pad, t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

between particle size ranges.

M. modiolus (Table 29: In general, byssus pads were longer than broad, and this was more pronounced at smaller particle size ranges. Byssus pads in the particle size range 0.5-1.0mm had a significantly larger shape factor than pads in the particle size range 8.0-16.0mm. Byssus pads in the particle size range<0.25 mm had a significantly larger shape factor than pads in the particle size ranges 4.0-8.0mm and 8.0-16.0mm. Finally, pads in the particle size ranges 1.0-2.0mm and 2.0-4.0mm had a significantly larger shape factor than pads in the particle size range 4.0-8.0mm.

T-tests were then performed on data to compare differences between species at each particle size range. The same conservative criterion of $P< 0.01$ was used for significance. The results (Table 30) showed that pads produced by M. modiolus had a significantly larger shape factor than pads produced by M. edulis in the particle size ranges 2-4mm, 1-2mm, 0.5-1.0mm and 0.25-0.5mm. There were no significant differences in the shape factor for pads produced in the particle size ranges 4-8mm and 8-16mm.

Comparison	t	d.f.	P
<0.25mm to 0.25-0.5mm	0.013	58	P> 0.9
<0.25mm to 0.5-1.0mm	2.264	58	0.05> P> 0.02
<0.25mm to 1.0-2.0mm	0.042	58	P> 0.9
<0.25mm to 2.0-4.0mm	0.235	58	0.9> P> 0.5
<0.25mm to 4.0-8.0mm	2.900	58	0.01> P> 0.001*
<0.25mm to 8.0-16.0mm	1.140	58	0.4> P> 0.2
0.25-0.5mm to 0.5-1.0mm	1.986	58	0.1> P> 0.05
0.25-0.5mm to 1.0-2.0mm	0.046	58	P> 0.9
0.25-0.5mm to 2.0-4.0mm	0.172	58	0.9> P> 0.5
0.25-0.5mm to 4.0-8.0mm	2.189	58	0.05> P> 0.02
0.25-0.5mm to 8.0-16.0mm	0.935	58	0.4> P> 0.2
0.5-1.0mm to 1.0-2.0mm	2.361	58	0.05> P> 0.02
0.5-1.0mm to 2.0-4.0mm	2.568	58	0.02> P> 0.01
0.5-1.0mm to 4.0-8.0mm	4.613	58	P< 0.001*
0.5-1.0mm to 8.0-16.0mm	3.089	58	0.01> P< 0.001*
1.0-2.0mm to 2.0-4.0mm	0.310	58	0.9> P> 0.5
1.0-2.0mm to 4.0-8.0mm	3.385	58	0.01> P> 0.001*
1.0-2.0mm to 8.0-16.0mm	1.274	58	0.4> P> 0.2
2.0-4.0mm to 4.0-8.0mm	3.032	58	0.01> P> 0.001*
2.0-4.0mm to 8.0-16.0mm	1.017	58	0.4> P> 0.2
4.0-8.0mm to 8.0-16.0mm	1.319	58	0.2> P> 0.1

Table 29. Students t-tests on the shape of byssus pads animals attached to sediment of different particle size ranges for Modiolus modiolus. Shape = length of pad/width of pad, t = students t, d.f. = degrees of freedom and P = probability. Probabilities of P< 0.01 are regarded as significant and are denoted by an asterisk (*).

Comparison	t	d.f.	P
0.25-0.5mm	2.721	58	$0.01 > P > 0.001^{*}$
0.5-1.0mm	4.374	58	$P < 0.001^{*}$
1.0-2.0mm	3.406	58	$0.01 > P > 0.001^{*}$
2.0-4.0mm	3.797	58	$P < 0.001^{*}$
4.0-8.0mm	0.413	58	$0.5 > P > 0.4$
8.0-16.0mm	0.072	58	$P > 0.9$

Table 30. Comparison between species. Students t-tests on the shape of byssus pads *Mytilus edulis* and *Modiolus modiolus* attached to sediments of different particle size range. Shape = length of pad/width of pad, t = students t, d.f. = degrees of freedom and P = probability.

GROUPS OF ANIMALS

The number of byssus threads animals attached to sediment, other animals, and the animal's own shell are shown in Table 31 (Mytilus edulis) and 32 (Modiolus modiolus). The total number of threads/animal are also included in each table. Tanks were numbered 1 to 5 for the particle size ranges <0.25mm, 0.25-0.5mm, 0.5-1.0mm, 1.0-2.0mm and 2.0-4.0mm respectively.

Mytilus edulis

Comparison within tanks (particle size ranges)

Animals attached most threads to other animals, with the exception of tank 1 (sediment of particle size range 2-4mm) where most threads were attached to sediment. In tanks 1 to 4 (sediment of particle size ranges <0.25mm to 1-2mm respectively) few animals attached threads to sediment or to the animals own shell. In tank 5 no animals attached threads to their own shell.

One-way analyses of variance and t-tests were performed on data to test for differences in the number of threads attached to different substrates (sediment, other animals and the animals own shell). These are shown in Tables 33 (anovars) and 34 (t-tests). There were significant differences between substrates for all tanks (Tables 33, M. edulis and 34, M. modiolus). Animals in tanks 1 to 4 (<0.25mm to 1.0-2.0mm respectively) attached significantly more threads to other animals than they did to sediment (Table 34). Animals in tanks 2 to 4 attached significantly more threads to other animals than they did to their own shell (Table 34). Animals in tank 5 (2.0-4.0mm), however attached significantly more threads to sediment than they did to other animals (Table 34).

Comparison between tanks (particle size ranges)

Animals in tank 5 (2.0-4.0mm) attached more threads to sediment particles and fewer threads to other animals than than did animals in

Tank	Particle size range	N	Threads to sediment		Threads to other animals		Threads to itself		Total number of threads	
			mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
1	<0.25mm	38	0	0	11.45	8.60	0.26	1.06	11.71	8.49
2	0.25-0.5mm	37	0.19	0.81	10.08	7.20	0.11	0.66	10.38	6.83
3	0.5-1.0mm	36	0.28	1.26	9.67	6.91	0.06	0.33	10.00	6.54
4	1.0-2.0mm	37	0.92	2.54	11.19	8.04	0.05	0.33	12.16	7.90
5	2.0-4.0mm	32	19.16	12.76	5.25	4.17	0	0	24.41	11.84

Table 31. The number of threads Mytilus edulis (groups of animals) attached to different substrates and the total number threads/animal in different particle size ranges of sediment. N = number of animals, s.d. = standard deviation.

Tank	Particle size range	N	Threads to sediment		Threads to other animals		Threads to itself		Total number of threads	
			mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
1	<0.25mm	5	86.6	108.3	27.8	36.3	0	0	114.4	89.6
2	0.25–0.5mm	4	93.0	36.1	30.0	32.6	0	0	123.0	56.8
3	0.5–1.0mm	5	123.0	56.8	15.4	34.4	0	0	138.4	35.6
4	1.0–2.0mm	4	160.5	80.3	24.5	24.2	0	0	185.0	75.0
5	2.0–4.0mm	5	224.0	54.8	13.2	16.7	0	0	229.2	51.0

Table 32. The number of threads *M. modiolus* attached to different substrates and the total number of threads/animal in different particle size ranges of sediment. N = number of animals, s.d. = standard deviation.

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
	Depth	2	2433.6	1216.8	69.02	P< 0.001
0.25-0.5mm	Error	108	1904.0	17.6		
	Total	110	4337.6			
	Depth	2	2166.9	1083.4	65.79	P< 0.001
0.5-1.0mm	Error	105	1729.1	16.5		
	Total	107	3896.0			
	Depth	2	2839.4	1419.7	59.79	P< 0.001
1.0-2.0mm	Error	108	2564.3	23.7		
	Total	110	5403.7			

Table 33. Mytilus edulis. One way analyses of variance comparing the number of threads groups of animals attached to several substrates for different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Comparison	t	d.f.	P
A	other animals to own shell	7.956	74	P< 0.001***
	sediment to other animals	8.308	72	P< 0.001***
B	sediment to own shell	0.472	72	0.90> P> 0.50
	other animals to own shell	8.394	72	P< 0.001***
	sediment to other animals	8.024	70	P< 0.001***
C	sediment to own shell	1.026	70	0.40> P> 0.20
	other animals to own shell	8.339	70	P< 0.001***
	sediment to other animals	7.408	72	P< 0.001***
D	sediment to own shell	2.052	72	0.05> P> 0.02 *
	other animals to own shell	8.416	72	P< 0.001***
E	sediment to other animals	5.858	62	P< 0.001***

Table 34. Students t-tests comparing the number of byssus threads groups of *Mytilus edulis* attached to several substrates for different particle size ranges of sediment. A = <0.25mm, B = 0.25-0.5mm, C = 0.5-1.0mm D = 1.0-2.0mm and E = 2-4mm. t = students t, d.f. = degrees of freedom and P = probability.

tanks 1 to 4 (<0.25mm, 0.25-0.50mm, 0.50-1.0mm, and 1.0-2.0mm). The total number of threads/animal in tank 5 was double that for tanks 1 to 4.

One-way analyses of variance and t-tests were performed on the data to test for differences in the number of threads attached to each substrate and for the total number of threads in different particle size ranges (Tables 35-37).

Threads attached to sediment (Table 36): Animals in tank 5 (2.0-4.0mm) attached significantly more threads to sediment than did animals in tanks 2 to 4 (0.25-0.5mm, 0.5-1.0mm and 1.0-2.0mm respectively. Animals in tank 1 (<0.25mm) did not attach threads to sediment. No other comparisons were significant.

Threads attached to other animals (Table 36): Animals in tank 5 (2-4mm) attached significantly fewer threads to other animals than did animals in tanks 1 to 4.

Threads attached to the animals own shell (Table 35): There were no significant differences between tanks 1 to 4. Animals in tank 5 did not attach threads to their own shells.

Total number of threads (Table 37): Animals in tank 5 produced significantly more threads than animals in tanks 1 to 4.

Modiolus modiolus

Comparison within tanks (particle size ranges)

Animals in all the tanks attached more threads to sediment than they did to other animals and did not attach threads to their own shell's.

The data for number of threads was found to have a non-normal distribution (using the rankit method to determine normality). Three transformations were used to assess which would be the best for normalising the data ($\log_{10}$ (x+1), $\sqrt{x}$ and arcsin). The best transformation was found to be $\log_{10}$ (x+1). Statistical analyses were

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Threads to sediment	Substrate	3	8673.2	2891.1	74.41	P< 0.001
	Error	138	5361.9	38.9		
	Total	141	14035.1			
Threads to other animals	Depth	4	836.8	209.2	4.01	0.005> P> 0.001
	Error	175	9139.8	52.2		
	Total	179	9976.6			
Threads to animals own shell	Substrate	3	1.094	0.356	0.81	0.50> P> 0.25
	Error	144	64.717	0.449		
	Total	147	65.811			
Total number of threads	Depth	4	4795.2	1198.8	16.88	P< 0.001
	Error	175	12431.3	71.0		
	Total	179	17226.4			

Table 35. Mytilus edulis. One way analyses of variance comparing the number of threads groups of animals produced in different particle size ranges of sediment. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Comparison	t	d.f.	P
A	0.25-0.5mm to 0.5-1.0mm	0.359	71	0.90> P> 0.50
	0.25-0.5mm to 1.0-2.0mm	1.663	72	0.20> P> 0.10
	0.25-0.5mm to 2.0-4.0mm	9.029	67	P< 0.001***
	0.5-1.0mm to 1.0-2.0mm	1.360	71	0.20> P> 0.10
	0.5-1.0mm to 2.0-4.0mm	8.835	66	P< 0.001***
	1.0-2.0mm to 2.0-4.0mm	8.508	67	P< 0.001***
B	<0.25mm to 0.25-0.5mm	0.745	73	0.50> P> 0.10
	<0.25mm to 0.5-1.0mm	0.979	72	0.40> P> 0.20
	<0.25mm to 1.0-2.0mm	0.134	73	0.90> P> 0.50
	<0.25mm to 2.0-4.0mm	3.721	68	P< 0.001***
	0.25-0.5mm to 0.5-1.0mm	0.251	71	0.90> P> 0.50
	0.25-0.5mm to 1.0-2.0mm	0.625	72	0.90> P> 0.50
	0.25-0.5mm to 2.0-4.0mm	3.340	67	0.01> P> 0.001 **
	0.5-1.0mm to 1.0-2.0mm	0.867	71	0.40> P> 0.20
	0.5-1.0mm to 2.0-4.0mm	3.142	66	0.01> P> 0.001 **
	1.0-2.0mm to 2.0-4.0mm	3.761	67	P< 0.001***

Table 36. Students t-tests comparing the number of byssus threads *Mytilus edulis* produced in different particle size ranges of sediment. A = threads attached to sediment and B = threads attached to other animals. t = students t, d.f. = degrees of freedom and P = probability.

Comparison	t	d.f.	P
<0.25mm to 0.25-0.5mm	0.747	73	0.50> P> 0.10
<0.25mm to 0.5-1.0mm	0.967	72	0.40> P> 0.20
<0.25mm to 1.0-2.0mm	0.238	73	0.90> P> 0.50
<0.25mm to 2.0-4.0mm	5.212	68	P< 0.001 ***
0.25-0.5mm to 0.5-1.0mm	0.242	71	0.90> P> 0.50
0.25-0.5mm to 1.0-2.0mm	1.039	72	0.40> P> 0.20
0.25-0.5mm to 2.0-4.0mm	6.128	67	P< 0.001 ***
0.5-1.0mm to 1.0-2.0mm	1.272	71	0.40> P> 0.20
0.5-1.0mm to 2.0-4.0mm	6.304	66	P< 0.001 ***
1.0-2.0mm to 2.0-4.0mm	5.115	67	P< 0.001 ***

Table 37. Students t-tests comparing the total number of byssus threads produced by Mytilus edulis in different particle size ranges. t = students t, d.f. = degrees of freedom and P = probability.

therefore performed on $\log_{10}$ (x+1) transformed data. In the particle size ranges 0.25-0.5mm and 1.0-2.0mm only four of the five animals produced threads. Animals which did not produce threads were not included in the statistical analyses.

T-tests were performed to test for differences in the numbers of threads attached to sediment and to other animals (Table 38). These showed that there was no significant difference in the number of threads between sediment and other animals for tanks 1 and 2 (particle size ranges <0.25mm and 0.25-0.5mm) and that in tanks 3-5 (0.5-1.0mm, 1.0-2.0mm and 2.0-4.0mm respectively) animals attached significantly more threads to sediment than they did to other animals.

Comparison between tanks (particle size ranges)

Animals in tanks 1 to 5 showed an increase in the number of threads with increasing particle size range (Table 32). There were no obvious differences in the number of threads attached to other animals between tanks. There was a corresponding increase in the total number of threads/animal with increasing particle size. One-way analyses of variance and t-tests were performed on the data to test for differences in the number of threads attached to each substrate and for the total number of threads in different tanks (Tables 39-40).

Threads attached to sediment (Table 40): Animals in tanks 2 and 3 (0.25-0.5mm and 0.5-1.0mm respectively) attached significantly fewer threads to sediment than did animals in tank 5 (2-4mm). The mean number of threads attached to sediment by animals in tank 1 (<0.25mm) was smaller than the means in tanks 2 and 3 but the comparison between tank 1 and tank 5 was not significant because the standard deviation in tank 1 was so large.

Threads attached to other animals (Table 39): There were no significant differences between tanks 1 to 5.

Total number of threads (Table 40): Animals in tank 5 produced

Comparison	t	d.f.	P
<0.25mm	1.052	8	0.40> P> 0.20
0.25-0.5mm	1.910	6	0.20> P> 0.10
0.5-1.0mm	4.365	8	0.01> P> 0.001**
1.0-2.0mm	2.574	6	0.05> P> 0.02*
2.0-4.0mm	5.167	8	P< 0.001***

Table 38. Students t-tests comparing the number of byssus threads groups of Modiolus modiolus attached to sediment and other animals for different particle size ranges of sediment ($\log_{10}$ (x+1) transformed data). t = students t, d.f. = degrees of freedom and P = probability.

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Threads to sediment	Substrate	4	1.967	0.492	2.26	0.25> P> 0.10
	Error	18	3.915	0.218		
	Total	22	5.882			
Threads to other animals	Depth	4	1.715	0.429	0.66	0.75> P> 0.50
	Error	18	11.624	0.646		
	Total	22	13.339			
Total number of threads	Depth	4	0.401	0.100	2.80	0.10> P> 0.05
	Error	18	0.645	0.036		
	Total	22	1.046			

Table 39. Modiolus modiolus. One way analyses of variance comparing the number of threads produced in different particle size ranges of sediment ($\log_{10}(x+1)$ transformed data). d.f. = degrees of freedom, F = variance ratio and P = probability.

significantly more threads than did animals in tanks 1 to 3. There was no significant difference between tanks 4 and 5.

	Comparison	t	d.f.	P
	<0.25mm to 0.25-0.5mm	0.933	7	0.40> P> 0.20
	<0.25mm to 0.5-1.0mm	1.356	8	0.40> P> 0.20
	<0.25mm to 1.0-2.0mm	1.356	7	0.40> P> 0.20
	<0.25mm to 2.0-4.0mm	2.034	8	0.10> P> 0.05
	0.25-0.5mm to 0.5-1.0mm	0.979	7	0.40> P> 0.20
A	0.25-0.5mm to 1.0-2.0mm	1.219	6	0.40> P> 0.20
	0.25-0.5mm to 2.0-4.0mm	3.738	7	0.01> P> 0.001**
	0.5-1.0mm to 1.0-2.0mm	0.569	1	0.90> P> 0.50
	0.5-1.0mm to 2.0-4.0mm	2.938	8	0.02> P> 0.01*
	1.0-2.0mm to 2.0-4.0mm	1.403	7	0.40> P> 0.20
	<0.25mm to 0.25-0.5mm	0.494	7	0.90> P> 0.50
	<0.25mm to 0.5-1.0mm	1.133	8	0.40> P> 0.20
	<0.25mm to 1.0-2.0mm	1.458	7	0.20> P> 0.10
	<0.25mm to 2.0-4.0mm	2.866	8	0.05> P> 0.02*
	0.25-0.5mm to 0.5-1.0mm	0.698	7	0.90> P> 0.50
B	0.25-0.5mm to 1.0-2.0mm	1.145	6	0.40> P> 0.20
	0.25-0.5mm to 2.0-4.0mm	3.005	7	0.02> P> 0.01*
	0.5-1.0mm to 1.0-2.0mm	0.849	7	0.50> P> 0.40
	0.5-1.0mm to 2.0-4.0mm	3.182	8	0.02> P> 0.01*
	1.0-2.0mm to 2.0-4.0mm	1.067	7	0.40> P> 0.20

Table 40. Students t-tests comparing the number of byssus threads groups of <u>Modiolus modiolus</u> produced in different particle size ranges ($\log_{10}$ (x+1) transformed data). A = threads attached to sediment and C = total number of threads. t = students t, d.f. = degrees of freedom and P = probability.

Clumping in *Mytilus edulis*

Only 5 *Modiolus modiolus* were used in each tank but it was clear that animals did not move towards one another.

The use of Nearest-neighbour analyses was originally employed to determine clumping in *M. edulis* (Pielou, 1977; Clark and Evans, 1954; Edgar and Meadows, 1969). The methods described in Clark and Evans (1954) were followed but they were not applicable to my data. I did not have enough time to pursue the method further.

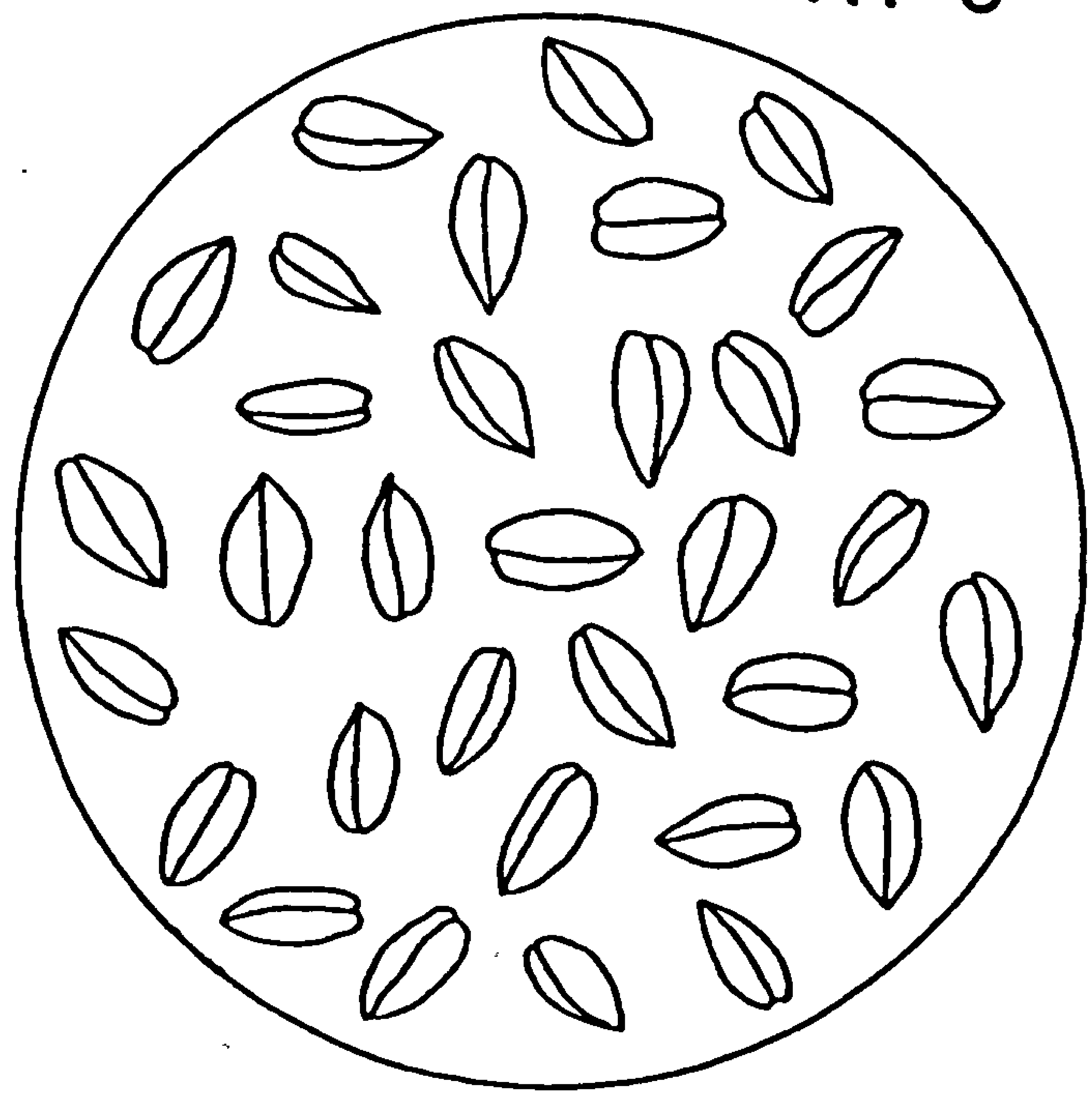
In all the tanks used in the experiment I have defined a group as a solitary animal or a clump of animals in which each animal touches at least one other member of the clump. The total number of groups, the number of groups containing 1 animal, 2 animals, 3 animals, 4 animals and >4 animals in different particle size ranges of sediment. for day 0 to day 12 is shown in Table 41. The mean number of animals/clump for days 0 to 12 are also shown in Table 41. This table and Figure 9 show that *M. edulis* had formed several clumps by day 1. In general, clumping continued at a slower rate from day 1 onwards. There appears to have been little change after 4-8 days.

Particle size range	Day	T	1	2	3	4	>4	Number of animals/group mean ± std dev
		Number of groups containing						
			animals					
<0.25mm	0	29	29	0	0	0	0	1.000 + ——
	1	21	24	0	0	0	1 (5)	1.381 ± 0.921
	2	16	8	5	2	0	1 (5)	1.813 ± 1.109
	4	15	6	6	2	0	1 (5)	1.933 ± 1.100
	8	11	4	4	1	0	2 (5,9)	2.636 ± 2.420
	12	13	4	4	1	1	2 (5,9)	2.636 ± 2.420
0.25-0.5mm	0	32	32	0	0	0	0	1.000 + ——
	1	14	5	4	2	2	1 (5)	2.286 ± 1.326
	2	13	5	2	2	3	1 (5)	2.462 ± 1.450
	4	11	3	2	1	4	1 (6)	2.909 ± 1.640
	8	8	2	2	0	3	1 (14)	4.000 ± 4.243
	12	8	2	2	0	3	1 (14)	4.000 ± 4.243
0.5-1.0mm	0	32	32	0	0	0	0	1.000 + ——
	1	20	13	3	3	1	0	1.600 ± 0.940
	2	18	10	5	1	1	1 (5)	1.778 ± 1.166
	4	14	4	6	1	2	1 (5)	2.286 ± 1.267
	8	12	2	4	3	2	1 (5)	2.667 ± 1.231
	12	11	1	4	2	3	1 (5)	2.909 ± 1.221
1.0-2.0mm	0	33	33	0	0	0	0	1.000 + ——
	1	19	11	5	1	1	1 (5)	1.738 ± 1.147
	2	15	8	2	2	1	2 (5,6)	2.200 ± 1.656
	4	12	5	4	1	0	2 (5,12)	2.750 ± 3.137
	8	10	3	3	1	1	2 (5,12)	3.300 ± 3.335
	12	9	2	3	1	1	2 (5,13)	3.667 ± 3.742
2.0-4.0mm	0	34	34	0	0	0	0	1.000 + ——
	1	24	17	4	3	0	0	1.417 ± 0.717
	2	20	13	2	3	2	0	1.700 ± 1.081
	4	14	7	3	0	2	2 (6,7)	2.249 ± 2.027
	8	12	4	3	1	2	2 (6,7)	2.833 ± 2.038
	12	11	3	1	2	0	2 (7,7)	3.091 ± 2.212

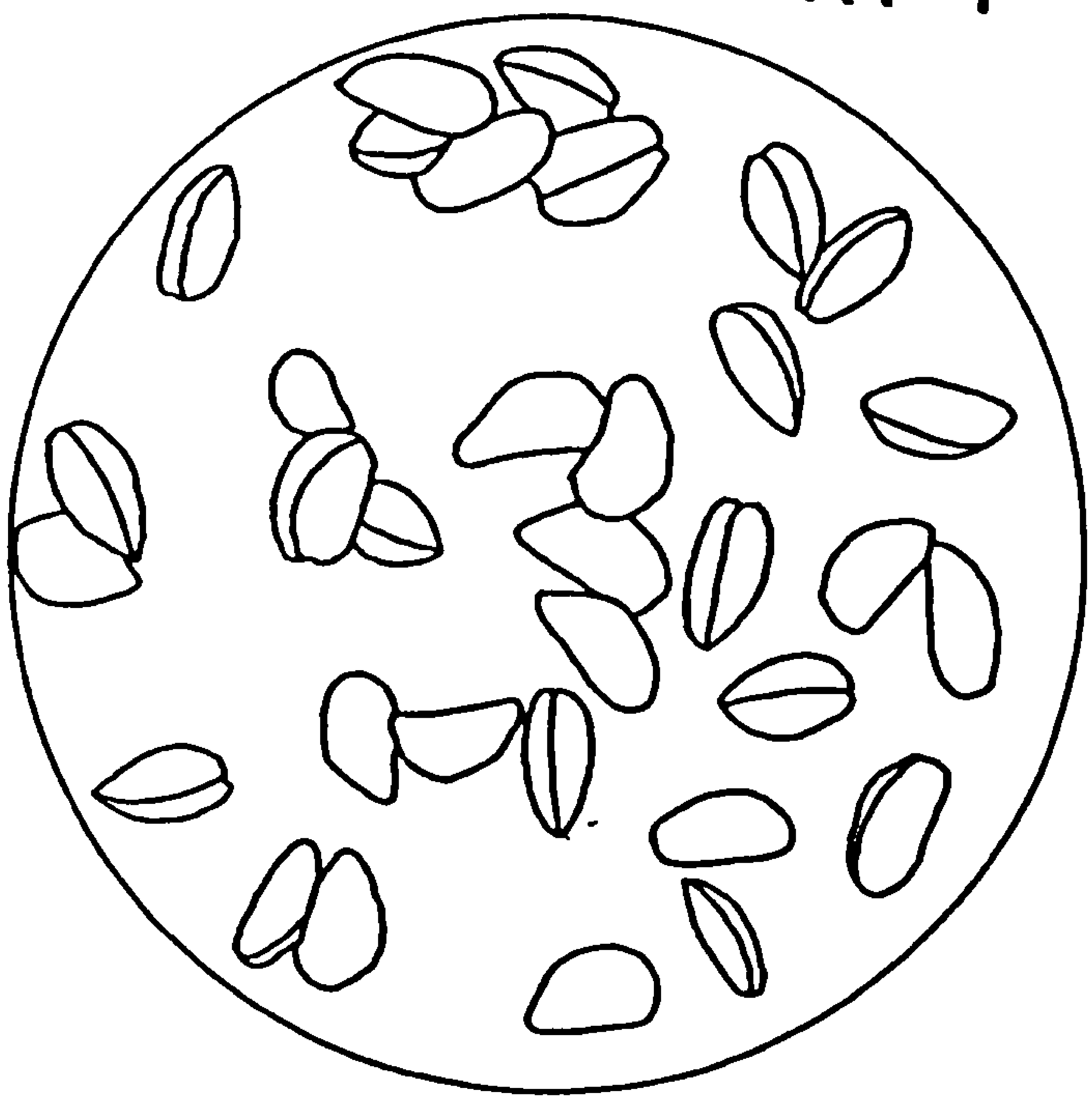
Table 41. The number of groups and mean number of animals/group (± standard deviation) for *M. edulis* in different particle size ranges of sediment. T = total number of groups and the numbers in brackets under the heading >4 animals are the number of animals in each clump.

Figure 9. Clumping in *Mytilus edulis* in sediment of particle size range 1.0-2.0mm. Animals were placed on the sediment surface at regular intervals (top). After 1 day (bottom) the animals had formed several small clumps.

DAY 0



DAY 1



PART 4. THE EFFECTS OF SEDIMENT WITH STONES PRESENT OR NOT PRESENT AT DIFFERENT DEPTHS ON BYSSUS THREAD FORMATION BY *Mytilus edulis* AND *Modiolus modiolus*

MATERIALS AND METHODS

Mytilus edulis and *Modiolus modiolus* were collected from Arrochar and Coilessan respectively. Sediment was collected from Arrochar. Details of animal and sediment collection are given on pages 64-65.

An area of sediment at Arrochar, close to the *Mytilus* site, was covered by small angular stones. The stones, approximately 5-20mm in diameter were also collected for the experiment.

COMPARISON OF ANIMALS FROM THE FIELD

In the laboratory threads were cut at the point of insertion between the two shell valves. A total of 18 *M. edulis* and 18 *M. modiolus* were collected but the threads with attached stones for 9 *M. edulis* and 10 *M. modiolus* were subsequently lost. The following details and measurements were obtained for the remaining 9 *Mytilus edulis* and 8 *Modiolus modiolus*:

1. The number of byssus threads and number of stones to which animals had attached byssus threads.

2. The length of 50 threads from the insertion point of the shell to the byssus pad.

3. The weight of stones to which threads were attached.

EXPERIMENT

Experimental sediments with stones present or not present at various depths in the sediment were prepared in the following way. Stones were wet-sieved between a 16mm and an 8mm sieve. The stones were then painted with a spot of white, green, red or blue Humbrol Enamel paint on the undersurface.

Sediment was wet-sieved through a 2mm sieve to obtain a large enough particle size difference between stones and sediment. Wet-sieving kept the sediment in as natural a state as possible.

The previous experiment (Part 3, Figure 5, p.86) showed that *M.*

modiolus readily attached byssus threads to sediment particles less than 2mm diameter whereas M. edulis attached few threads to sediment particles smaller than 2mm. The aim of this experiment was therefore to determine the response of both species to the presence or absence of stones at different depths in the sediment.

Sediment and stones were added to 18 clear perspex tanks(size 30 x 20 x 20cm). Eight combinations of up to 4 layers of painted stones were placed in the sediment at depths of 0-1cm(white), 3-4cm(green), 6-7cm(red), and 15-16cm(blue) for 8 pairs of tanks. In addition, one pair of tanks contained stones at each 1cm layer from 0cm down to 15cm. This gave 9 pairs of tanks, one of each pair for Mytilus edulis and one for Modiolus modiolus (figures 10-11). Each tank was marked at 1cm intervals from the sediment surface to a depth of 15cm.

The height of 100 stones was measured to determine whether the stones at the top of each 1cm layer touched the bottom of the layer. The mean height of stones $\pm$ SD was 0.724cm $\pm$ 0.226. Animals could therefore search through the sediment between stone layers in tank 9 (Figure 11) because the stones in different layers do not touch.

The perspex tanks were placed in larger tanks containing a continuous flow of water at 10^{o}C. Two M. edulis were added to each of nine tanks containing a different experimental sediment. This procedure was repeated for M. modiolus in the remaining 9 tanks. All animals were placed on the sediment surface at least 6cm apart, and left for 12 days.

The small tanks containing the sediment and mussels were removed after 12 days. Sediment was carefully removed with the aid of paintbrushes and weak water jets from syringes. Byssus threads were traced from the mussel to the attachment pad. The following

Figure 10. Explanation of experimental tanks used in experiment 2. The hatched areas represent layers of stones (A-D) in the sediment. The sediment in each tank was divided into four depths i.e. I = 0-2cm (includes the A layer); II = 2-5cm (includes the B layer); III = 5-8cm (includes the C layer); IV = 8-16cm (includes the D layer). All tanks were marked at 1cm intervals from 0 to 15cm.

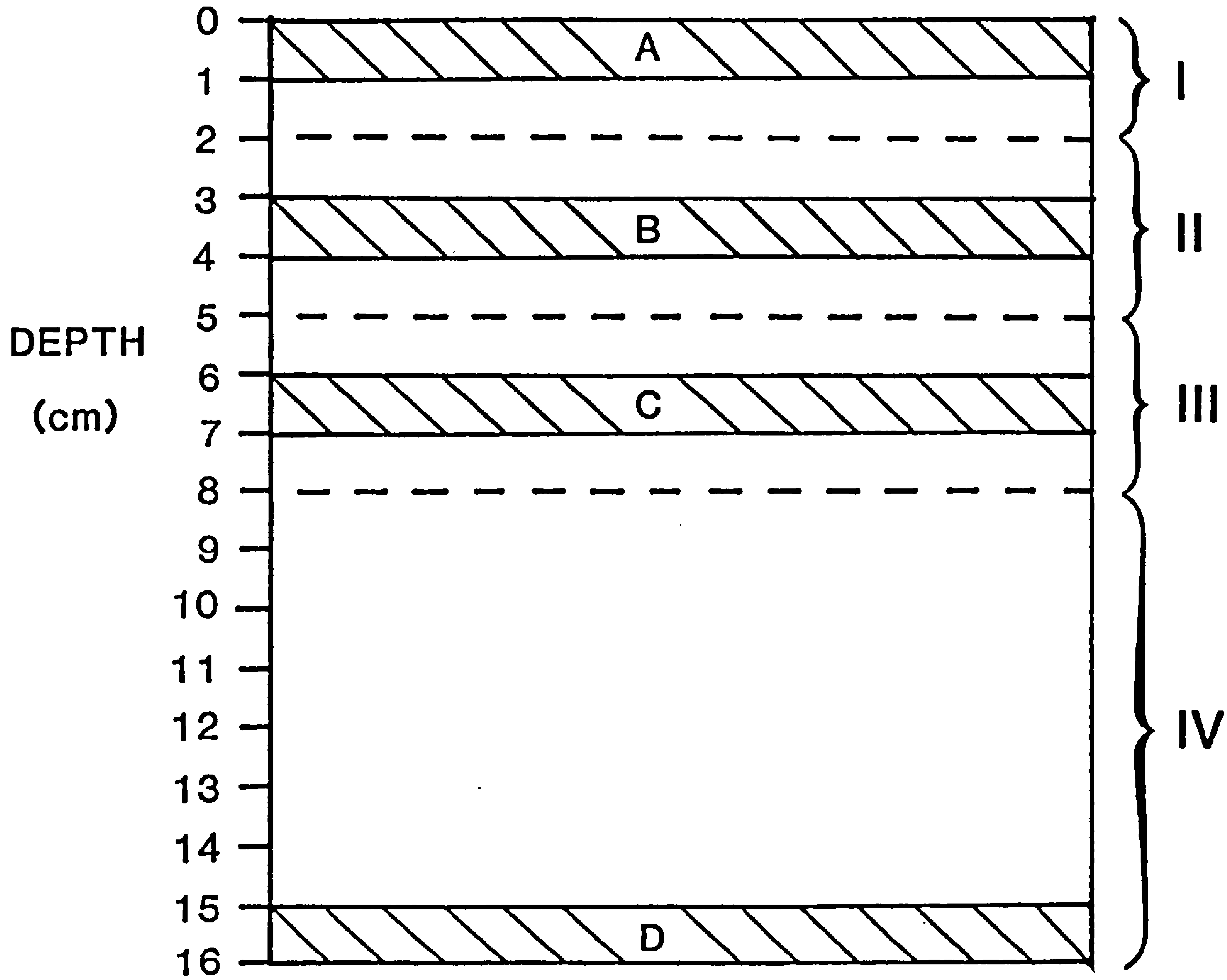

DEPTH
(cm)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
A
B
C
D
I
II
III
IV

Figure 11. Experimental tanks used in experiment 2. Each tank contains stone layer D (15-16cm).

Tank 1 = stone layer A (0-1cm) present in sediment

Tank 2 = stone layer B (3-4cm) present in sediment

Tank 3 = stone layer C (6-7cm) present in sediment

Tank 4 = stone layers A and B present in sediment

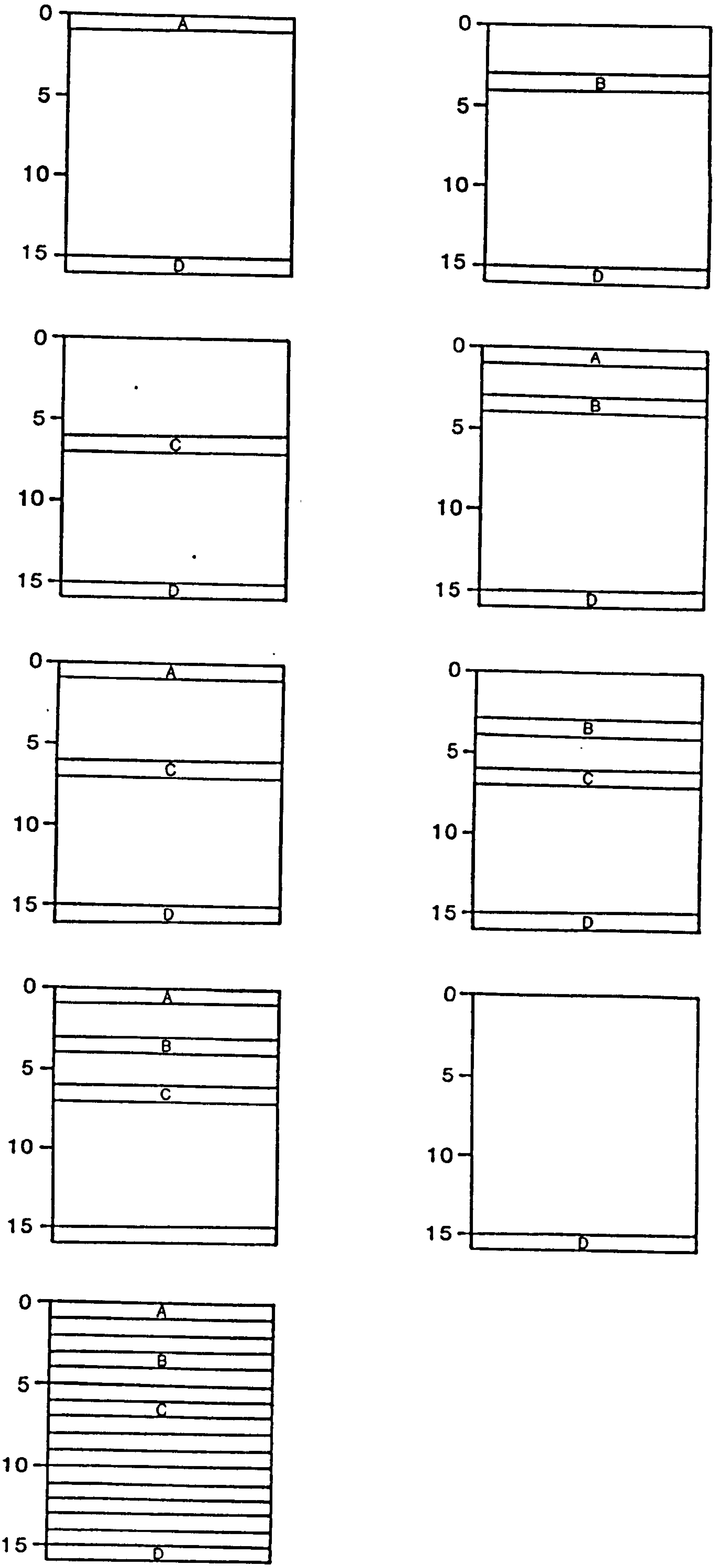
Tank 5 = stone layers A and C present in sediment

Tank 6 = stone layers B and C present in sediment

Tank 7 = stone layers A, B and C present in sediment

Tank 8 = control sediment

Tank 9 = stone layers present at each 1cm interval from 0 to 15cm in the sediment.



0
5
10
15
A
B
C
D

measurements were then taken.

1. The vertical depth of the thread from the sediment surface to each byssus pad.

2. The length of each thread from the pad to the point of insertion between the shell valves.

3. Plan view x and y co-ordinates were obtained with the aid of a clear perspex grid. These two co-ordinates, with the vertical depth of the thread gives a 3 dimensional co-ordinate for each thread.

A computer programme was written in MBasic to determine the plan, side and end view angles with corresponding length of vectors for each byssus thread (Appendix 2). Angles were calculated using x, y and d co-ordinates to determine the tan of the angle as follows:

tan A (plan view angle) = y/x

tan B (side view angle) = d/x

tan C (end view angle) = d/y

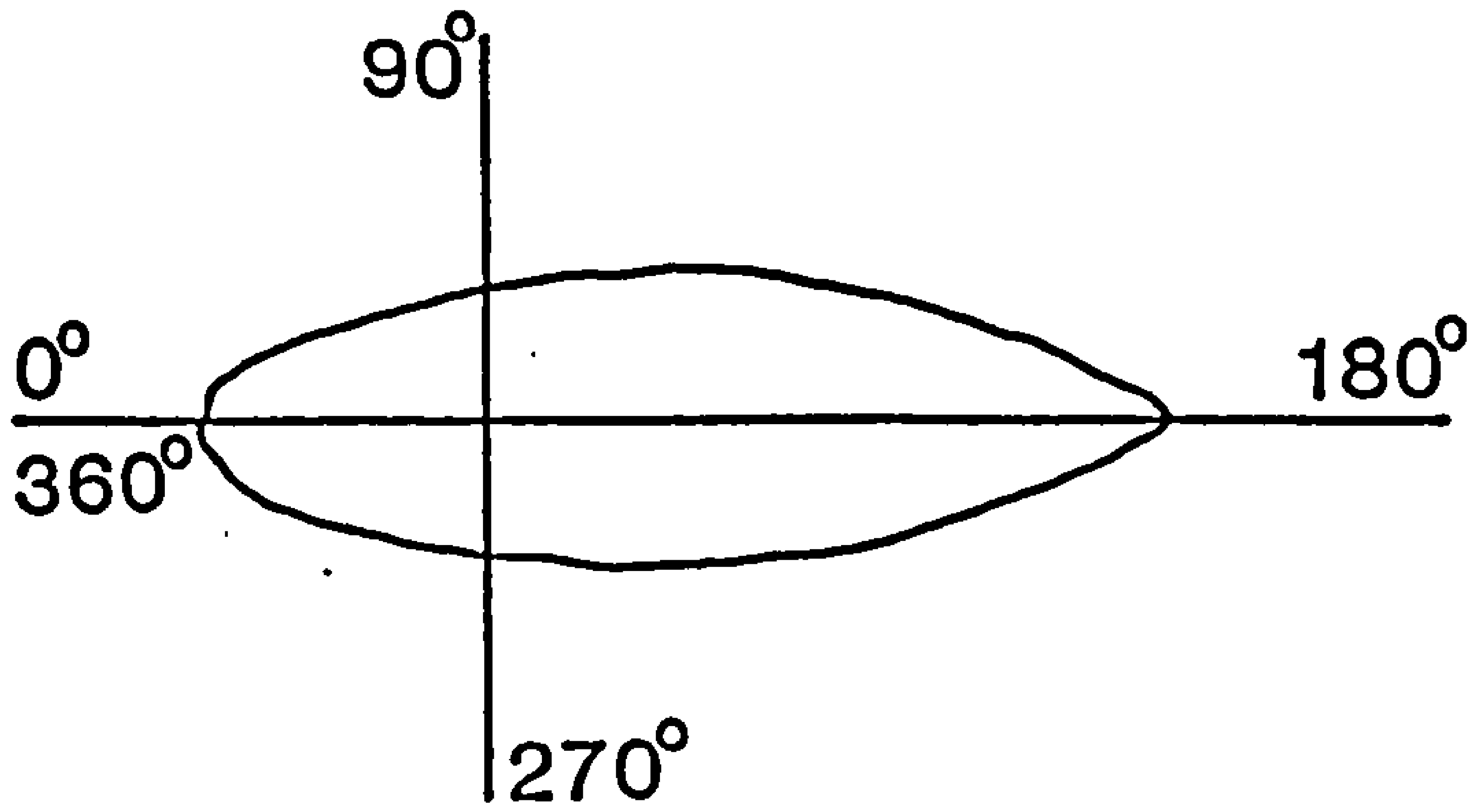
The angle calculated using the tangents of co-ordinates gives values for 0^{O} to 90^{O}. To obtain the true angle from 0 to 360^{O} (figure 12) the computer programme corrected the value obtained. The following are examples of the calculations for the x, y and depth co-ordinates (+5.0cm, -3.0cm, -2.0cm).

The computer programme calculates the angle in radians and this is converted to degrees using the following equation;

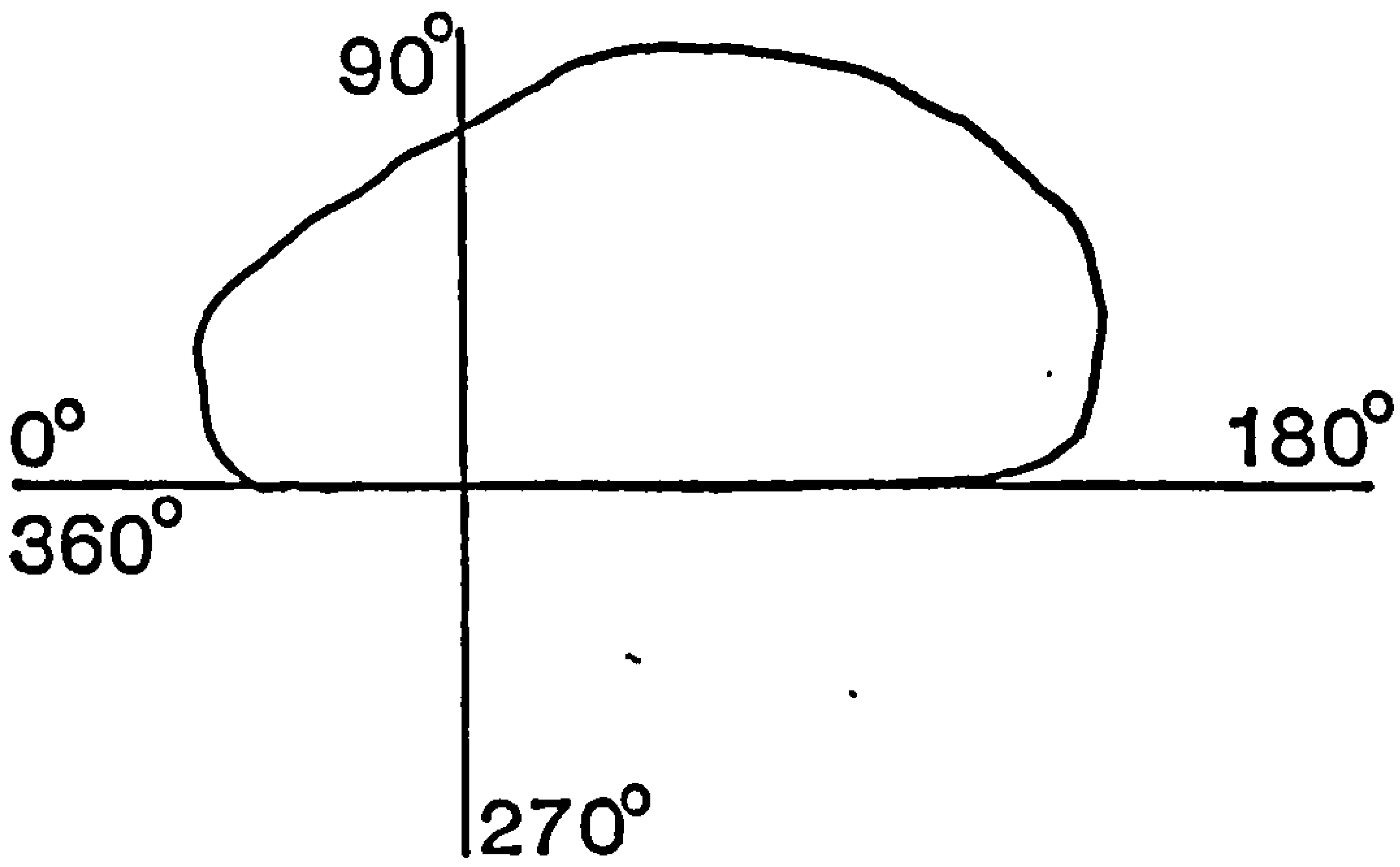
$$\text{Angle (degrees)} = \frac{\text{Angle (radians)} \times 360}{6.28318}$$

If the x co-ordinate for Angles A and B or the y co-ordinate for Angle C < 0 the angle is subtracted from 180^{O}. This is a mirror image across the $90^{O}/270^{O}$ line. If the y co-ordinate for Angle A or the d co-ordinate for Angles B and C < 0 the angle is then subtracted from 360^{O}. This is a mirror image across the $0^{O}/180^{O}$ line. If both of the above conditions occur (e.g. Angle A with x and y co-ordinates (+5.0,-

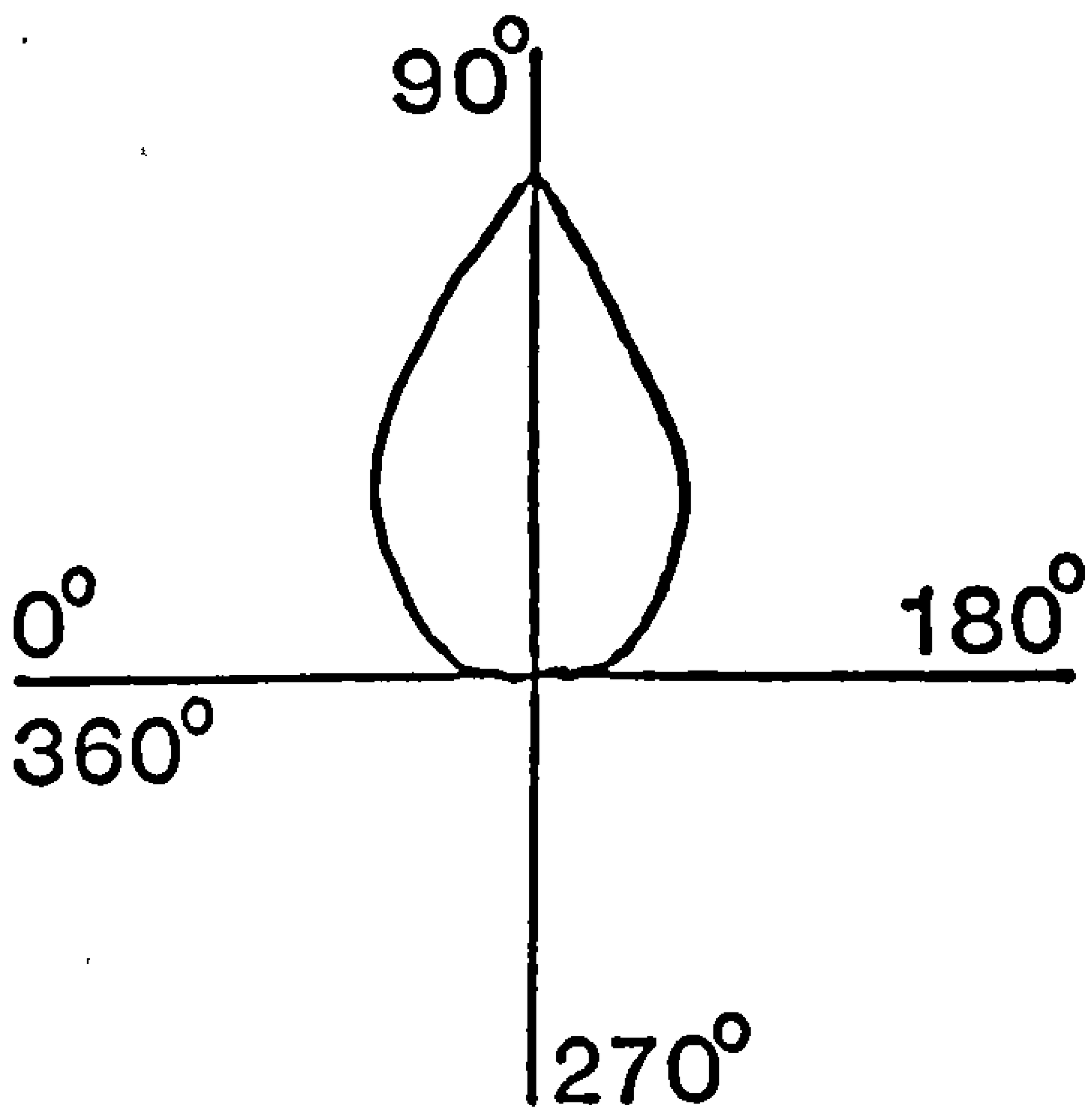
Figure 12. The angle of byssus threads from the animal to the attachment pad as seen in plan, side and end views of *Mytilus edulis* and *Modiolus modiolus*.



PLAN VIEW



SIDE VIEW



END VIEW

3.0)) the angle is subtracted from 180° and then subtracted from 360°.

I. Angle A (5.0, -3.0). The angle is between 180° and 270°

$\tan A = -3.0/+5.0 = -0.6$ Ignoring the sign,

arctan (radians)= 0.540

arctan (degrees)= (0.540*360)/6.28318 =30.940°

$x>0$ therefore 180°-30.940° = 149.06°

$y<0$ therefore Angle A = 360°-149.06° = 210.94°

II. Angle B (5.0, -2.0). The angle is between 180° and 270°

$\tan B = -2.0/+5.0 = -0.4$ Ignoring the sign,

arctan (radians)= 0.381

arctan (degrees) = (0.381*360)/6.28318 =21.830°

$x>0$ therefore B = 180°-21.830° = 158.17°

$d<0$ therefore Angle B = 360°-158.17° = 201.83°

III. Angle C (-3.0, -2.0) The angle is between 270° and 360°

$\tan C = -2.0/-3.0 = 0.666$ Ignoring the sign,

arctan (radians) = 0.588

arctan(degrees) = (0.588*360)/6.28318 =33.690°

Angle C = 360°-33.69° = 326.31°

An example of angles obtained for plan, side and end views of animals are shown in Figure 13(a).

The length of the vector for each angle was calculated in the following way:

Length of vector A (plan view) = $\sqrt{x^2 + y^2}$

Length of vector B (side view) = $\sqrt{x^2 + d^2}$

Length of vector C (end view) = $\sqrt{y^2 + d^2}$

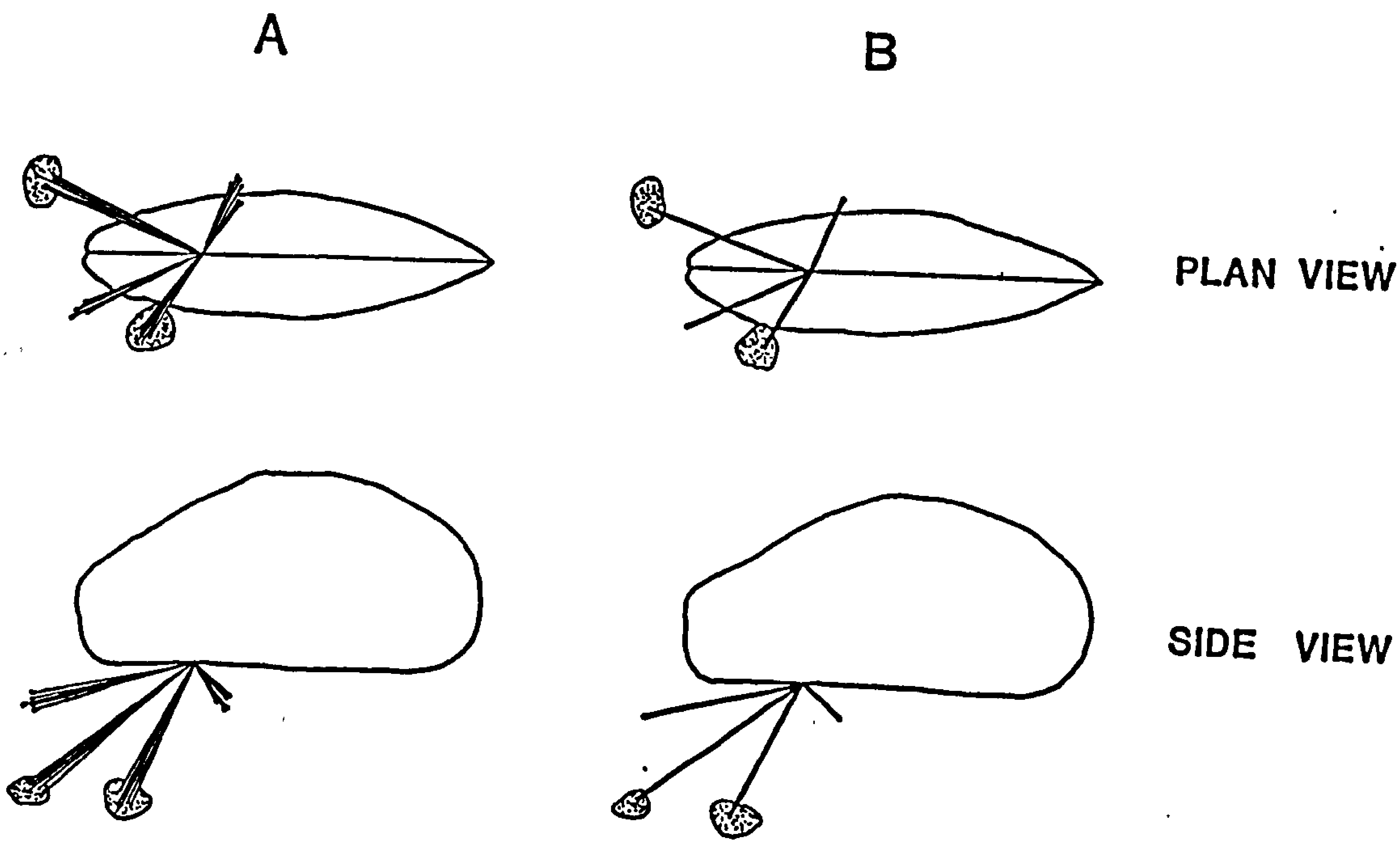
Using the co-ordinates on page 8,

Length of vector A (plan view) = $\sqrt{25 + 9} = 5.831$

Length of vector B (side view) = $\sqrt{25 + 4} = 5.385$

Length of vector C (end view) = $\sqrt{9 + 4} = 3.606$

Figure 13. Plan and side view vectors of byssus threads in experimental tanks. Diagram A: vectors of individual byssus threads attached to stones and sediment. Each vector is a combination of the angle of the byssus thread as seen from above (plan view) or the side (side view) and length of the vector as calculated from 2-dimensional co-ordinates. Diagram B: Each line (=mean vector) represents a group of byssus threads attached to a stone (both species)or to sediment (mainly Modiolus). The mean vector is a combination of the mean angle of n threads and mean length of n vectors.


A
B
PLAN VIEW
SIDE VIEW

It is clear from this worked example that the vector length does not represent the true length of the thread but represents the observed length of the thread from one of the three views. A diagramatic representation of vectors for individual threads for plan and side views of one animal is shown in Figure 13 (a). Groups of byssus threads form discrete clumps attached to a single stone (both species) or sediment (mainly Modiolus). The mean angle and length of these clumps of threads defines the mean vector of the clump. Plan and side views of the mean vectors are shown in Figure 13 (b) where each mean vector represents n threads attached to a single stone or clump of threads attached to sediment. The mean vector is therefore a combination of the mean angle of n threads and mean length of n vectors.

RESULTS

The results are divided into three main parts. The first part gives the results for animals taken from the sample sites in the field. The second gives the results for laboratory experiments with single animals. The third gives the results from experiments with groups of animals.

FIELD RESULTS

Comparison of the number of byssus threads, the number of attached stones and the number of threads/stone for *Mytilus edulis* and *Modiolus modiolus* in the field.

A total of 18 *M. edulis* and 18 *M. modiolus* were collected but the threads with attached stones for 9 *M. edulis* and 10 *M. modiolus* were subsequently lost. Statistical analyses were therefore performed on data obtained from the remaining samples.

The number of byssus threads, number of attached stones and the number of threads/stone for 9 *Mytilus edulis* and 8 *Modiolus modiolus* are shown in Tables 42 (*M. edulis*) and 43 (*M. modiolus*). In each table the number of threads are shown in column 2, stones in column 3 and threads/stone in column 4.

Number of threads and number of stones

The data for number of threads and number of stones were found to have a non-normal distribution (using the rankit method to determine normality; Sokal and Rholf, 1981). Three transformations were therefore performed on the data ($\log_{10}(x)$, $\sqrt{x}$ and arcsin). The best transformations were found to be $\log_{10}(x)$ for the number of threads and $\sqrt{x}$ for the number of stones.

Students t-tests were performed on the number of threads and the number of stones (transformed data) to test differences between

Animal	Number of threads	Number of stones	Number of threads/stone mean ± s.d.	Weight of stones mean ± s.d.	Total weight of stones(g)
1	76	51	1.490 ± 0.925	0.701 ± 2.373	35.752
2	61	47	1.298 ± 0.907	0.507 ± 1.692	23.852
3	236	64	3.688 ± 4.580	1.312 ± 2.967	83.977
4	129	35	3.686 ± 7.161	1.173 ± 4.997	41.065
5	68	18	3.778 ± 6.682	5.092 ± 19.79	91.652
6	124	69	1.797 ± 1.324	0.766 ± 4.781	52.852
7	193	95	2.032 ± 2.075	0.295 ± 1.590	28.043
8	127	52	2.442 ± 1.742	0.714 ± 0.766	37.100
9	112	38	2.947 ± 5.550	2.635 ± 13.55	100.127

Table 42. The number of threads, number of attached stones, number of threads/stone, weight of attached stones and the total weight of attached stones for *Mytilus edulis* taken from the field.

Animal	Number of threads	Number of stones	Number of threads/stone mean ± s.d.	Weight of stones (g) mean ± s.d.	Total weight of stones(g)
1	861	137	6.28 ± 10.40	1.069 ± 3.708	146.48
2	506	34	14.88 ± 23.46	5.279 ± 14.16	179.48
3	339	20	16.95 ± 22.31	3.660 ± 8.743	73.21
4	602	31	19.42 ± 34.86	1.544 ± 2.775	47.86
5	1193	133	8.97 ± 20.49	1.952 ± 6.215	259.57
6	2447	200	12.24 ± 22.44	1.821 ± 4.471	364.21
7	1459	91	16.03 ± 23.72	2.244 ± 4.584	204.23
8	1006	77	13.06 ± 18.50	1.869 ± 5.245	143.93

Table 43. The number of threads, number of attached stones, number of threads/stone, weight of attached stones and the total weight of attached stones for *Modiolus modiolus* taken from the field.

species. The following results were obtained.

1. M. modiolus produced significantly more byssus threads per animal than M. edulis ($P< 0.001$, Table 44).

2. M. modiolus did not attach byssus threads to significantly more stones than did M. edulis ($0.20> P> 0.10$ Table 44).

Number of threads/stone for Mytilus edulis and Modiolus modiolus in the field. Comparison within and between species.

A two-way analysis of variance was performed in which factor A was the fixed factor (species ie.M. edulis and M. modiolus), and factor B was the random factor (individuals). This is a 2 by 8 mixed model two-way nested analysis of variance (Sokal and Rohlf, 1981, pp.271-272 and Table 10.2,p.287). A two-way analysis of variance is normally performed on data of equal sample size. To obtain 8 subclasses for both species, and all subclasses (sample) of equal size, the following procedure was used:

1. To obtain 8 subclasses, each Mytilus edulis was numbered from 1 to 9. I chose one animal using random number tables. The data for this animal was discarded for the analysis, thus reducing the number of animals to that of M. modiolus (8 animals).

2. To obtain equal sample sizes the animal with the smallest sample size, n (where n equals the number of stones to which an animal attaches byssus threads) was chosen as the subclass size. The smallest sample size for an animal, hence subclass size was 18. The data for the other animals were numbered from 1 to n, where n was the sample size (number of stones). I then used random number tables to choose 18 values from the data for each animal. The 18 values obtained for each animal were used for the analysis.

The analysis showed that there was no significant differences between individuals ($0.50> P> 0.25$) but that there was a significant difference between species ($P< 0.001$, Table 45).

Data compared	t	d.f.	P
Number of byssus threads/animal	7.7596	15	P< 0.001***
Number of stones/animal to which byssus threads are attached.	1.4799	15	0.20>P> 0.10

Table 44. Students t-tests comparing the number of threads and the number of attached stones for M. edulis and M. modiolus. t = Student's t, d.f. = degrees of freedom and P = probability.

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Indiv.	7	1502	215	1.102	0.50> P> 0.25
Factor B: Species	1	6300	6300	32.307	P< 0.001
Interaction	7	714	102	0.523	0.90> P> 0.75
Error	272	53016	195		
Total	287	61533			

Table 45. Two-way analysis of variance comparing the number of threads/stone for Mytilus edulis and Modiolus modiolus from the field. d.f.= degrees of freedom, F= variance ratio and P= probability. Factor A (fixed): species (2 species= 2 levels); Factor B (random): individuals (8 individuals= 8 levels).

	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Indiv.	8	346.9	43.4	3.48	P< 0.001
	Error	460	5723.8	12.4		
	Total	468	6070.6			
Modiolus modiolus	Indiv.	7	9656	1380	3.17	0.01> P> 0.001
	Error	715	310988	435		
	Total	722	320646			

Table 46. One-way analyses of variance comparing the number of threads/stone for Mytilus edulis and for Modiolus modiolus taken from the field. Indiv.= individuals, d.f.= degrees of freedom, F= variance ratio and P= probability.

One way analyses of variance were then performed on the complete set of data for each animal to test for differences between animals. These showed that there was a significant difference between individuals for both species (Mytilus edulis, P< 0.001; Modiolus modiolus, 0.005> P> 0.001, Table 46).

The two-way anovar did not show a significant difference between animals. In contrast the one-way anovar showed a significant difference between individuals for both species. This is because the two-way analysis used only 18 values for each animal and the test was therefore less sensitive to differences between animals than the one-way anovar. Small differences are therefore less likely to be found significant. The between species comparison using two-way analysis of variance was very significant, highlighting the large difference between species.

Comparison of the weight of attached stones and the total weight of stones/animal for Mytilus edulis and Modiolus modiolus from the field.

The mean weight of stones/animal and total weight of stones/animal are shown in Tables 42 (M. edulis) and 43 (M. modiolus).

Weight of individual stones

A two-way analysis of variance was performed to determine differences between individuals and between species. In this analysis, factor A was the fixed factor (species) and factor B was the random factor (individuals). Equal subclass sizes were obtained in the same way as for the number of threads/stone. The analysis showed that there was no significant difference between individuals (0.75> P> 0.50) or between species (0.50> P> 0.10, Table 47).

One-way analyses of variance were performed on the complete set of data for each animal to determine differences between animals. These showed that there was no significant difference between animals for

Mytilus edulis ($0.25 > P > 0.10$), but that there was a significant difference between animals for Modiolus modiolus ($0.025 < P < 0.01$, Table 48).

The two-way analysis of variance used oly 18 values and did not show a significant difference between animals. In contrast, the one-way analysis of variance showed a significant difference between animals for M. modiolus. The two-way anovar was therefore probably less sensitive to differences between animals than the one-way anovar.

Total weight of stones/animal

The data for total weight of stones was found to have a non-normal distribution (using the rankit method to determine normality; Sokal and Rohlf, 1981). Three transforations were therefore performed on the data ($\log_{10}(x)$, $\sqrt{x}$ and arcsin. The best transformation was found to be $\sqrt{x}$. Statistical analyses were therefore performed on square-root transformed data.

A Students t-test was performed on the data to test for differences between species. This showed that M. modiolus attached byssus threads to a significantly greater total weight of stones than did M. edulis ($t = 3.835$, d.f. = 15 and $0.01 > P > 0.001$).

There was a significant difference between species for the total weight of stones (see above) but no significant difference in the number of stones (Table 44) or weight of individual stones (Table 48). One explanation for this may be that M. modiolus attached threads to a higher proportion of heavier stones than did M. edulis. To test this the number of stones to which each species attached threads were divided into two size classes (< 0.99g and > 1.0g). The number of stones > 1.00g for each animal was changed to a proportion of the total number of stones/animal. These are shown in Table 49. The arcsin transformation was then applied to the proportion (arcsin transformation = arcsin $\sqrt{P}$). A t-test was performed on transformed

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Indiv.	7	224.7	32.1	0.6978	0.75> P> 0.50
Factor B: Species	1	63.6	63.6	1.3826	0.25> P> 0.10
Interaction	7	363.6	51.9	1.128	0.50> P> 0.25
Error	272	12513.4	46.0		
Total	287	13165.2			

Table 47. Two-way analysis of variation comparing the weight of stones to which Mytilus edulis and Modiolus modiolus attached byssus threads in the field. d.f. = degrees of freedom, F = variance ratio and P = probability. Factor A (fixed): species (2 species= 2 levels); Factor B (random): individuals (8 individuals= 8 levels).

Species	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Indiv.	8	487.1	60.9	1.64	0.25> P> 0.10
	Error	460	17090.8	37.2		
	Total	468	17578.0			
Modiolus modiolus	Indiv.	7	558.5	79.8	2.46	0.025> P> 0.01
	Error	715	23227.5	32.5		
	Total	722	23786.0			

Table 48. One-way analyses of variance comparing the weight of stones to which field Mytilus edulis and Modiolus modiolus attached byssus threads taken from the field. Indiv. = individuals, d.f.= degrees of freedom, F= variance ratio and P= probability.

	Animal	0-0.99g	>1.00g
		Size class	
Mytilus edulis	1	41	10
	2	43	4
	3	29	6
	4	15	3
	5	63	6
	6	87	8
	7	29	23
	8	29	8
Modiolus modiolus	1	102	35
	2	19	16
	3	12	8
	4	15	16
	5	98	35
	6	113	77
	7	35	56
	8	53	24

Table 49. The number of stones in different weight classes to which *Mytilus edulis* and *Modiolus modiolus* attached byssus threads in the field.

Comparison	t	d.f.	P
Proportion of stones > 1.0g.	3.779	14	$0.01 > P > 0.001^{***}$

Table 50. Comparison between species. Students t-test on the proportion of stones > 1.00g for *M. edulis* and *M. modiolus* from the field (arcsin transformed data). t = students t, d.f. = degrees of freedom and P = probability.

data to compare differences between M. edulis and M. modiolus. This showed that M. modiolus attached byssus threads to a significantly higher proportion of heavier stones (> 1.00g) than did M. edulis (0.01> P> 0.001, Table 50).

Comparison of the length of byssus threads produced by Mytilus edulis and Modiolus modiolus in the field.

The mean length (± std dev) of 50 threads for each animal are shown in Table 51.

A two-way analysis of variance was performed on the data to determine differences between animals and between species. In this analysis, factor A was the fixed factor and factor B was the random factor (animals).

To obtain 8 subclasses for each species I used random number tables to choose the data for one of the nine Mytilus edulis. Data for the chosen animal was discarded for this analysis.

The results showed that the Interaction of Factor A (species) and Factor B (individuals) was significant (P< 0.001, Table 52). Hence no deductions could be made about significances of the two main factors, and one-way anovars were needed.

One-way analyses of variance were then performed on the lengths of 50 threads/animal for M. edulis and for M. modiolus to determine differences in thread length between individuals. These showed that there was a highly significant difference between individuals for M. edulis (P< 0.001) and for M. modiolus (P< 0.001 Table 53).

The animals for each species were then numbered from 1 to 8. I used random number tables to pair each M. edulis with one M. modiolus. Students t-tests were performed on the paired animals to test for differences between species. In all comparisons these showed that M. modiolus produced significantly longer byssus threads than did M. edulis (P< 0.001 for all comparisons, Table 54).

Animal	*M. edulis*		*M. modiolus*	
	Mean	std dev	Mean	std dev
1	1.024 ± 0.381		3.905 ± 1.363	
2	0.970 ± 0.348		2.966 ± 0.937	
3	1.419 ± 0.505		2.431 ± 0.975	
4	1.217 ± 0.487		2.619 ± 0.987	
5	1.323 ± 0.403		3.438 ± 1.254	
6	0.826 ± 0.384		3.696 ± 1.240	
7	1.610 ± 0.484		3.377 ± 0.945	
8	1.101 ± 0.397		2.547 ± 1.030	
9	0.996 ± 0.352		----	----

Table 51. The mean length of byssus threads produced by *Mytilus edulis* and *Modiolus modiolus* in the field. 30 threads were measured for each animal.

Comparison	d.f.	Sum of squares	Mean of squares	F	P
Species	1	776.637	776.637	1133.77	Not applicable
Individuals	7	73.756	10.537	15.38	Not applicable
Interaction	7	70.766	10.109	14.75	P< 0.001
Error	784	537.278	0.685		
Total	799	1458.437			

Table 52. Two-way analysis of variance on the length of byssus threads produced by Mytilus edulis and Modiolus modiolus in the field. d.f. = degrees of freedom, F = variance ratio and P = probability. Factor A (fixed): species (2 species = 2 levels); Factor B (random): individuals (8 individuals = 8 levels).

Species	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus edulis	Indiv.	8	24.683	3.085	18.56	P< 0.001
	Error	441	73.327	0.166		
	Total	449	98.011			
Modiolus modiolus	Indiv.	7	124.26	17.750	14.59	P< 0.001
	Error	392	476.99	1.22		
	Total	399	601.25			

Table 53. One-way analyses of variance comparing the length of byssus threads produced in the field for Mytilus edulis and for Modiolus modiolus. Indiv. = individuals, d.f. = degrees of freedom, F = variance ratio and P = probability.

Animals compared *M. edulis*	*M. modiolus*	t	d.f.	P
Animal 1	to animal 4	11.037	98	P< 0.001***
Animal 2	to animal 5	13.264	98	P< 0.001***
Animal 3	to animal 3	6.914	98	P< 0.001***
Animal 4	to animal 1	12.857	98	P< 0.001***
Animal 5	to animal 2	14.942	98	P< 0.001***
Animal 6	to animal 8	5.787	98	P< 0.001***
Animal 7	to animal 7	15.684	98	P< 0.001***
Animal 8	to animal 6	14.793	98	P< 0.001***

Table 54. Comparison between species. Students t-tests on the length of byssus threads produced by animals in the field. t = students t, d.f. = degrees of freedom and P = probability.

LABORATORY EXPERIMENTS: SINGLE ANIMALS

Position of byssus pads in sediment with stones present or not present at different depths

The mean angles for groups of byssus threads attached to stones at different depths and to sediment for three Mytilus edulis and three Modiolus modiolus are shown in Tables 55 and 56. Each table shows the results for one animal in tanks 7 (stone layers present at depths of 0-1cm, 3-4cm and 6-7cm), 6 (stone layers present at depths 3-4cm and 6-7cm) and 8 (no stone layers present). In addition, Figures 14 and 15 show plan, side and end views for the mean angles and vector lengths of threads for each animal. The mean angles and vector lengths of threads for the remaining animals are given in Appendix 3A.

Several interesting points can be shown from Tables 55-56 and Figures 14-15. M. edulis readily attached threads to stones but rarely attached threads to sediment. Animals only attached threads when a stone layer was not present at the surface. Hence, when a stone layer was not present at the sediment surface very few or no threads were produced. When stones were present at the surface animals pulled stones upwards, towards the animal's own shell. M. modiolus attached many threads to stones and to sediment even when stones were not present in the sediment. Animals attached threads to stones present at the three depths (0-1cm, 3-4cm and 6-7cm). The searching and burrowing activities of animals caused stones from the surface (0-1cm) to be forced deeper in the sediment.

It is clear that both species modify their sedimentary environment, M. edulis attaching threads at the surface and M. modiolus at the surface and down to depths of about 7cm. The movement of stones above (M. edulis) and below (M. modiolus) the surface changes the physical composition of the sediment. Statistical analyses on byssus thread production will now be reported.

Table 55. Mytilus edulis. The mean plan, side and end view angles for groups of byssus threads attached to stones and to sediment. A is the plan view angle, B is the side view angle and C is the end view angle. AA, BB and CC are the corresponding vector lengths for each group of threads. One animal from each of three tanks are shown. Tank 7 contains stone layers at the depths 0-1cm (a layer), 3-4cm (b layer) and 6-7cm (c layer). Tank contains stone layers at the depths 3-4cm and 6-7cm. Tank 8 is the control tank with no stone layers present.

Substrate	number of threads	Angle	mean	sd	Vector	mean	sd
Tank 7 (a,b,c stone layers) animal 1							
stone 1 (a layer)	5	A	176.74	9.00	AA	1.135	0.594
		B	177.21	3.75	BB	1.125	0.588
		C	183.00	0.17	CC	0.186	0.166
stone 2 (a layer)	3	A	159.43	49.43	AA	0.726	0.251
		B	157.22	23.68	BB	0.611	0.377
		C	108.82	78.13	CC	0.366	0.117
stone 3 (a layer)	9	A	120.24	41.14	AA	0.499	0.175
		B	212.48	58.16	BB	0.582	0.180
		C	199.62	53.06	CC	0.551	0.186
stone 4 (a layer)	2	A	151.07	0.06	AA	0.688	0.001
		B	189.19	0.71	BB	0.610	0.002
		C	196.31	1.17	CC	0.347	0.004
stone 5 (a layer)	2	A	51.60	1.63	AA	0.701	0.032
		B	30.24	15.70	BB	0.519	0.079
		C	154.61	15.00	CC	0.621	0.036
stone 6 (a layer)	12	A	134.76	29.26	AA	0.564	0.188
		B	225.30	21.82	BB	0.492	0.252
		C	219.42	25.45	CC	0.464	0.180
Tank 6 (b,c layers)							
sediment	1	A	347.78	——	AA	0.246	——
		B	291.74	——	BB	0.648	——
		C	274.94	——	CC	0.604	——
sediment	1	A	342.71	——	AA	0.411	——
		B	326.85	——	BB	0.468	——
		C	295.48	——	CC	0.284	——
Tank 8 animal 1							
sediment	4	A	113.33	13.65	AA	0.888	0.242
		B	256.02	10.77	BB	1.534	0.101
		C	242.03	3.18	CC	1.662	0.054

Table 56. Modiolus modiolus. The mean plan, side and end view angles for groups of byssus threads attached to stones and to sediment. A is the plan view angle, B is the side view angle and C is the end view angle. AA, BB and CC are the corresponding vector lengths for each group of threads. One animal from each of three tanks are shown. Tank 7 contains stone layers at the depths 0-1cm (a layer), 3-4cm (b layer) and 6-7cm (c layer). Tank 6 contains stone layers at the depths 3-4cm and 6-7cm. Tank 8 is the control tank with no stone layers present.

Substrate	number of threads	Angle	mean	sd	Vector	mean	sd
Tank 7 (a,b,c stone layers) animal 1							
stone 1 (a layer)	2	A	192.22	2.92	AA	0.624	0.080
		B	215.87	4.67	BB	0.752	0.061
		C	286.51	1.21	CC	0.457	0.018
stone 2 (a layer)	11	A	17.28	6.93	AA	1.531	0.201
		B	336.70	2.46	BB	1.578	0.174
		C	235.14	12.03	CC	0.784	0.120
stone 3 (b layer)	2	A	349.32	0.88	AA	1.455	0.033
		B	320.01	0.63	BB	1.867	0.021
		C	282.68	1.29	CC	1.230	0.006
stone 4 (b layer)	6	A	324.51	0.61	AA	0.956	0.059
		B	300.31	2.13	BB	1.553	0.194
		C	292.66	1.96	CC	1.454	0.194
sediment	7	A	314.66	11.14	AA	2.689	0.225
		B	316.80	6.20	BB	2.544	0.408
		C	317.27	6.62	CC	2.556	0.239
sediment	7	A	300.91	0.97	AA	2.885	0.068
		B	320.21	0.76	BB	1.928	0.039
		C	333.50	0.78	CC	2.766	0.082
sediment	9	A	235.58	1.74	AA	0.796	0.021
		B	262.50	0.41	BB	3.445	0.007
		C	280.88	0.41	CC	3.478	0.008
sediment	1	A	308.66	——	AA	0.384	——
		B	273.96	——	BB	3.479	——
		C	274.94	——	CC	3.484	——
sediment	1	A	67.65	——	AA	0.973	——
		B	279.73	——	BB	2.189	——
		C	247.36	——	CC	2.338	——
sediment	17	A	190.48	3.03	AA	1.205	0.074
		B	225.80	0.72	BB	1.696	0.081
		C	280.21	2.98	CC	1.237	0.065
sediment	1	A	71.57	——	AA	0.949	——
		B	277.13	——	BB	2.417	——
		C	249.44	——	CC	2.562	——
sediment	1	A	258.69	——	AA	1.020	——
		B	267.17	——	BB	4.055	——
		C	283.87	——	CC	4.172	——
sediment	1	A	82.11	——	AA	2.039	——
		B	273.77	——	BB	4.260	——
		C	244.58	——	CC	4.707	——

Substrate	number of threads	Angle	mean	sd	Vector	mean	sd
Tank 6; animal 1							
stone 1 (b layer)	1	A	330.95	——	AA	0.618	——
		B	280.92	——	BB	2.850	——
		C	276.12	——	CC	2.814	——
stone 2 (b layer)	1	A	189.57	——	AA	1.805	——
		B	230.01	——	BB	2.770	——
		C	276.12	——	CC	2.814	——
stone 3 (b layer)	5	A	59.04	1.58	AA	1.784	0.079
		B	292.75	0.09	BB	2.369	0.007
		C	235.02	1.62	CC	2.668	0.055
stone 4 (b layer)	5	A	65.88	1.08	AA	1.810	0.034
		B	287.13	0.91	BB	2.513	0.122
		C	235.47	0.39	CC	2.915	0.131
stone 5 (b layer)	1	A	27.02	——	AA	2.818	——
		B	311.67	——	BB	3.775	——
		C	245.59	——	CC	3.100	——
stone 6 (c layer)	13	A	122.70	10.65	AA	0.977	0.040
		B	263.99	1.70	BB	4.938	0.034
		C	260.64	1.28	CC	4.976	0.038
sediment	5	A	78.61	1.08	AA	1.781	0.028
		B	287.04	1.25	BB	1.213	0.014
		C	213.38	4.49	CC	2.102	0.135
sediment	2	A	124.93	1.55	AA	2.166	0.150
		B	249.73	1.59	BB	3.583	0.106
		C	242.15	0.66	CC	3.801	0.129
sediment	3	A	146.64	18.81	AA	1.655	0.275
		B	218.02	1.60	BB	1.655	0.044
		C	230.61	22.11	CC	1.444	0.275
sediment	30	A	144.76	3.79	AA	1.349	0.147
		B	194.41	26.55	BB	1.310	0.359
		C	200.60	33.43	CC	1.043	0.319
Tank 8 (control); animal 1							
sediment	1	A	276.98	——	AA	2.881	——
		B	274.88	——	BB	4.111	——
		C	304.92	——	CC	4.997	——
sediment	6	A	309.96	3.51	AA	1.799	0.262
		B	300.03	4.41	BB	2.344	0.480
		C	304.47	1.64	CC	2.466	0.569

Table 56 (cont.)

Substrate	number of threads	Angle	mean	sd	Vector	mean	sd
Tank 8 (cont.)							
sediment	15	A B C	243.49 258.91 292.29	7.78 22.16 4.31	AA BB CC	0.775 1.665 1.784	0.280 0.391 0.471
sediment	25	A B C	57.32 283.31 249.62	3.84 0.60 1.93	AA BB CC	0.793 1.858 1.926	0.054 0.237 0.218
sediment	9	A B C	33.75 295.85 252.00	3.40 1.21 2.32	AA BB CC	1.554 2.978 2.816	0.176 0.492 0.441
sediment	1	A B C	39.07 317.45 228.51	—— —— ——	AA BB CC	1.301 1.371 1.238	—— —— ——
sediment	22	A B C	132.83 252.67 251.59	6.81 5.31 4.79	AA BB CC	1.170 2.810 2.819	0.161 0.674 0.651
sediment	3	A B C	132.21 258.63 257.49	0.27 1.53 1.73	AA BB CC	1.012 3.482 3.496	0.050 0.388 0.386
sediment	6	A B C	49.18 285.69 251.99	0.36 0.08 0.11	AA BB CC	1.323 3.200 3.239	0.371 0.084 0.088
sediment	5	A B C	67.25 286.03 235.59	0.66 0.63 0.25	AA BB CC	2.197 3.077 3.584	0.039 0.020 0.023
sediment	7	A B C	57.31 307.40 220.40	3.82 10.17 7.81	AA BB CC	2.490 2.315 2.831	0.401 0.570 0.730
sediment	45	A B C	143.86 185.82 188.21	2.13 2.93 4.23	AA BB CC	2.734 2.237 1.616	0.781 0.688 0.417

Table 56 (cont.)

Figure 14. The plan, side and end views of Mytilus edulis byssus threads attached to stones and sediment. The first animal (opposite) is in sediment with stone layers at the depths 0-1cm (a layer), 3-4cm (b layer) and 6-7cm (c layer). The second animal (page 181) is in sediment with stone layers at 3-4cm and 6-7cm. The third animal (page 183) is in control sediment with no stone layers present.

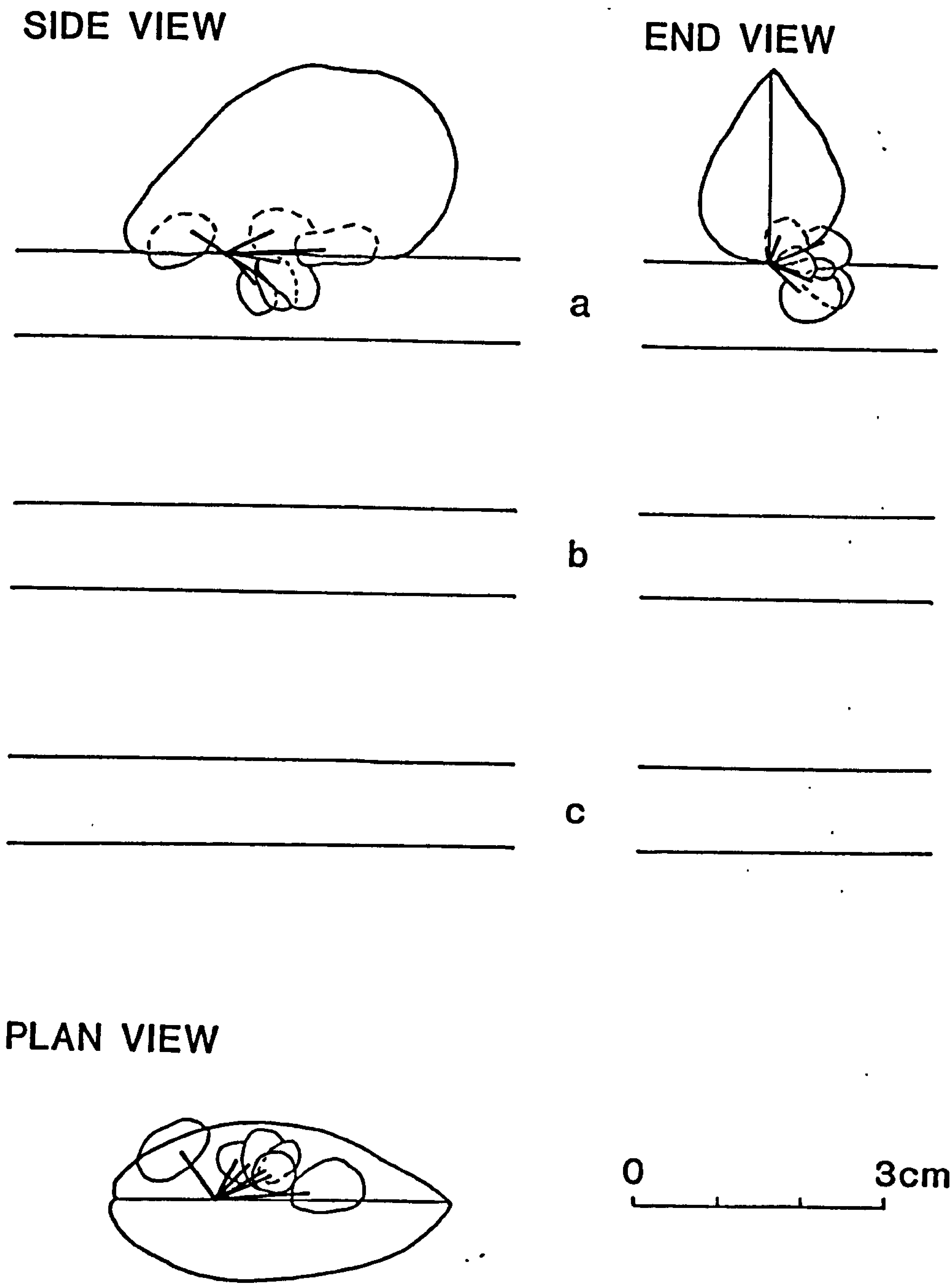
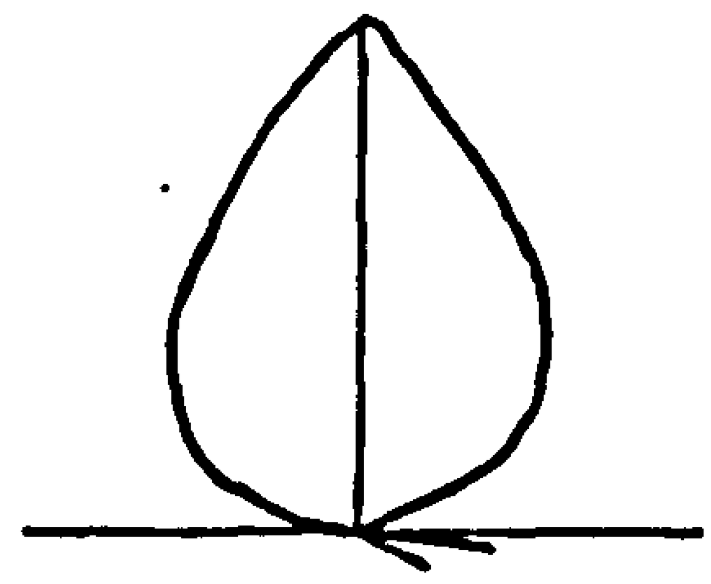

SIDE VIEW
END VIEW
a
b
c
PLAN VIEW
0
3cm

Figure 14 (cont.).

SIDE VIEW

END VIEW



b

c

PLAN VIEW

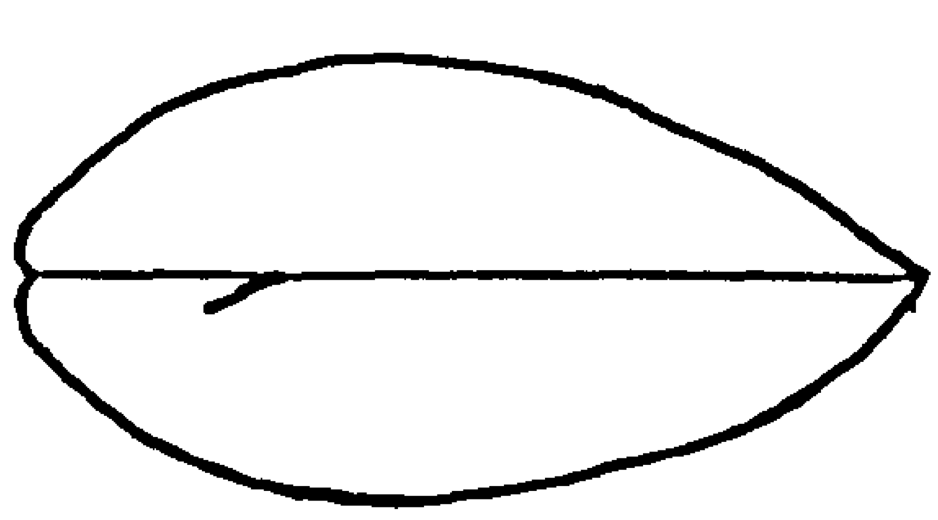


Figure 14 (cont.).

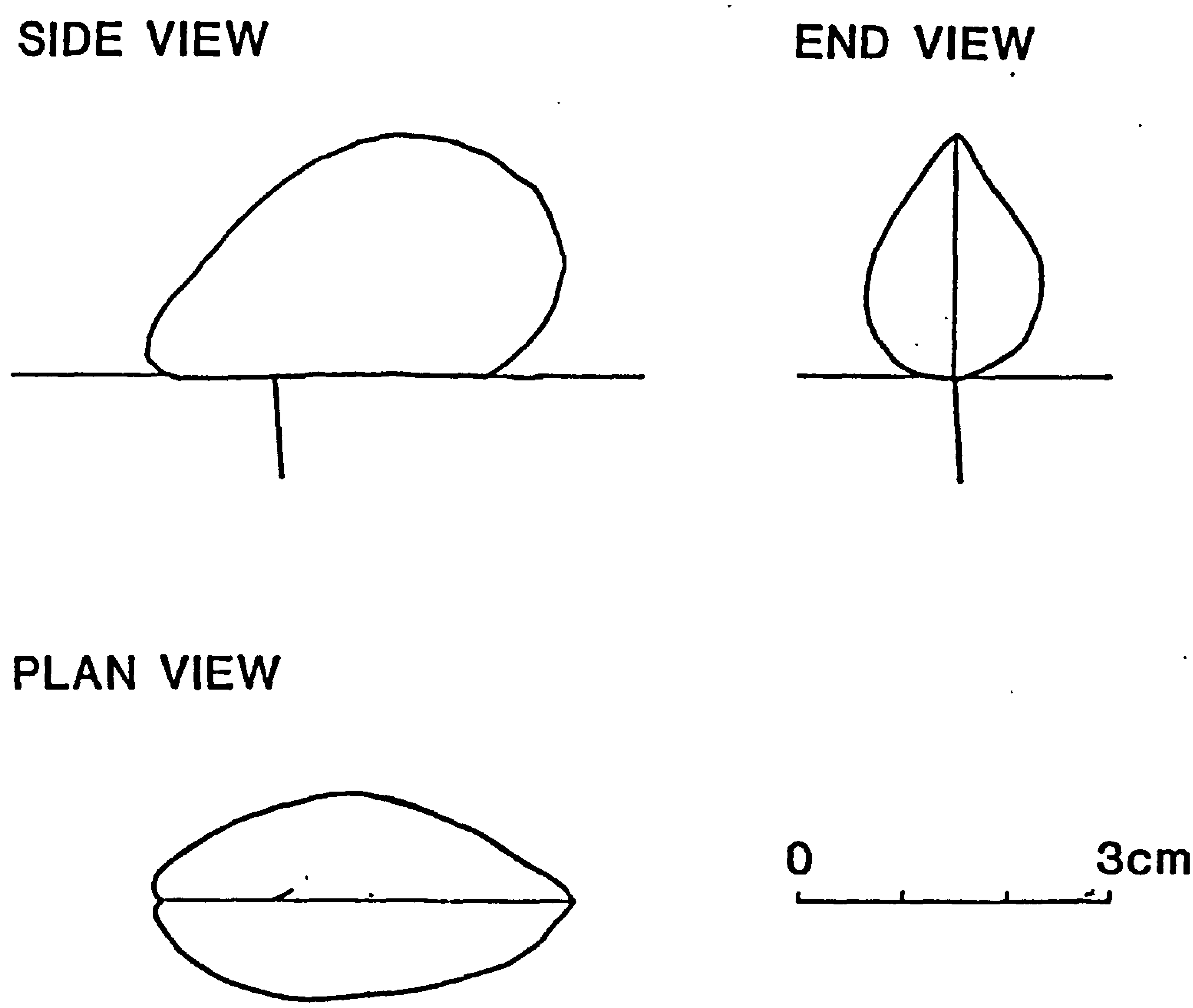

SIDE VIEW
END VIEW
PLAN VIEW
0
3cm

Figure 15. The plan, side and end views of _Modiolus modiolus_ byssus threads attached to stones and sediment. The first animal (opposite) is in sediment with stone layers at the depths 0-1cm (a layer), 3-4cm (b layer) and 6-7cm (c layer). The second animal (page 189) is in sediment with stone layers at 3-4cm and 6-7cm. The third animal (page 191) is in control sediment with no stone layers present.

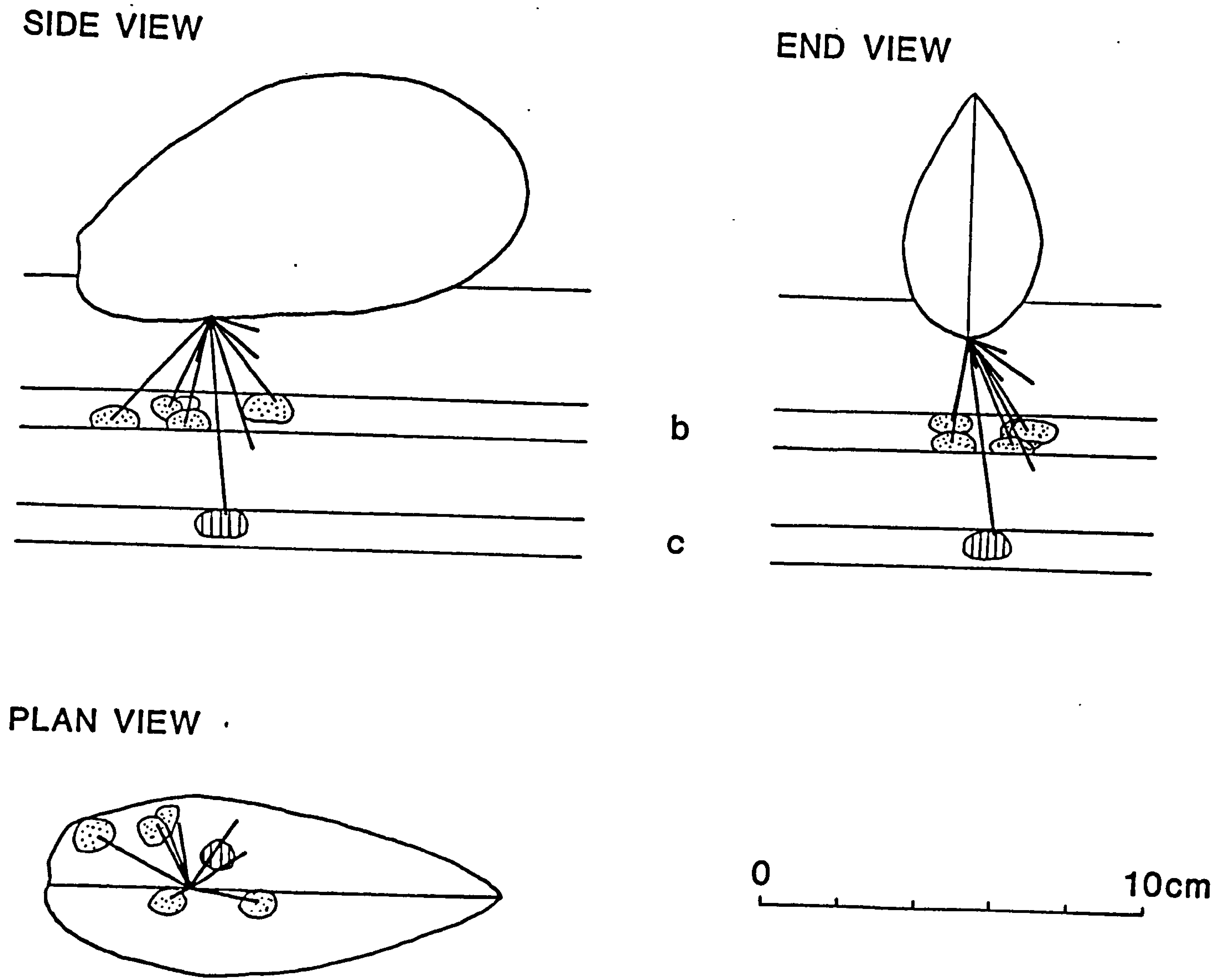

SIDE VIEW
END VIEW
b
c
PLAN VIEW
0
10cm

Figure 15 (cont.).

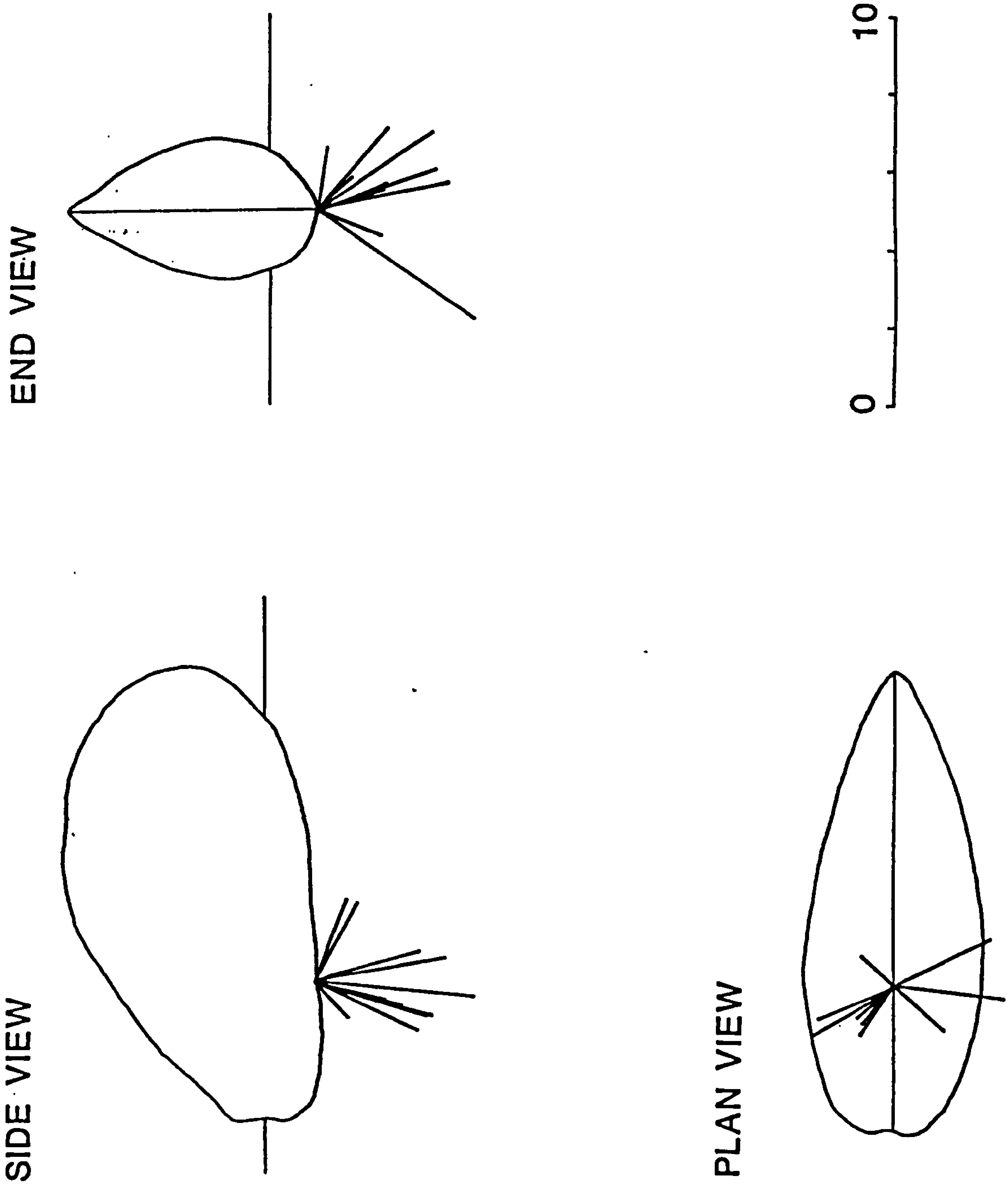
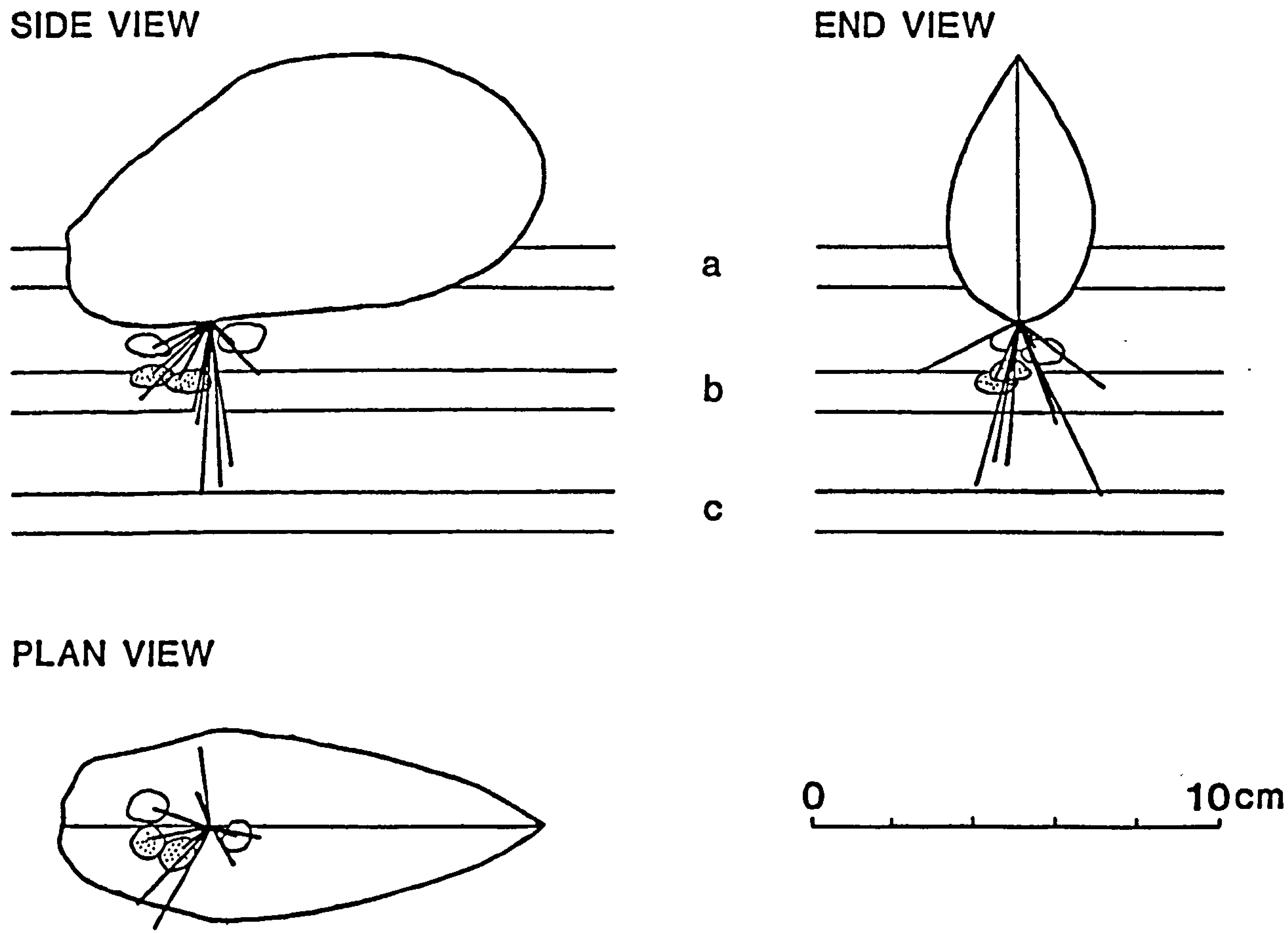

END VIEW
SIDE VIEW
PLAN VIEW
0
10cm

Figure 15 (cont.).


SIDE VIEW
END VIEW
a
b
c
PLAN VIEW
0
10cm

Total number of byssus threads attached to stones and sediment. Comparison between depths.

The total number of byssus threads Mytilus edulis and Modiolus modiolus attached to stones and sediment in different experimental tanks are shown in Tables 57 and 58 and figure 16.

The results for M. edulis clearly show that animals readily produced threads when stones were present at 0-1cm (a layer) but rarely produced threads when stones were not present at 0-1cm. The results for M. modiolus were not so clear. To determine differences in the number of threads/animal for M. modiolus at each depth in different tanks several non parametric statistical analyses were considered. These were the X^2 test, Kruskal-Wallis one way analysis of variance, Mann-Whitney U test, Kendall Coefficient of Concordance, Sign test and Wilcoxon matched-pairs signed-ranks test.

The Wilcoxon matched-pairs signed-ranks test was the most powerful test of those which could be used for the small sample size of the data. A discussion of the other tests is given in Appendix 1. I have used the test to determine whether different animals show a preference for attaching byssus threads at the same depth (for a comparison between two depths) in different experimental tanks. Two animals were present in each experimental tank. Therefore a comparison of animals for three experimental tanks actually compares six animals. In comparing animals from different experimental tanks I have considered the effect of the sediments with stones at different depths on byssus thread production at each of the three depths. This test utilizes information about the direction of differences in the number of threads within pairs of depths (the difference between two depths of the number of threads/ animal is either +ve or -ve) and the relative magnitude of these differences. It gives more weight to a pair which shows a large difference between the two depths than to a

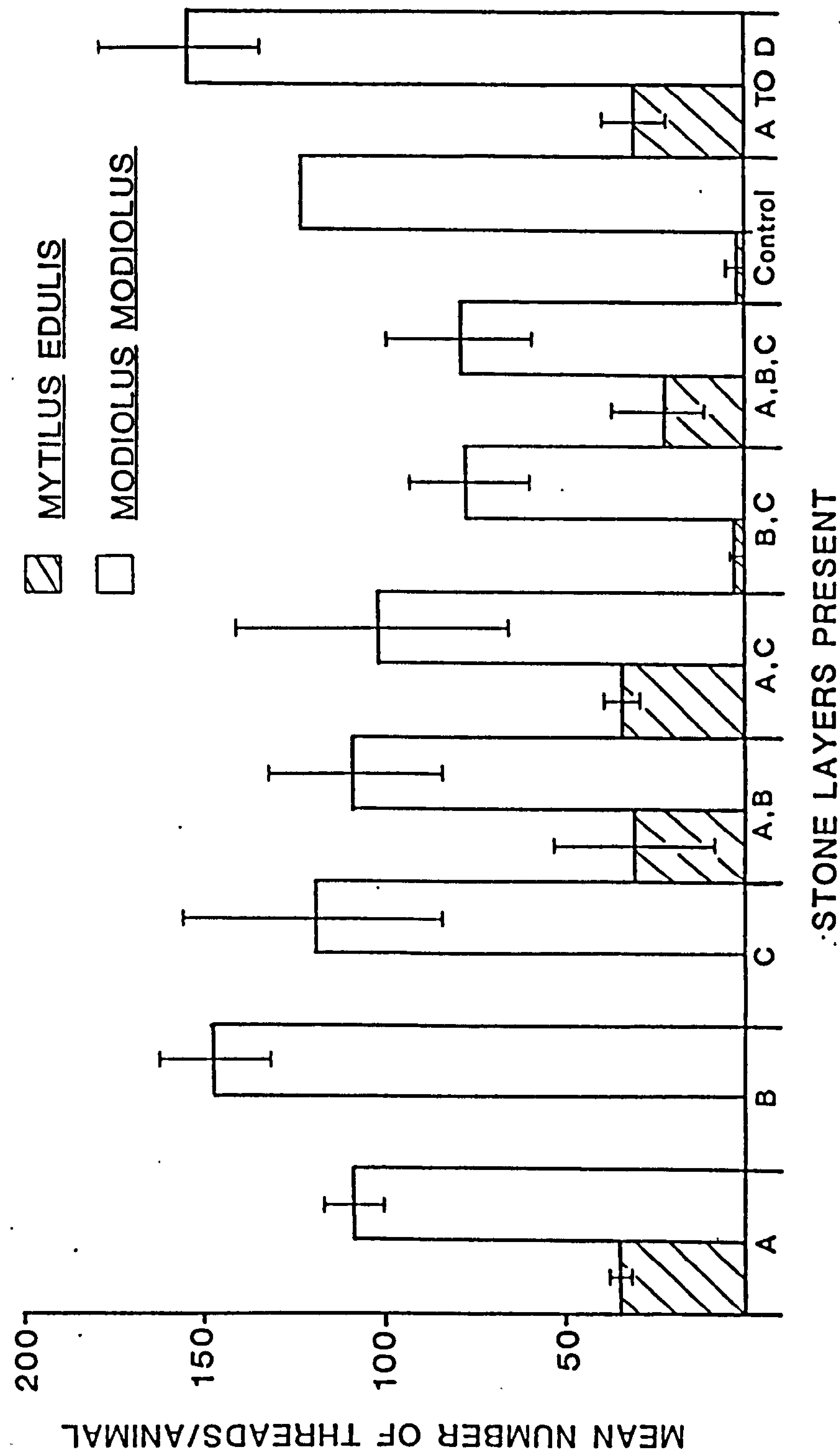
Tank	Animal	Stone layer present	Total number of byssus threads 0-2cm	2-5cm	5-8cm
1	1	a	33	0	0
	2		37	0	0
2	1	b	0	0	0
	2		0	0	0
3	1	c	0	0	0
	2		0	0	0
4	1	a+b	15	0	0
	2		47	0	0
5	1	a+c	38	0	0
	2		31	0	0
6	1	b+c	2	0	0
	2		0	4	0
7	1	a+b+c	33	0	0
	2		15	0	0
8	1	control	0	0	0
	2		0	4	0
9	1	all 1cm layers	38	0	0
	2		24	0	0

Table57. The number of byssus threads *Mytilus edulis* attached to stones and sediment at different depths in experimental tanks with stones present or not present at each depth. Stone layers (a) = 0-1cm, (b) = 3-4cm and (c) = 6-7cm.

Tank	Animal	Stone layer present	Total number of byssus threads 0-2cm	2-5cm	5-8cm	Total
1	1	a	115	0	0	115
	2		91	13	0	104
2	1	b	58	78	0	136
	2		30	128	0	158
3	1	c	51	72	0	123
	2		0	78	16	94
4	1	a+b	71	54	0	125
	2		56	31	4	91
5	1	a+c	17	111	2	130
	2		66	11	0	77
6	1	b+c	0	47	41	89
	2		20	33	13	66
7	1	a+b+c	2	52	12	66
	2		47	31	18	96
8	1	control	0	0	0	0
	2		45	98	2	145
9	1	all 1cm layers	65	72	0	137
	2		81	91	0	172

Table 58. The number of byssus threads Modiolus modiolus attached to stones and sediment at different depths in experimental tanks with stones present or not present at each depth. Stone layers (a) = 0-1cm, (b) = 3-4cm and (c) = 6-7cm depth.

Figure 16. The mean number of threads produced by animals in sediment with stones present or not present at different depths. A, B and C represent stone layers at the depths 0-1cm, 3-4cm and 6-7cm respectively. Scale bars represent the standard deviations.


MYTILUS EDULIS
MODIOLUS MODIOLUS
MEAN NUMBER OF THREADS/ANIMAL
200
150
100
50
A
B
C
A,B
A,C
B,C
A,B,C
Control
A TO D
STONE LAYERS PRESENT

pair which shows a small difference.

Three sets of comparisons were performed (0-2cm to 2-5cm, 0-2cm to 5-8cm and 2-5cm to 5-8cm). Each set compared animals in the following tanks:

1. All tanks
2. Tanks with 1 stone layer present (a, b and c layers).
3. Tanks with 2 stone layers present (a+b, a+c, and b+c layers)
4. Tanks with 1-2 stone layers present which include the a layer (a, a+b and a+c).
5. Tanks with 1-2 stone layers present which include the b layer (b, a+b and b+c).
6. Tanks with 1-2 stone layers present which include the c layer (c, a+c and b+c).
7. Tanks with 1-2 stone layers present and which do not contain an a layer (b, c and b+c).

The results of the Wilcoxon matched-pairs signed-ranks tests are shown in Table 59. These are as follws:

1. Total number of animals (comparison 1). There was a significant preference for producing more threads at a depth 0-2cm than at 5-8cm and at the depth 2-5cm than 5-8cm.
2. Tanks with 1-2 stone layers present (comparisons 2 to 7).
   (a). There was a significant preference for producing more threads at a depth of 0-2cm than at 2-5cm in comparison 7 (tanks which do not contain an a layer).
   (b). There was a significant preference for producing more threads at the depth 0-2cm than at 5-8cm in comparison 4 (tanks which contain an a stone layer).
   (c). There was a significant preference for producing more threads at the depth 2-5cm than at 5-8cm in all tanks.

Comparison	Tanks in comparison	Number of animals	Depths compared					
			0-2cm to 2-5cm		0-2cm to 5-8cm		2-5cm to 5-8cm	
			T	P	T	P	T	P
1	All tanks	18	66	$p > 0.05$	16	$p < 0.01$	0	$p < 0.01$
2	a,b,c	6	7	$p > 0.05$	1	$p > 0.05$	0	$p = 0.05$
3	a+b,a+c,b+c	6	10	$p > 0.05$	3	$p > 0.05$	0	$p = 0.05$
4	a,a+b,a+c	6	5	$p > 0.05$	0	$p = 0.05$	0	$p = 0.05$
5	b,a+b,b+c	6	5	$p > 0.05$	3	$p > 0.05$	0	$p = 0.05$
6	c,a+c,b+c	6	4	$p > 0.05$	7	$p > 0.05$	0	$p = 0.05$
7	b,c,b+c	6	0	$p = 0.05$	6	$p > 0.05$	0	$p = 0.05$

Table 59. Comparison between animals. Wilcoxon matched-pairs signed-ranks test on the number of byssus threads Modiolus modiolus attaches to sediment and stones at different depths in different experimental tanks. Each tank contains 2 animals. T = total ranks of less frequent sign (see pp 75-83 and Table G in Siegal (1956)) and P = probability. For sample sizes of 6 the t value is significant if all 6 animals produce most threads at one particular depth, and P = 0.05.

The number of threads _M. edulis_ attached to their own shells are shown in Table 60. The 8 animals in sediment with no stones present at the surface (a layer) attached between 1 and 23 threads to their own shells. Only 1 of the 10 animals with stones present at the surface attached threads to it's own shell.

Tank	Animal	Stone layer present	Number of threads attached to animals own shell
1	1	a	0
	2		0
2	1	b	12
	2		1
3	1	c	8
	2		23
4	1	a+b	0
	2		0
5	1	a+c	7
	2		0
6	1	b+c	11
	2		16
7	1	a+b+c	0
	2		0
8	1	control	3
	2		21
9	1	all 1cm layers	0
	2		0

Table 60. The number of byssus threads Mytilus edulis attached to the animals own shell in sediment with stones present or not present at different depths.

Comparisons of the number of byssus threads attached to stones and sediment

The number of byssus threads attached to stones and sediment for *Mytilus edulis* and *Modiolus modiolus* are shown in Tables 61 and 62 respectively. The tables have been prepared in the following way. Each of the sediment layers I to IV (figure 10, p.149) have been divided into 2 categories i.e. Type I and Type II sediment layers. The sediment layer is called a Type I sediment layer when stones are present and a Type II sediment layer when stones are not present. The Type I sediment layer is divided into threads attached to stones and threads attached to sediment (Type I sediment), shown in columns 1 to 6 and 7 to 11 respectively. The Type II sediment layer = type II sediment, shown in columns 12 to 16. This is illustrated by *M. modiolus* in tank 5. At 0-2cm animal 1 attaches 17 threads to stones and 0 threads to sediment. These are placed under Type I sediment (columns 3 and 8 respectively). No stone layer is present at 2-5cm, therefore the number of threads (111) are placed under Type II sediment (column 13). A stone layer is present at 5-8cm and the number of threads attached to stones (0 threads) and sediment (2 threads) are placed under Type I sediment (columns 3 and 8 respectively). Tank 5 is therefore composed of Type I sediment layers at 0-2cm and 5-8cm and a type II sediment layer at 2-5cm. The data has in fact been organised into groups of identical sediment layers from different tanks for statistical analyses.

The following sections give the statistical analyses preformed. Sections 1 to 4 analyse the numbers of byssus threads attached to stones and sediment (Tables 61 and 62). Sections 1 and 2 compare differences between depths and species in the number of byssus threads attached to stones (section 2) and to Type I and Type II sediment layers (section 3). Section 4 compares threads attached to stones and

Depth (cm)	TYPE I SEDIMENT LAYERS: Threads attached to stones — Tank no.	Number of threads/animal for each tank 1	Number of threads/animal for each tank 2	T	N	Mean number of threads/animal ± standard deviation	Threads attached to sediment — Number of threads/animal for each tank 1	Number of threads/animal for each tank 2	T	N	Mean number of threads/animal ± standard deviation	TYPE II SEDIMENT LAYERS: Threads attached to sediment — Tank no.	Number of threads/animal for each tank 1	Number of threads/animal for each tank 2	T	N	Mean number of threads/animal ± standard deviation	Total number of threads
0–2 cm	1	33	35	247	8	30.875 ± 10.960	0	2	2	8	0.250 ± 0.707	2	0	0	2	8	0.250 ± 0.707	222
	4	15	47				0	0				3	0	0				
	5	38	31				0	0				6	2	0				
	7	33	15				0	0				8	0	0				
2–5 cm	2	0	0	4	8	0.500 ± 1.414	0	0	0	8	0	1	0	0	4	8	0.500 ± 1.414	8
	4	0	0				0	0				3	0	0				
	6	0	4				0	0				5	0	0				
	7	0	0				0	0				8	0	4				
5–8 cm	3	0	0	0	8	0	0	0	0	8	0	1	0	0	0	8	0	0
	5	0	0				0	0				2	0	0				
	6	0	0				0	0				4	0	0				
	7	0	0				0	0				8	0	0				
8–16 cm	No threads were attached to stones or sediment																	

Table 61. Number of byssus threads *Mytilus edulis* attached to stones and sediment in different experimental tanks.

TYPE I SEDIMENT LAYERS												TYPE II SEDIMENT LAYERS						
	Threads attached to stones						Threads attached to sediment					Threads attached to sediment						
Depth (cm)	Tank no.	Number of threads/animal for each tank 1	2	T	N	Mean number of threads/animal $\pm$ standard deviation	Number of threads/animal for each tank 1	2	T	N	Mean number of threads/animal $\pm$ standard deviation	Tank no.	Number of threads/animal for each tank 1	2	T	N	Mean number of threads/animal $\pm$ standard deviation	Total number of threads
0–2 cm	1	34	14	214	8	26.750 $\pm$ 22.790	81	76	249	8	31.125 $\pm$ 34.510	2	58	30	204	8	25.500 $\pm$ 24.166	667
	4	71	3				0	53				3	45	0				
	5	17	37				0	29				6	0	20				
	7	2	36				0	10				8	0	51				
2–5 cm	2	0	16	132	8	16.500 $\pm$ 14.900	78	112	320	8	40.000 $\pm$ 38.348	1	0	13	383	8	48.875 $\pm$ 46.520	835
	4	5	6				49	25				3	98	78				
	6	47	13				0	20				5	111	11				
	7	19	26				32	4				8	0	72				
5–8 cm	3	0	0	57	8	7.125 $\pm$ 11.789	2	16	46	8	5.750 $\pm$ 5.898	1	0	0	4	8	0.500 $\pm$ 1.414	107
	5	0	0				2	0				2	0	0				
	6	33	13				8	0				4	0	4				
	7	0	11				12	6				8	0	0				
8–16 cm	No threads were attached to stones or sediment																	

Table 62. Number of byssus threads *Modiolus modiolus* attached to stones and sediment in different experimental tanks.

sediment in Type I sediment layers. Section 5 compares threads produced in Type I sediment layers and Type II sediment layers. No statistical analyses were performed on data for 8-16cm because both species did not produce threads at these depths (Tables 61 and 62).

These sections inevitably involve repetion of statistical procedures. This was thought necessary to analyse the results sufficiently.

The data for number of threads was found to have a non-normal distribution (using the rankit method to determine normality). Three transformations were therefore used to assess which would be the best for normalising the data ($\log_{10}(x)$, square-root and arcsin). The best transformation was found to be $\sqrt{x}$. All statistical analyses were therefore performed on square-root transformed data.

A general description of the results is given at the beginning of each subsection followed by statistical analyses of the data.

SECTION 1:

Number of byssus threads attached to stones. Comparison between depths and between species.

The results in this section are shown in Tables 61 and 62, columns 1 to 6. There was a decrease in the number of byssus threads both species attached to stones at increasing depths. M edulis showed a sharper decrease than Modiolus modiolus. In addition there were differences between species at stone layers below 0-1cm, M. modiolus having attached more byssus threads to stones than did M. edulis. These effects were analysed statistically by analyses of variance and t-tests on square-root transformed data. No statistical analyses were performed for M. edulis (6-7cm) because animals did not attach byssus threads at this depth (see Tables 61 and 62).

A two-way analysis of variance was performed on the data in which Factor A was species (M. edulis and M. modiolus) and Factor B was depth (0-1cm and 3-4cm). The data for 6-7cm was excluded from this analysis because M. edulis did not attach byssus threads to stones at this depth (see Table 61). Technically, Factor A is a fixed factor and Factor B a random factor; the whole anovar is hence termed a mixed model nested analysis of variance (Sokal and Rohlf 1981, pp 271-272 and Table 10.2, p.287). The analysis (Table 63) showed that the Interaction of Factor A (species) and Factor B (depth) was significant (0.005> P> 0.001). Hence no deductions can be made about the significances of the two main factors and one-way analyses of variance are needed.

One-way analyses of variance were performed on data to test differences between the number of threads attached to stones at different depths. These anovars (Table 64) showed that there were significant differences between depths for M. modiolus and that M.

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Species	1	12.77	12.77	4.434	Not applicable
Factor B: Depth	1	79.64	79.64	27.653	Not applicable
Interaction	1	34.01	34.01	11.809	0.005> P> 0.001
Error	28	80.70	2.88		
Total	31	207.13			

Table 63. Two way analysis of variance comparing the number of byssus threads animals attached to stones at different depths in the sediment (square-root transformed data). F = variance ratio, and P = probability. Factor A (fixed): species (2 species = 2 levels): Factor B (random): depth (2 depths = 2 levels).

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Mytilus	Depth	1	108.874	108.874	134.18	P< 0.001
edulis	Error	14	11.359	0.811		
	Total	15	120.233			
Modiolus	Depth	2	39.16	19.58	3.87	0.05> P> 0.02
modiolus	Error	21	106.28	5.06		
	Total	23	145.44			

Table 64. One way analyses of variance comparing the number of byssus threads animals attached to stones at different depths in sediment (square-root transformed data). d.f. = degrees of freedom, F = variance ratio and P = probability.

edulis attached significantly more threads to stones at 0-1cm than at 3-4cm ($P < 0.001$).

T-tests were then performed on transformed data to compare differences between pairs of depths for M. modiolus. These tests (Table65) showed that there was no significant difference between 0-1cm and 3-4cm ($0.4 > P > 0.2$) or between 2-5cm and 6-7cm ($0.1 > P > 0.05$) but that animals attached significantly more byssus threads to stones at 0-1cm depth than at 6-7cm ($0.02 > P > 0.01$).

T-tests were performed on the data for 0-1cm and 3-4cm to compare differences between species at each depth. These are shown in Table 66. There was no significant difference between species at 0-1cm but M. modiolus attached significantly more byssus threads to stones at 3-4cm than did Mytilus edulis. No test was performed for 6-7cm because M. edulis did not attach byssus threads to stones at this depth.

Comparison	t	d.f.	P
0-1cm to 3-4cm	0.983	14	0.40> P> 0.20
0-1cm to 6-7cm	2.639	14	0.02> P> 0.01*
2-5cm to 5-8cm	1.826	14	0.10> P> 0.05

Table 65. Students t-tests comparing the number of byssus threads Modiolus modiolus attached to stones at different depths in sediment (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Comparison	t	d.f.	P
0-1cm	0.867	14	0.50> P> 0.40
3-4cm	4.317	14	P> 0.001***

Table 66. Students t-tests comparing the number of byssus threads Mytilus edulis and Modiolus modiolus attached to stones at different depths in sediment (square-root transformed data). t = students t, d.f. = degrees of freedom and p = probability.

SECTION 2

Number of byssus threads attached to sediment. Comparison between depths, between species and between sediment with stones present (type I sediment) or absent (type II sediment)

The results in this section are shown in Tables 61 and 62, columns 7 to 11 and 12 to 17. In general these showed that Mytilus edulis attached very few byssus threads to sediment and that Modiolus modiolus attached large numbers of byssus threads to sediment (particle size range 0-2mm). M. modiolus showed a decrease in the number of byssus threads/animal with increasing depth at depths below 2-5cm. In addition there were no obvious differences in the number of byssus threads M. modiolus attached to type I sediment and type II sediment. These effects were analysed statistically by analyses of variance and t-tests on the square root of the number of byssus threads/animal. No statistical analyses were performed on M. edulis (2-5cm - type I sediment only, 5-8cm - type I and II sediment) because at these depths animals did not attach byssus threads to sediment.

A. Comparison within sediment types, between depths and between species

A two-way analysis of variance was performed on the data for type II sediment in which Factor A was species (M. edulis and M. modiolus) and factor B was depth (0-2cm and 2-5cm). The analysis (Table67) showed that there was no significant difference within species ($0.5 > P > 0.25$) and that M. modiolus attached significantly more byssus threads to sediment than did M. edulis ($P < 0.001$).

One-way analyses of variance were then performed on the data to test for differences in the number of byssus threads attached to sediment at different depths for thype I sediment and for type II sediment. These anovars showed that there was no significant

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Species	1	165.05	165.05	21.052	P< 0.001
Factor B: Depth	1	5.99	5.99	0.764	0.5> P> 0.25
Interaction	1	5.02	5.02	0.640	0.5> P> 0.25
Error	28	219.41	7.84		
Total	31	395.47			

Table 67. Type II sediment. Two way analysis of variance comparing the number of byssus threads animals attached to sediment at different depths (square-root transformed data). F = variance ratio, and P = probability. Factor A (fixed): species (2 species = 2 levels); Factor B (random): depth (2 depths = 2 levels).

difference between depths for M. edulis - type II sediment (P> 0.75, Table 68) and M. modiolus - type I sediment (0.25> P> 0.10, Table 69) but that there was a significant difference between depths for Modiolus modiolus - type II sediment (p= 0.01, Table 69).

T-tests were then performed on data to compare differences between pairs of depths for M. modiolus. The results were as follows:

Type I sediment. The tests (Table 70) showed no significant differences between 0-2cm and 2-5cm (0.9> P> 0.5) or 0-2cm and 5-8cm (0.2> P> 0.1) but showed that M. modiolus attached significantly more byssus threads to sediment at 2-5cm than to sediment at 5-8cm (0.02> P> 0.01).

Type II sediment. The tests (Table 70) showed no significant difference between 0-2cm and 2-5cm (p=0.40) but showed that M. modiolus attached significantly more byssus threads to sediment at 0-2cm than 5-8cm (0.01> P> 0.001) and at 2-5cm than 5-8cm (0.01> P> 0.001). No tests were performed for M. edulis.

T-tests were performed on data to compare differences between species at each depth. The test on type I sediment layers (Table 70) showed that M. modiolus attached significantly more byssus threads than did M. edulis to sediment at 0-2cm (0.02> P> 0.01). The tests on type II sediment showed that M. modiolus attached significantly more byssus threads to sediment than did M. edulis at 0-2cm and 2-5cm (0-2cm 0.01> P> 0.001; 2-5cm 0.01> P> 0.001).

Comparison between type I sediment and type II sediment

A two-way analysis of variance was performed on the data for M. modiolus in which factor A was substrate (type I and type II sediment) and factor B was depth (0-2cm, 2-5cm and 5-8cm). The analysis (Table 72) showed that there was a significant difference between depths (0.05> P> 0.025) but no significant difference between sediments (0.50> P> 0.25).

Sediment	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Type II sediment	Depth	1	0.021	0.021	0.06	P> 0.75
	Error	14	5.249	0.375		
	Total	15	5.271			

Table 68. Mytilus edulis. One way analysis of variance comparing the number of byssus threads animals attached to sediment at different depths (square-root transformed data). d.f. = degrees of freedom, F = variance ratio and P = probability.

Sediment	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Type I sediment	Depth	2	50.24	25.12	2.55	0.25> P> 0.10
	Error	21	207.03	9.86		
	Total	23	257.27			
Type II sediment	Depth	2	119.30	59.60	5.75	p= 0.01
	Error	21	217.70	10.40		
	Total	23	336.90			

Table 69. Modiolus modiolus. One way analyses of variance comparing the the number of byssus threads animals attached to type I sediment and to type II sediment at different depths (square-root transformed data). d.f. = degrees of freedom, F = variance ratio and P = probability.

	Comparison	t	d.f.	P
Type I sediment	0-2cm to 2-5cm	0.676	14	0.90> P> 0.50
	0-2cm to 5-8cm	1.510	14	0.20> P> 0.10
	2-5cm to 5-8cm	2.634	14	0.02> P> 0.01*
Type II sediment	0-2cm to 2-5cm	0.848	14	0.50> P> 0.40
	0-2cm to 5-8cm	3.000	14	0.01> P> 0.001**
	2-5cm to 5-8cm	3.410	14	0.01> P> 0.001**

Table 70. Modiolus modiolus. Students t-tests comparing the number of byssus threads animals attached to sediment at different depths for type I sediment and type II sediment (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

	Comparison	t	d.f.	P
Type I sediment	0-1cm	2.865	14	0.02> P> 0.01*
Type II	0-1cm	3.092	14	0.01> P> 0.001**
sediment	3-4cm	3.410	14	0.01> P> 0.001**

Table 71. Students t-tests comparing the number of byssus threads Mytilus edulis and Modiolus modiolus attached to sediment at different depths for type I sediment and for type II sediment (square-root transformed data). t = Students t, d.f. = degrees of freedom and P = probability.

One way analyses of variance and students t-tests comparing depths have been described and are shown on pages 205-209 of this section.

T-tests were then performed on data to compare differences between type I and type II sediments at each depth for M. modiolus. These tests (Table 73) showed that there were no significant differences in the number of byssus threads between type I and type II sediment at 0-2cm and at 2-5cm (0-2cm 0.9> P> 0.5; 2-5cm P> 0.90) and that M. modiolus attached significantly more byssus threads to type I sediment than to type II sediment at 6-7cm (0.02> P> 0.01). No tests were performed for M. edulis.

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Substrate	1	4.40	4.40	0.436	0.75> P> 0.50
Factor B: Depth	2	162.06	81.00	8.020	0.01> P> 0.005
Interaction	2	7.40	3.70	0.366	0.75> P> 0.50
Error	42	424.70	10.10		
Total	47	598.60			

Table 72. Modiolus modilous. Two way analysis of variance comparing the number of byssus threads animals attached to type I sediment and type II sediment at different depths (square-root transformed data). F = variance ratio and P = probability. Factor A (fixed) = substrate (2 substrates = 2 levels): Factor B = random = depth (3 depths = 3 levels).

Comparisons	t	d.f.	P
0-2cm	0.145	14	0.9> P> 0.50
3-4cm	0.072	14	P> 0.90
6-7cm	2.897	14	0.02> P> 0.01*

Table 73. Modiolus modiolus. Students t-tests comparing the number of byssus threads attached to type I and type II sediment at different depths (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

SECTION 3

Comparisons of data within type I sediment layers

The results in this section are shown in Tables 61 and 62, columns 1 to 6 and 7 to 11. In general these show that with few exceptions Mytilus edulis attached byssus threads to stones but only rarely to sediment and that Modiolus modiolus attached similar numbers of byssus threads to stones and sediment. These effects were analysed statistically by analyses of variance and t-tests on square root transformed data. No statistical analyses were performed for M. edulis (2-5cm - sediment, 5-8cm and 8-16cm - stones and sediment) because animals did not attach byssus threads at these depths (see Tables 61 and 62).

A two-way analysis of variance was performed on data in which Factor A was the type of substrate (stones or sediment) and factor B was depth (0-2cm, 2-5cm and 5-8cm). The analyses (Table 74) showed that there was a significant difference within substrates ($0.01 > P > 0.005$) but no significant difference between stones and sediment ($0.50 > P > 0.25$).

One way analyses of variance and students t-tests comparing depths have been described and are found on pages 209-211.

T-tests were performed on data to compare differences between stones and sediment at each depth. These tests (Table 75) showed that M. edulis attached significantly more byssus threads to stones than to sediment at 0-2cm ($P < 0.001$) and that there was no significant difference between the number of byssus threads M. modiolus attached to stones and sediment at all depths (0-2cm $0.9 > P > 0.5$; 2-5cm $0.4 > P > 0.2$; 5-8cm $0.9 > P > 0.5$). No other t-tests were performed for M. edulis.

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Substrate	1	4.10	4.10	0.550	0.50> P> 0.25
Factor B: Depth	2	78.12	39.06	5.2363	0.01> P> 0.005
Interaction	2	11.28	5.64	0.756	0.50> P> 0.25
Error	42	313.31	7.46		
Total	47	406.81			

Table 74. Two way analysis of variance comparing the number of byssus threads/animal attached to stones and to sediment at different depths for type I sediment layers at different depths (square-root transformed data). F = variance ratio and P = probability. Factor A (fixed) = substrate (2 substrates = 2 levels): Factor B (random) = depth (3 depths = 3 levels).

Species	Comparisons	t	d.f.	P
Mytilus edulis	0-2cm	12.772	14	P< 0.001***
Modiolus modiolus	0-2cm	0.293	14	0.90> P> 0.50
	3-4cm	1.316	14	0.40> P> 0.20
	6-7cm	0.374	14	0.90> P> 0.50

Table 75. Students t-tests comparing the number of byssus threads attached to stones and sediment for different depths in type I sediment (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

SECTION 4

Comparisons of the total number of threads produced in Type I and Type II sediment layers.

The results in this section are shown in Tables 61 and62. The number of byssus threads attached to stones (column 3) were added to the number of byssus threads attached to sediment with stones present at the same depth (column 8). This addition gave the total number of byssus threads/animal at each depth for Type I sediment layers. These were then compared to the number of byssus threads attached to Type II sediment layers, where Type II sediment layer = type II sediment (column 13). Broadly speaking <u>Mytilus edulis</u> produced more byssus threads in Type I sediment layers than Type II sediment layers at 0-2cm depth but it is not clear whether <u>Modiolus modiolus</u> produced more byssus threads in Type I sediment layers than Type II sediment layers. The results were analysed statistically by analyses of variance and t-tests on the square root of the number of byssus threads/animal. No statistical analyses were performed for <u>M. edulis</u> (5-8cm) because animals did not attach byssus threads at this depth.

A Two-way analysis of variance was performed on data for <u>Modiolus</u> in which Factor A was the substrate (type I sediment layers and type II sediment layers) and factor B was depth (0-2cm, 2-5cm and 5-8cm). The analyses (Table 76) showed that there was significant differences within substrates ($P > 0.001$) and between substrates ($0.01 > P > 0.005$). No analysis was performed for <u>M. edulis</u>.

One way analyses of variance were performed on data to test differences between the number of byssus threads produced in type I sediment layers at different depths. These anovars (Table 77) showed that there was a significant difference between depths for <u>M. edulis</u> and <u>M. modiolus</u> (<u>M. edulis</u> $P < 0.001$; <u>M. modiolus</u> $0.025 > P > 0.01$).

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Sediment	1	77.86	77.86	9.720	0.005> P> 0.001
Factor B: Depth	2	205.54	102.77	12.830	P< 0.001
Interaction	2	4.52	2.26	0.282	0.75> P> 0.50
Error	42	336.25	8.01		
Total	47	624.17			

Table 76. Two way analysis of variance comparing the number of byssus threads animals produced in type I sediment and type II sediment layers for Modiolus modiolus (square-root transformed data). F = variance ratio and P = probability. Factor A (fixed) = substrate (2 substrates = 2 levels): Factor B = depth (3 depths = 3 levels).

Species	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Mytilus edulis	Depth	1	109.747	109.747	132.22	P< 0.001
	Error	14	11.534	0.824		
	Total	15	121.280			
Modiolus modiolus	Depth	2	90.810	45.400	8.04	0.025> P> 0.01
	Error	21	118.59	5.65		
	Total	23	209.40			

Table 77. One way analyses of variance comparing the number of byssus threads animals produced in type I sediment layers at different depths. d.f. = degrees of freedom, F = variance ratio and P = probability.

One-way analyses and t-tests for type II sediment layers have been described and are shown in Section 2, pages 209-211.

T-tests were then performed on data to compare differences between pairs of depths for M. modiolus. These tests (Table 78) showed that the number of byssus threads produced at 0-2cm depth was not significantly different from the number produced at 2-5cm (0.1> P> 0.05) but that animals produced significantly more threads at 0-2cm and 2-5cm depth than at 5-8cm depth (0-2cm to 2-5cm, 0.01> P> 0.005; 2-5cm to 5-8cm, 0.005> P> 0.001).

T-tests were performed on data to compare differences between the substrates at each depth. The results for M. edulis (Table 79) showed that animals produced more byssus threads when stones were present in Type I sediment layers than Type II sediment layers 0-2cm (P< 0.001). The results for M. modiolus showed that there were no significant differences at 0-2cm and at 2-5cm (0-2cm, 0.1> P> 0.05; 2-5cm, 0.4> P> 0.2) and that at 5-8cm M. modiolus produced more byssus threads in type I sediment layers than in type II sediment layers (0.01> P> 0.001).

Comparison	t	d.f.	P
0-2cm to 2-5cm	0.174	14	0.10> P> 0.05
0-2cm to 5-8cm	3.144	14	0.01> P> 0.005**
2-5cm to 5-8cm	4.238	14	0.005> P> 0.001**

Table 78. Modiolus modiolus. Students t-tests comparing the number of byssus threads produced at different depths in type I sediment layers (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Species	Comparisons	t	d.f.	P
Mytilus edulis	0-2cm	11.513	14	P< 0.001***
Modiolus modiolus	0-2cm	2.523	14	0.05> P> 0.02*
	3-4cm	1.930	14	0.10> P> 0.05
	6-7cm	3.2926	14	0.01> P> 0.001*

Table 79. Students t-tests comparing the number of byssus threads produced in type I and type II sediment layers for Mytilus edulis and Modiolus modiolus (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Number of stones to which animals attach byssus threads. Comparison between depths and between species.

The number of stones to which animals attach byssus threads are shown in Table 80. The table has been prepared in the same way as Tables 61 and 62 (pages 202-203). In general the number of stones to which animals attached byssus threads decreased with increasing depth. Mytilus edulis showed a sharper decrease than Modiolus modiolus. In addition there were clear differences between species at stone layers below 0-1cm, Modiolus having attached byssus threads to a larger number of stones than did M. edulis. These were analysed statisticaly by analyses of variance and t-tests on square root transformed data. Statistical analyses were not performed for M. edulis (6-7cm) because animals did not attach byssus threads at this depth (see Table 80).

The data was found to have a non-normal distribution (using the rankit method to determine normality, Sokal and Rholf, 1981). Three transformations were therefore used to assess which would be the best for normalising the data ($\log_{10}(x)$, square-root and arcsin). The best transformation was found to be $\sqrt{x}$. All statistical analyses were therefore performed on square-root transformed data.

A two-way analysis of variance was performed on the data in which factor A was the fixed factor (species ie. M. edulis and M. modiolus) and factor B was the random factor (depth ie. 0-1cm and 3-4cm). This analysis (Table 81) showed that the Interaction of Factor A (species) and Factor B (depth) was significant ($0.01 > P > 0.005$). Hence no deductions can be made about the significance of the two main factors and one-way analyses of variance are needed.

One-way analyses of variance were performed on the data to test differences between the number of stones at different depths. These anovars (Table 82) showed that there were significant differences between depths for both species (Mytilus edulis $P<0.001$; Modiolus

Species	Depth (cm)	Tank no.	Number of stones/animal for each tank 1	2	T	N	Number of stones/animal (mean $\pm$ standard deviation)	Number of threads/stone (mean $\pm$ standard deviation)
Mytilus edulis	0-2 cm	1 4 5 7	5 3 3 6	7 9 4 8	44	8	5.625 $\pm$ 2.264	5.614 $\pm$ 5.569
	2-5 cm	2 4 6 7	0 0 0 0	0 0 1 0	1	8	0.125 $\pm$	4.000 $\pm$ 0.000
	5-8 cm	3 5 6 7	0 0 0 0	0 0 0 0	0	8	0	—
	8-16 cm	1 2 3 8	0 0 0 0	0 0 0 0	0	8	0	—
Modiolus modiolus	0-2 cm	1 4 5 7	3 10 5 1	4 2 7 7	39	8	4.875 $\pm$ 2.997	5.462 $\pm$ 4.987
	2-5 cm	2 4 6 7	0 2 9 3	2 3 5 3	27	8	3.375 $\pm$ 1.414	3.814 $\pm$ 3.886
	5-8 cm	3 5 6 7	0 0 2 0	0 0 1 2	5	8	0.625 $\pm$ 0.916	11.400 $\pm$ 7.700
	8-16 cm	1 2 3 8	0 0 0 0	0 0 0 0	0	8	0	—

Table 80. Number of stones/animal and mean number of threads/stone for *Mytilus edulis* and *Modiolus modiolus* in 8 tanks of sediment with stones present or not present at different depths. T = total number of stones for all animals at the relevant depth and N = number of animals.

Comparisons	d.f.	Sum of squares	Mean of squares	F	P
Factor A: Species	1	1.163	1.163	3.304	Not applicable
Factor B: Depth	1	7.288	7.288	20.705	Not applicable
Interaction	1	2.742	2.742	7.790	0.01> P> 0.005
Error	28	9.852	0.352		
Total	31	21.045			

Table 81. Two way analysis of variance comparing the number of stones to which animals attached byssus threads at different depths in the sediment (square-root transformed data). F = variance ratio, and P = probability. Factor A (fixed): species (2 species = 2 levels); Factor B (random): depth (2 depths = 2 levels).

	Source of Variation	d.f.	Sum of squares	Mean of squares	F	P
<u>Mytilus edulis</u>	Depth	1	9.486	9.486	37.80	P< 0.001
	Error	14	3.513	0.251		
	Total	15	12.999			
<u>Modiolus modiolus</u>	Depth	2	6.512	3.256	9.13	0.01> P> 0.005
	Error	21	7.492	0.357		
	Total	23				

Table 82. One way analyses of variance comparing the number of stones to which animals attached byssus threads at different depths in sediment. d.f. = degrees of freedom, F= variance ratio and P= probability.

modiolus, 0.025> P> 0.005).

T-tests were then performed to test differences between pairs of depths for *M. modiolus*. The results (Table 83) showed that there was no significant difference between 0-1cm and 3-4cm (0.4> P> 0.2) but that animals attached threads to significantly more stones at 0-1cm and at 3-4cm than at 6-7cm (P< 0.001 for both comparisons).

T-tests were performed on the data for 0-1cm and 3-4cm to compare differences between species at each depth (Table 84). These showed that there was no significant difference between species at 0-1cm (0.9> P> 0.5) but that *M. modiolus* attached threads to significantly more stones than did *M. edulis* at 3-4cm (0.02> P> 0.01).

Comparison	t	d.f.	P
0-1cm to 3-4cm	1.0967	14	0.40> P> 0.20
0-1cm to 6-7cm	4.4947	14	P< 0.001***
3-4cm to 6-7cm	3.1270	14	P< 0.001***

Table 83. Students t-tests comparing the number of stones to which Modiolus modiolus attached byssus threads at different depths in sediment square-root transformed data). t= students t, d.f. = degrees of freedom and p = probability.

Comparison	t	d.f.	P
0-1cm	0.7106	14	0.90> P> 0.90
3-4cm	3.1639	14	0.02> P> 0.01*

Table 84. Students t-tests comparing the number of stones to which Mytilus edulis and Modiolus modiolus attached byssus threads (square-root transformed data). t = students t, d.f. = degrees of freedom and P = probability.

Number of threads/stone for *Mytilus edulis* and *Modiolus modiolus*. Comparison between depths and between species.

The number of threads/stone (mean ± std dev) for each depth are shown in Table 85. T-tests were performed on the data to test differences in the number of threads/ stone at different depths for *M. modiolus*. These showed that there was no significant difference in the number of threads/stone between the depths 0-1cm and 3-4cm but that animals attached significantly more threads/stone at 6-7cm than at 0-1cm and at 3-4cm (Table 85). A t-test was performed on the data to test for differences between species at 0-1cm. This showed that there was no significant difference in the number of threads/ stone between species at 0-1cm (Table 86).

Depth of stones with attached threads

The depth of each stone with attached threads was estimated by calculating the mean depth of threads attached to each stone for the a (0-1cm), b (3-4cm) and c (6-7cm) stone layers in each tank. These are shown in Table 87. The mid-point of each stone layer was used as the expected depth (0.5cm for 0-1cm, 3.5cm for 3-4cm and 6.5cm for 6-7cm).

Chi-squared tests were performed to determine whether there was a change in depth of stones due to the activity of animals. These showed that there was no significant difference for *M. edulis* (a layer) or *M. modiolus* (b and c layers) but that there was a significant change in depth for stones with threads attached at 0-1cm for *M. modiolus* (Table 88).

Species	0-1cm N	0-1cm Mean	0-1cm std dev	3-4cm N	3-4cm Mean	3-4cm std dev	6-7cm N	6-7cm Mean	6-7cm std dev
Mytilus edulis	44	5.61	4.60	1	4.00	——	0	——	——
Modiolus modiolus	39	5.46	4.98	27	3.81	3.88	5	11.4	7.70

Table 85. The mean number of threads/stone for threads attached to stones at different depths in sediment. N = number of stones.

	Comparison	t	d.f.	P
	0-1cm to 3-4cm	0.501	64	$0.70 > P > 0.50^{ns}$
A	0-1cm to 6-7cm	2.360	42	$0.05 > P > 0.02^{*}$
	3-4cm to 6-7cm	2.919	30	$0.01 > P > 0.001^{***}$
B	*M. e.* to *M. m.*	0.145	81	$0.90 > P > 0.70^{ns}$

Table 86. Students t-tests comparing the number of threads/stone at different depths for *Modiolus modiolus* (A) and the number of threads/stone at 0-1cm for *Mytilus edulis* and *Modiolus modiolus* (B). t = students t, d.f. = degrees of freedom and P = probability.

Species	Stone layer	Number of stones	Mean depth (cm)	std dev
Mytilus edulis	a (0-1cm)	58	0.063	0.377
	b (3-4cm)	1	3.212	——
Modiolus modiolus	a (0-1cm)	52	1.797	0.881
	b (3-4cm)	29	3.336	0.509
	c (6-7cm)	5	6.129	1.018

Table 87. The depth of stones with attached byssus threads for *Mytilus edulis* and for *Modiolus modiolus*.

Comparison		X^2 statistic	d.f.	P
M. edulis	0-1cm	38.337	56	0.20> P> 0.10
M. modiolus	0-1cm	254.050	50	P< 0.001***
M. modiolus	3-4cm	2.297	27	P> 0.99
M. modiolus	6-7cm	0.800	3	0.90> P> 0.80

Table 88. Statistical analyses comparing the depth of stones with attached byssus threads to stones with no attached byssus threads (control) for *Mytilus edulis* and *Modiolus modiolus*. d.f. = degrees of freedom.

Length of byssus threads

The length of byssus threads produced by Mytilus edulis and Modiolus modiolus are shown in Tables 89 and 90 respectively.

One way analyses of variance were performed on the data to determine whether there were differences between animals. These showed that there were significant differences in thread length between animals for M. edulis and for M. modiolus (Table 91). A careful study of Tables 89 and 90 shows that there is no relationship between sediment type and length but that significant differences are due to variation between individuals.

Comparison between field data and laboratory data

In the results for field data I stated (page 160) that the data for about half the animals had been lost. T-tests were therefore performed on the available data to compare the length of threads produced by animals in field and laboratory conditions. In most comparisons there was no significant difference in thread length between an animal taken from the field and the same animal in the laboratory (Table 91).

Tank	Stone layer present	Animal	Number of threads	Mean	std dev
1	(a layer)	1	33	1.350	0.592
		2	37	1.694	0.487
3	(c layer)	1	4	1.028	0.397
4	(a,b layers)	1	15	1.151	0.290
		2	47	1.157	0.481
5	(a,c layers)	1	38	1.128	0.468
		2	31	1.369	0.310
6	(b,c layers)	1	2	0.685	0.069
		2	4	2.881	0.154
7	(a,b,c layers)	1	33	1.025	0.356
		2	37	1.658	0.606
8	(control)	1	4	2.225	0.206
9	(all 1cm layers)	1	38	1.220	0.315
		2	24	1.165	0.346

Table 89. The length of byssus threads produced by <u>Mytilus edulis</u> in tanks of sediment with stones present or not present at different depths. The stone layers a, b and c occur at the depths 0-1cm, 3-4cm and 6-7cm respectively.

Tank	Stone layer present	Animal	Number of threads	Mean	std dev
1	(a layer)	1	115	2.84	0.90
		2	104	3.07	1.22
2	(b layer)	1	136	3.60	1.44
		2	158	4.21	1.66
3	(c layer)	1	94	4.66	0.99
		2	123	3.76	1.21
4	(a,b layers)	1	125	4.70	1.43
		2	93	3.42	0.98
5	(a,c layers)	1	130	5.82	2.00
		2	77	4.46	1.79
6	(b,c layers)	1	89	5.33	1.53
		2	66	2.42	0.70
7	(a,b,c layers)	1	66	2.91	1.00
		2	97	4.26	1.64
8	(control)	1	145	3.33	0.87
9	(all 1cm layers)	1	137	3.61	1.13
		2	172	3.81	1.15

Table 90. The length of byssus threads produced by Modiolus modiolus in tanks of sediment with stones present or not present at different depths. The stone layers a, b and c occur at the depths 0-1cm, 3-4cm and 6-7cm respectively.

Species	Source of variation	d.f.	Sum of squares	Mean of squares	F	P
Mytilus	Size range	13	27.947	2.150	11.37	P< 0.001
edulis	Error	311	58.820	0.189		
	Total	324	86.767			
Modiolus	Size range	16	1347.67	84.23	47.34	P< 0.001
modiolus	Error	1910	3398.66	1.78		
	Total	1926	4746.32			

Table 91. One way analyses of variance comparing the length of byssus threads produced by Mytilus edulis and Modiolus modiolus in sediment with stones present or not present at different depths. d.f. = degrees of freedom, F = variance ratio and P = probability.

Tank	Animal	t	d.f.	P
Mytilus edulis				
3	1	0.296	63	0.90> P> 0.70
4	2	0.629	95	0.90> P> 0.50
5	1	0.707	86	0.50> P> 0.30
5	2	0.721	79	0.50> P> 0.30
7	1	0.291	81	0.90> P> 0.70
7	2	0.296	85	0.90> P> 0.70
9	1	3.099	86	0.01> P> 0.001**
9	2	1.975	72	0.10> P> 0.05
Modiolus modiolus				
1	1	0.810	163	0.50> P> 0.30
1	2	2.618	152	0.01> P> 0.01**
2	2	1.236	206	0.40> P> 0.20
3	2	1.552	171	0.20> P> 0.10
6	2	1.131	114	0.40> P> 0.20
7	1	1.568	114	0.20> P> 0.10
8	1	0.321	193	0.90> P> 0.70
9	1	0.436	185	0.70> P> 0.50

Table 92. Students t-tests comparing the length of byssus threads produced by animals in the field and laboratory. t = students t, d.f. = degrees of freedom and P = probability.

GROUPS OF ANIMALS

The number of byssus threads animals attached to sediment, other animals, and the animal's own shell are shown in Table 93 (Mytilus edulis) and 94 (Modiolus modiolus).

Mytilus edulis

Comparison within tanks

In tank 1 (a,b and c stone layers) equal numbers of threads were attached to stones and to other animals. Animals only attached threads to stones at the surface (a layer). In tanks 2 (b and c stone layers) and 3 (no stone layers) the largest number of threads were attached to other animals. Small numbers of threads were attached to sediment. Only 2 of the 60 animals in tank 2 attached threads to the animals own shell and animals did not attach threads to stones (b or c layers).

One-way analyses of variance and t-tests were performed on data to test for differences in the number of threads attached to different substrates (sediment, stones, other animals and its own shell). These are shown in Tables 95-96. There were significant differences in the number of threads attached to different substrates in all tanks. In tank 1 (a,b and c stone layers) animals attached significantly more threads to stones (a stone layer) and to other animals than to sediment. In tanks 2 and 3, animals attached significantly more threads to other animals than to sediment. In tank 2, animals attached significantly more threads to other animals than the animals own shell.

Comparison between tanks

In general animals only attached threads to stones when a stone layer was present at the surface (a stone layer). There were fewer threads attached to other animals in tank 1 (a,b and c stone layers) than in tanks 2 (b and c stone layers) and 3 (no stone layers) but the total number of threads/animal was larger in tank 1 than in tanks 2

Stone layer present	N	Type of substrate threads to which threads are attached									
		sediment		stones		other animals		to itself		Total	
		mean	s.d.	mean	s.d.	mean	s.d.	mn	s.d.	mean	s.d.
a+b+c	62	0.40	1.45	9.81	7.60	10.1	8.6	0	0	20.3	9.9
b+c	60	0.65	1.35	—	—	14.5	11.3	0.08	0.46	15.3	10.9
control	66	2.03	5.28	—	—	13.8	10.9	0	0	15.8	11.2

Table 93. The number of threads/animal for groups of *Mytilus edulis* in different experimental sediments. N = number of animals.

Stone layer present	N	Threads to sediment		Threads to stones a layer		Threads to stones b layer		Threads to stones c layer		Threads to stones Total		Threads to other animals		Threads to own shell	Total number of threads	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	mean	s.d.
a+b+c layers	10	107.5	69.9	5.30	7.29	11.70	15.00	16.00	18.20	34.0	29.30	4.20	8.12	0	144.1	66.5
b+c layers	10	94.3	35.6	—	—	5.50	5.97	9.60	9.54	15.1	8.13	4.60	6.31	0	85.3	40.3
control	10	88.4	58.6	—	—	—	—	—	—	—	—	2.10	6.64	0	90.5	62.1

Table 94. The number of threads/animal for groups of *Modiolus modiolus* in different experimental sediments. N = number of animals.

Comparison	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Tank 1 Stone layers a, b and c	Substrate	2	3764.4	1882.2	42.37	P< 0.001
	Error	183	8129.2	44.4		
	Total	185	11893.6			
Tank 2 Stone layers b and c	Depth	2	8034.4	4018.7	93.31	P< 0.001
	Error	177	7623.2	43.1		
	Total	179	15660.6			
Tank 3 Control tank	Depth	1	4585.5	4585.5	62.61	P< 0.001
	Error	130	9521.8	73.2		
	Total	131	14107.2			

Table 95. Groups of Mytilus edulis. One way analyses of variance comparing the number of threads attached to different substrates. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Comparison	t	d.f.	P
	stones to sediment	9.574	122	P< 0.001***
A	stones to other animals	0.189	122	0.20> P> 0.10
	sediment to other animals	8.766	122	P< 0.001***
	sediment to other animals	9.469	118	P< 0.001***
B	sediment to own shell	3.075	118	0.01> P> 0.001**
	other animals to own shell	9.917	118	P< 0.001***

Table 96. Groups of *Mytilus edulis*. Students t-tests comparing the number of byssus threads attached to different substrates. A = tanks with stone layers at 0-1cm(a), 3-4cm(b) and 6-7cm(c), B = tanks with stone layers at 3-4cm and 6-7cm. t = students t, d.f. = degrees of freedom and P = probability.

and 3.

One-way analyses of variance and t-tests were performed on the number of threads attached to the different substrates and on the total number of threads in tanks. These are shown in Tables 97-98.

Threads attached to sediment: Animals in tank 1 (a, b and c stone layers) attached significantly fewer threads to sediment than did animals in tank 3 (no stone layers). No other comparisons were significant (Table 98).

Threads attached to stones: Animals only attached threads to stones when a stone layer was present at the surface (a stone layer).

Threads attached to other animals: Animals in tank 1 (a, b and c stone layers) attached significantly fewer threads to other animals than did animals in tanks 2 (b and c layers) and 3 (no stone layers).

Threads attached to the animals own shell: Only 2 animals in tank 2 (b and c stone layers attached threads to the animal's own shell.

Total number of threads: Animals in tank 1 produced significantly more threads than did animals in tanks 2 and 3 (Table 98).

Modiolus modiolus

Comparison within tanks

In general, animals attached the largest number of threads to sediment, with much fewer threads attached to stones and only a small number attached to other animals. Animals did not attach threads to their own shell's. In tank 1 (a,b and c stone layers) more threads were attached to stones in the c layer than to stones in the a and b stone layers, and in the b layer than in the a layer. In tank 2 (b and c stone layers) more threads were attached to stones in the c layer than in the b layer.

One-way analyses of variance and t-tests were performed on data to test for differences in the number of threads animals attached to different substrates. These are shown in Tables 99-100. In all three

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Threads to sediment	Substrate	2	99.0	49.5	4.47	0.025> P> 0.01
	Error	185	2048.5	11.1		
	Total	187	2147.5			
Threads to other animals	Depth	2	707.0	354.0	3.32	0.05> P> 0.025
	Error	185	19693.0	106.0		
	Total	187	20400.0			
Total number of threads	Depth	2	941	471	4.10	0.025> P> 0.01
	Error	185	21231	115		
	Total	187	22172			

Table 97. Groups of Mytilus edulis. One way analyses of variance comparing the number of threads attached to different substrates in different experimental tanks. d.f. = degrees of freedom, F = variance ratio and P = probability.

Comparison		t	d.f.	P
	tank 1 to tank 2	0.971	120	0.20> P> 0.10
A	tank 1 to tank 3	2.344	126	0.05> P> 0.01*
	tank 2 to tank 3	1.967	124	0.10> P> 0.05
	tank 1 to tank 2	2.460	120	0.02> P> 0.01*
B	tank 1 to tank 3	2.148	126	0.05> P> 0.02*
	tank 2 to tank 3	0.362	124	0.20> P> 0.10
	tank 1 to tank 2	2.664	120	0.01> P> 0.001**
C	tank 1 to tank 3	2.378	126	0.025> P> 0.01*
	tank 2 to tank 3	0.278	124	0.20> P> 0.10

Table 98. Groups of Mytilus edulis. Students t-tests comparing the number of byssus threads animals attach to various substrates in different experimental tanks. A = threads attached to sediment, B = threads attached to other animals and C = total number of threads. t = students t, d.f. = degrees of freedom and P = probability.

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Stone layers a, b and c	Substrate	3	56835	28418	14.63	P< 0.001
	Error	27	52483	1942		
	Total	30	109273			
Stone layers b and c	Substrate	2	29022	1454	23.88	P< 0.001
	Error	27	16407	608		
	Total	29	45429			
Control tank	Depth	1	37238	37238	21.43	P< 0.001
	Error	18	31279	1738		
	Total	19	68518			

Table 99. Groups of Modiolus modiolus. One way analyses of variance comparing the number of threads attached to different substrates. d.f. = degrees of freedom, F = variance ratio and P = probability.

	Comparison	t	d.f.	P
	stones to sediment	3.104	18	0.01> P> 0.001**
A	stones to other animals	2.969	18	0.01> P> 0.001**
	sediment to other animals	4.642	18	P< 0.001***
	stones to sediment	4.501	18	P< 0.001***
B	stones to other animals	3.226	18	0.01> P> 0.001**
	sediment to other animals	5.326	18	P< 0.001***

Table 100. Groups of Modiolus modiolus. Students t-tests on the number of byssus threads animals attach to different substrates. A = tanks with stone layers at 0-1cm(a layer), 3-4cm(b layer) and 6-7cm(c layer), B = tanks with stone layers at 3-4cm and 6-7cm. t = students t, d.f. = degrees of freedom and P = probability.

	Comparison	t	d.f.	P
	a layer to b layer	1.213	18	0.40> P> 0.20
A	a layer to c layer	1.724	18	0.20> P> 0.10
	b layer to c layer	0.756	18	0.70> P> 0.50
B	b layer to c layer	1.206	18	0.40> P> 0.20

Table 101. Groups of Modiolus modiolus. Students t-tests comparing the number of byssus threads animals attached to stones at different depths in the sediment. Stone layer a layer = 0-1cm, b layer = 3-4cm and c layer = 6-7cm depth. t = students t, d.f. = degrees of freedom and P = probability.

tanks significantly more threads were attached to sediment than to stones (total number of stones) or to other animals (Tables99-100). Significantly more threads were attached to stones (total number of stones) than to other animals (Tables99-100). There were no significant differences in the number of threads attached to stones at different depths (Table 101).

Comparison between tanks

In general more threads were attached to sediment and to stones (total number of stones) in tank 1 than in tanks 2 or 3. There were no differences in the number of threads attached to other animals. Thus more threads were produced in tank 1 than in tanks 2 and 3.

One-way analyses of variance and t-tests were performed on the number of threads attached to the different substrates to test for differences between tanks. These are shown in Tables 102-103. There were no significant differences in the numbers of threads attached to sediment, to stones (b stone layer, c stone layer and total number attached to stones) between species However, animals in tank 1 produced significantly more threads than did than animals in tank 2 (Table 103).

	Source of variation	d.f.	Sum of squares	Sum of squares	F	P
Threads to sediment	Substrate	2	8544	4272	1.23	0.50> P> 0.20
	Error	27	93413	3460		
	Total	29	101957			
Threads to other animals	Depth	2	36.1	18.0	0.36	0.75> P> 0.50
	Error	27	1348.9	50.0		
	Total	29	1385.0			
Total number of threads	Depth	2	21191	10596	3.21	0.10> P> 0.05
	Error	27	89108	3300		
	Total	29	110299			

Table 102. Modiolus modiolus. One way analyses of variance comparing the number of threads attached to several substrates in different experimental tanks. d.f. = degrees of freedom, F = variance ratio and P = probability.

Comparison		t	d.f.	P
	tank 1 to tank 2	0.123	18	P> 0.90
A	tank 1 to tank 3	0.633	18	0.70> P> 0.50
	tank 2 to tank 3	0.863	18	0.40> P> 0.20
	tank 1 to tank 2	1.567	18	0.20> P> 0.10
B	tank 1 to tank 3	0.662	18	0.70> P> 0.50
	tank 2 to tank 3	0.947	18	0.40> P> 0.20
C	tank 1 to tank 2	0.231	18	0.40> P> 0.20
D	tank 1 to tank 2	0.984	18	0.40> P> 0.20
E	tank 1 to tank 2	1.845	18	0.10> P> 0.05
	tank 1 to tank 2	2.392	18	0.05> P> 0.01*
F	tank 1 to tank 3	1.864	18	0.10> P> 0.05
	tank 2 to tank 3	0.222	18	0.90> P> 0.70

Table 103. Groups of Modiolus modiolus. Students t-tests comparing the number of byssus threads animals attach to various substrates in different experimental tanks. A = threads attached to sediment, B = threads attached to other animals and C = numbar of threads attached to stones in the b layer (3-4cm), D = number of threads attached to stones in the c layer (6-7cm), E = total number of threads attached to stones and F = total number of threads. t = students t, d.f. = degrees of freedom and P = probability.

Comparison between species

T-tests were performed on the number of threads/animal to determine differences between species for each of the three experimental tanks. These are shown in Table 104. In all three tanks *M. modiolus* attached significantly more threads to sediment and significantly fewer threads to other animals than did *M. edulis*. In tanks 1 (a,b and c stone layers) and 2 (b and c stone layers) *M. modiolus* attached significantly more threads to stones (total number of stones) than did *M. edulis*. In tank 1 there was no significant difference in the number of threads attached to stones in the a layer (0-1cm) between *M. edulis* and *M. modiolus*. *M. edulis* did not attach threads to stones in the b layer (3-4cm depth). *M. modiolus* produced significantly more threads/animal than did *M. edulis* in all three tanks.

Comparison		d.f.	t	P
A	sediment	70	12.521	P< 0.001***
	stones (a layer)	70	1.750	0.10> P> 0.05
	stones (total)	70	4.766	P< 0.001***
	other animals	70	2.027	0.05> P> 0.02*
	total	70	14.203	P< 0.001***
B	sediment	68	14.428	P< 0.001***
	other animals	68	2.705	0.01> P> 0.001**
	total	68	14.075	P< 0.001***
C	sediment	74	12.109	P< 0.001***
	other animals	74	3.299	0.01> P> 0.001**
	total	74	9.134	P< 0.001***

Table 104. Students t-tests comparing the number of byssus threads attached to different substrates by *Mytilus edulis* and *Modiolus modiolus*. A = tank 1 (stones at 0-1cm, 3-4cm and 6-7cm - a+b+c stone layers), B = tank 2 (b+c stone layers) and C = tank 3 (control). t = students t, d.f. = degrees of freedom and P = probability.

COMPARISON BETWEEN SINGLE ANIMALS AND GROUPS OF ANIMALS

Mytilus edulis

The number of threads/animal for single animals andfor groups of animals in tanks with stone layers present or not present at different depths was strongly dependent on whether a stone layer was present or not present at the surface (Table 57 and Figure 16, single animals; Table 93, groups of animals). The number of threads /animal were therefore pooled for tanks with a stone layer present at the surface (a layer) and for tanks with no stone layer present at the surface.

Students t-tests were performed on the two sets of pooled data to determine whether there were significant differences between single animals and groups of animals for each set of pooled data. These are shown in Table 105. In sediment with stones present at the surface, single animals produced significantly more threads than did groups of animals. In sediment with stones not present at the surface, single animals produce significantly fewer threads than did groups of animals.

Modiolus modiolus

The number of threads/animal for single animals and for groups of animals in tanks with stone layers present at various depths was not dependent on the presence or absence of any stone layers (Table 58 and figure 17, single animals; Table 94, groups of animals). The number of threads/animal for single animals and for groups of animals were therefore pooled for all tanks.

Students t-tests were performed to determine whether there were significant differences in the number of threads/animal for single animals and groups of animals. These showed that there were no significant differences in the number of threads/animal between single animals and groups of animals (Table 105).

Comparison	d.f.	t	P
Mytilus edulis			
tanks pooled for;			
stone layer present at surface	70	3.164	0.01> P> 0.001 ***
stone layer absent at surface	70	3.533	P< 0.001 ***
Modiolus modiolus			
all tanks pooled	70	0.229	0.90> P> 0.50

Table 105. Students t-tests comparing the number of threads produced by single animals and groups of animals in sediment with stones present or not present at different depths.

Clumping in Mytilus edulis and Modiolus modiolus

Only 5 Modiolus modiolus were used in each tank but it was clear that animals did not move towards one another.

The use of Nearest-neighbour analyses was originally employed to determine clumping in M. edulis (Pielou, 1977; Clark and Evans, 1954; Edgar and Meadows, 1969). The methods described in Clark and Evans (1954) were followed but they were not applicable to my data. I did not have enough time to pursue the method further.

In all the tanks used in the experiment I have defined a group as a solitary animal or a clump of animals in which each animal touches at least one other member of the clump for the following results. The total number of groups, the number of groups containing >1 animal and the number of groups >2 animals in tanks with stones present or not present at different depths for day 0 to day 12 is shown in Table 106. The mean number of animals/clump are also shown for days 0 to 12 in each tank.

Table 106 shows that M. edulis had formed several clumps by day 1. In general, this clumping continues at a slower rate from day 1 onwards. There appears to be little change after 4-8 days.

Stone layers present	Tank	Day	Number of groups T	containing 1 animals	2	3	4	>4	Mean number of animals/group ± std dev
a + b + c	1	0	32	32	0	0	0	0	1.00 ± ——
		1	13	7	1	3	1	1 (10)	2.46 ± 2.50
		2	12	7	2	1	0	2 (7,11)	2.67 ± 3.14
		4	13	7	2	2	1	1 (11)	2.46 ± 2.76
		8	12	6	2	2	1	1 (12)	2.67 ± 3.11
		12	13	7	2	2	1	1 (11)	2.46 ± 2.76
	2	0	32	32	0	0	0	0	1.000 ± ——
		1	17	1	3	1	2	1 (5)	1.882 ± 1.317
		2	16	8	4	1	2	1 (5)	2.000 ± 1.317
		4	15	8	1	3	2	1 (5)	2.133 ± 1.407
		8	13	5	2	3	2	1 (5)	2.358 ± 1.387
		12	14	6	3	2	2	1 (5)	2.214 ± 1.369
b+c	1	0	30	30	0	0	0	0	1.000 ± ——
		1	16	8	5	2	0	1 (6)	1.875 ± 1.310
		2	14	6	4	2	1	1 (6)	2.143 ± 1.460
		4	10	3	3	1	1	2 (6,8)	3.000 ± 2.357
		8	9	2	2	2	1	2 (6,8)	3.333 ± 2.345
		12	9	2	1	4	0	2 (6,8)	3.333 ± 2.291
	2	0	31	31	0	0	0	0	1.000 ± ——
		1	24	18	5	1	0	0	1.292 ± 0.550
		2	21	14	4	3	0	0	1.476 ± 0.750
		4	16	6	6	3	1	0	1.938 ± 0.929
		8	13	5	2	4	1	1 (6)	2.385 ± 1.502
		12	12	3	3	4	1	1 (6)	2.583 ± 1.443
control no stone layers	1	0	33	33	0	0	0	0	1.000 ± ——
		1	21	15	3	3	0	0	1.429 ± 0.746
		2	17	8	3	5	1	0	1.941 ± 1.029
		4	14	5	2	5	1	1 (5)	2.357 ± 1.277
		8	15	7	1	5	1	1 (5)	2.200 ± 1.320
		12	15	7	1	5	1	1 (5)	2.200 ± 1.320
	2	0	33	33	0	0	0	0	1.000 ± ——
		1	19	10	6	1	2	0	1.737 ± 0.991
		2	17	8	4	3	2	0	1.941 ± 1.088
		4	17	8	4	3	2	0	1.941 ± 1.088
		8	15	7	4	1	1	2 (5,6)	2.200 ± 1.612
		12	14	6	4	1	0	3 (5,5,6)	2.357 ± 1.737

Table106. The number of groups and mean number of animals/group (± standard deviation) for M. edulis in sediment with stones present or not present at different depths. Stone layers a, b and c represent the depths 0-1cm, 3-4cm and 6-7cm respectively. T = total number of groups and the numbers in brackets are number of animals in each clump.

DISCUSSION

Mytilus edulis and Modiolus modiolus produce byssus threads as a means of attachment to hard substrates. Both species are found attached to rocky substrates and to stones in sediment, M. edulis intertidally and M. modiolus subtidally.

Distribution

Kuenen (1942) found that M. edulis on areas of loose sand were moved by tidal currents. They were moved in the direction of the flood current which which had a greater maximum current than the ebb. Thus currents, if strong enough can transport or remove unattached animals. Mussels cannot form beds in the intertidal region where tidal currents are strong unless there is a firm base (Kuenen, 1942; Maas Gesteranus, 1942). This appears to account for the distribution of M. edulis only where a suitable attachment site is present ie. rocky shores or on sediment containing stones at or near the surface.

The collecting sites for M. edulis and M. modiolus (Arrochar and Coilessan respectively) contained many stones at and below the surface. It is to these stones that animals attached byssus threads. Both sites are relatively sheltered areas although the M. edulis site probably experiences more erosion due to the tidal cycle and from freshwater runoff in the spring.

Clumping

Young (1983) found that groups of M. edulis in mud and sand attached threads to each other, sometimes in a matter of hours, forming well defined clumps. Animals on gravel did not form clumps with the regularity of animals on smaller particles. They attached threads to the substrate itself and when they did attach to one another it was normally in pairs. Larger groups were occasionally formed towards the end of 1 week. In contrast, I found that clumping was not related to particle size. Animals in the particle size range

2.0-4.0mm did attach larger numbers of threads to the substrate but this did not slow down the rate of clumping. In the field, M. edulis occurs in clumps on rocky shores and on sediment although single animals and small groups are not uncommon. Clumping is initially due to aggregated settling behaviour but adult animals also appear to prefer this aggregated distribution.

Martella (1974) found that more M. edulis produced threads when clumped with other M. edulis than M. edulis maintained in separate containers. These results are very unusual since M. edulis readily attaches threads to a variety of substrates in laboratory conditions. The only exceptions I have observed is when an animal's byssal apparatus appears to have been damaged. There is no advantage in single animals not producing threads.

Maas Gesteranus (1942) found that young animals prefer surfaces where two planes make an angle than flat surfaces. In the experiment with stones present or not present at the surface animals had pulled several stones towards their own shell's. This resulted in the animal being surrounded by several stones. Adult animals on sediment therefore appear to modify their environment. This modification may give the animal some protection from currents and possibly from predators in the same way that cracks and crevices protect young animals. Groups of animals in the laboratory and in the field compete for the best position. In the experiments with groups of M. edulis I noted that the inhalent and exhalent siphons of some animals were barely above the sediment surface, due to the attachment of threads by, and positions of, other animals.

M. modiolus attaches threads to stones deeper in the sediment than does M. edulis. This is not only due to the large difference in size between species but also a difference in behaviour. M. modiolus makes it's way into the sediment by a combination of sediment displacement and thread production. When threads are produced the animal can pull on the threads with the result that it will pull itself into the sediment. In the field, animals are most frequently found with only about one third of the shell above the sediment surface. Adult animals would preferentially attach threads to stones deeper in the sediment than to other animals at the surface. In addition, no small animals were found in Loch Long at depths of 10-15 metres. It is probable that small animals which are found in shallower water gradually make their way into deeper water. M. modiolus occurs in the sample site at low densities and so few clumps would result from animals moving downslope.

Number of threads

In field observations of M. edulis, Young (1983) found that animals attached a mean number of 87 threads/animal on a rocky substatum and 48 threads/animal on a muddy substratum with stones. M. edulis did not attach to particles smaller than 0.85mm in diameter. Clumps characteristic of mussel beds in the field were formed on finer substrates. Few clumps were formed on sediment >0.85mm diameter.

In my experiments the number of threads produced by M. edulis and M. modiolus was related to particle size. In all the particle size ranges M. edulis produced significantly fewer threads than M. modiolus. Adult M. edulis readily attached threads to sediment of particle size ranges greater than 1mm but rarely attach threads to smaller particle size ranges. This is broadly in agreement with the results obtained by Young (1983), mentioned above. M. modiolus readily attached threads to sediment of particle sizes greater than 0.25mm. Below this particle size thread production is reduced. The contrast between M. modiolus which attached a large number of threads to sediment of particle size <2.00mm and M. edulis which rarely attached threads to the same particle size, is an interesting one. M. edulis would not benefit by attaching threads to small particles. Animals attach threads at or near the sediment surface and this attachment would not give the animal any resistance to strong water currents. M. modiolus, however, does appear to benefit by attaching threads to relatively small particles deeper in the sediment. A moderate amount of force was required to pull or to move animals which had attached threads to sediment. It is clear that the attachment of large numbers of threads to sediment particles would not give the same support as threads attached to stones, but it is possible that they give the animal enough stability and support in relatively strong currents until or stones can be found. Another reason for the difference between species may be that adult M. edulis can shed it's byssus complex and move to a more suitable site wheras adult M. modiolus does not, to my knowledge, shed it's byssus complex or move across the sediment surface.

M. modiolus attaches large numbers of threads in a straight line, to stones and to sediment particles. It then retracts its foot and may search in a new area, attaching more threads to sediment particles or to a stones present in the sediment.

A larger number of threads/stone were found on stones deeper in the sediment. When an animal finds a suitable substrate it therefore maximises the production of threads.

Groups of M. edulis produce fewer threads than single animals of the same species. It would be interesting to determine whether the number of threads produced by each animal added to the number attached to the same animal is similar to the total number produced by single animals. The resulting network of threads and stones is attractive to other invertebrates (Tsuchiya and Nishihiri, 1985). Groups of M.

modiolus produced approximately the same number of threads/animal as did single animals. M. modiolus will attach threads to other animals but concentrate on searching for suitable substrates deeper in the sediment.

Length of threads

The length of threads varies greatly between animals of the same size and species. There is no relationship between number of threads produced and thread length. This difference may have important evolutionary consequences. Animals which produce longer threads may have an advantage during winter storms, particularly if threads can be attached to large stones in the sediment which are too deep for other animals to reach. In addition the longer the threads an animal can produce the greater the circumference for attachment to a suitable substrate. Alternatively, animals producing shorter threads may have greater reproductive success. If animals put more energy into gonad production and less into thread production there is a greater chance that more animals will survive to metamorphosis and adult life. These ideas are speculative, but such variation in species with planktonic larvae will allow at least a few individuals to survive in adverse conditions.

The experimental results obtained in this study show that M. edulis and M. modiolus produce longer threads in smaller particle size ranges. This is probably because animals search with their foot over a wider area when stones cannot be found nearby.

Size of byssus pads

Allen et al (1976) found that the size of byssus pads produced by M. edulis was very variable. This is true for animals in this study, but it is also clear that smaller pads are produced in the smaller particle size ranges by both species. Pads produced by M. edulis do not change shape with decreasing particle size whereas those of M.

modiolus become very much narrower. M. modiolus changed the shape of byssus pads as a response to smaller particle size ranges. In addition M. modiolus attached pads to smaller particle size ranges than did M. edulis. It appears that M. edulis "chooses" not to attach pads to smaller particle size ranges because of the lack of support the particles would give.

Sedimentation

It is unlikely that M. modiolus could survive in areas where sedimentation rates are high or in areas where subsidence of slopes occurs frequently. The animals at Coilessan are on a gentle sediment slope where currents are relatively weak compared to those of the exposed open coastline. Maas Geesteranus (1942) reports that M. edulis which are buried under up to 2cm of sediment can work their way up to the surface. Adult Modiolus modiolus are large and relatively much heavier than adult M. edulis. It is unlikely that M. modiolus could do the same. In Loch Long animals show a tendency to face down-slope. Sediment falling down the slope is therefore less likely to cover animals especially the siphons since the sediment will roll over the animal. The quick closing of the shell also produces a current of water which keeps the shell opening clear of sediment (personnal observation).

Summary

M. edulis is an intertidal species of mussel which attaches to rocks and to stones in sediment. Animals attach threads to stones at or close to the sediment surface and to other animals. They form characteristic mussel beds in areas where a suitable substrate is found. The formation of mussel beds is caused by aggregation of animals in suitable areas and may afford the animals some protection against predation and erosion. M. modiolus is a subtidal species of mussel which also attaches to rocks and to stones in the sediment. In areas where stones are relatively more scarce they probably attach to sediment particles. Animals attach threads to stones and sediment near the surface but preferentially attach threads to stones below the surface. They can make their way deeper into the sediment, leaving only the front of the shell with inhalent and exhalent siphons above the sediment surface. This may give the animal protection against predation and against destabilisation of the slope.

SECTION 3

THE EFFECTS OF THE MUSSELS *Mytilus edulis* AND *Modiolus modiolus* ON MARINE SEDIMENT STABILITY

INTRODUCTION

The dynamics of sediment transport in moving water are not simple (Miller et al, 1977; Dyer, 1979; Frostick and McCave, 1979; Grant, 1981; Lambiase, 1980; Larsen et al, 1981; Postma, 1967; Reineck and Singh, 1980; Brayshaw et al, 1983; Neilson, 1983; Komar and Clemens, 1986). Relationships between critical erosion velocities (the current velocity at which a few particles start to move over the bed surface) have been developed by Hjulstrom (1935, 1939) and re-examined by Sundborg (1956).

Shields (1936) worked on the entrainment of quartz density particles. The Shields entrainment function written in terms of fluid velocity is

$$\frac{pU_m^{\,2}}{(p_s-p)gD} = \frac{\tau}{(p_s-p)gD}$$

where p_s and p are the sediment and fluid densities, respectively, g is accelaration due to gravity ($9.81ms^{-2}$) and D is the mean grain diameter. U_m is the fluid velocity at a designated distance (normally 1m) above the seabed. The Shields function is the ratio of the shear stress across the sediment ($\tau = pUm^2$) to the stabilising force of gravity on the sediment particles ((ps-p)gD). When a certain minimum current velocity is reached particles start to move across the surface. At this point the Shields function is denoted by θ_t and is called the Shields criterion. This criterion is a dimensionless relationship. It applies for any fluid flow and sediment characteristics so long as the sediment is cohesionless.

Larsen et al (1981) investigated the applicability of the Shields function to the threshold of grain motion produced by ocean waves and currents. They concluded that Shields entrainment function for unidirectional flow can be used to predict the threshold of grain motion for oscillatory flow conditions on the continental shelf.

In a series of flume experiments, Parthenaides (1965) found that erosion rates of clays were independent of the shear strength of the bed, but was strongly related to the shear stress exerted by the current on the sediment surface. Shear stress values are therefore probably more meaningful for experimental work on sediment stability.

Importance of biological factors in sediment stability

Sedimentologists and engineers place a considerable amount of importance on the study of primary depositional structures. Bioturbation, however, produces the dominant structural components in many areas of sedimentary deposition (Reineck, 1977; Rhoads, 1963; 1967; McCall and Tevesz, 1982). In some cases the primary stratification is completely destroyed by burrowing (eg. Rhoads, 1963; Allen and Curren, 1974).

Many workers have shown that the activities of benthic organisms modify the physical and chemical nature of marine sediments. The effects of micro-organisms, plants and animals are reviewed below. Emphasis is given to the effects of animals since this forms the subject of my work. This review also covers some areas of research not included in my work. These are included because the results of any study of bioturbation have to be interpreted in relation to the sedimentary environment as a whole.

The effect of micro-organisms on sediment stability

The main influence of terrestial micro-organisms is thought to be their effects on soil stability (Martin and Wakesman, 1940; Aspiras et al, 1971). Bacteria and fungi are resposible for the degradation of biological material. This breakdown produces polysaccharides and humic substances which form polymer bridges between soil particles, thus stabilising soil aggregates (Hayes, 1980). Fungi bind sediment by forming hyphae between particles (Aspiras et al., 1971). The effects of micro-organisms on terrestial soil erodability has been reviewed by Gaspero-Mago and Troeh (1979).

Marine sediments are generally more mobile than terrestial soils. Marine bacteria, however, like their terrestial counterparts secrete polysaccharides for attachment to surfaces (Sutherland, 1980). The presence of bacterial films may therefore modify the properties of marine sediments. Microalgae produce organic films on the sediment surface which increase the adhesion of particles and reduce resuspension of sediment (Black, 1933; Frankel and Mead, 1973; Holland et al, 1974).

The effects of plants on sediment stability

The ability of plants to modify their physical environment has been well documented. The initial stabilisation of sand dunes by marram grass is one of the best examples of the way in which plants can stabilise sediment (Odum, 1959). Terrestial grasses protect the soil on slopes by their physical presence above the soil surface and the root-systems binding sediment below the soil surface (Branson and Owen, 1970).

Marine algae stabilise sediments by the production of one of two structures above or in the sediment.

(a). Baffles. Dense colonies of sea-grasses, benthic algae or aerial mangrove roots reduce the velocity of bottom currents. This decreases erosion of the sediment and allows finer grained particles to settle (Ginsburg and Lowenstram, 1958; Scoffin, 1970; Frostick and McCave, 1979; Ward et al, 1984).

(b). Framework structures. Both macro- and microalgae produce filaments and mats in the sediment which act as a rigid supporting skeleton protecting the underlying sediment (Bathurst, 1967; Neuman et al, 1970; Scoffin, 1970). Frostick and McCave (1979) studied the seasonal shifts of sediment within an estuary in relation to algal growth. Their results showed an accretion of about 5cm between April and September during algal growth and erosion of that amount during autumn and winter. This was due to the growth of filamentous algae (Enteromorpha) on the sediment surface which inhibit erosion by slowing down the flow, and the secretion of mucilage which binds sediment particles. Intact areas of dense Enteromorpha mat in the Bahamas can withstand currents five times stronger than those that erode loose unbound sand grains (Scoffin, 1970).

The effects of animals on sediment stability

Benthic invertebrates affect sediment stability by reworking the sediment during movement and feeding and by burrow and tube-building (Rhoads, 1974; Donahue, 1971; Featherstone and Risk, 1977 Meadows and Tufail, 1986). Demersal fish and marine mammals affect sediment stability by disturbing the sediment surface during feeding (Dillon and Zimmerman, 1970; Summers, 1980; Nelson and Johnson, 1987) and burrowing (Twitchell et al, 1985).

Reworking

Reworking results mainly from the movement and feeding activities of mobile and burrowing deposit feeders. This alters the spatial arrangement of sediment particles, mixing interstitial water and gases (Lee and Swartz, 1980). This in turn modifies the physical and chemical properties of the sediment (Baas Becking et al, 1960; Rhoads, 1963; 1967; Rhoads and Young, 1971; Cullen, 1973; Aller, 1982).

Many species show rates of sediment reworking up to 5 Kg/m^2/year (Gordon, 1966; Rhoads, 1963,1967; Bubnova, 1971; Guinasso and Schink, 1975; Kraeuter, 1976), some species up to about 54 Kg/m^2/year (Rhoads, 1967). The amount of reworking is related to temperature (Rhoads, 1963; Gordon, 1966; Powell, 1977) and varies seasonally (Nichols, 1974; Cadee, 1976; Grant et al, 1982). Deposit feeders may change the physical constitution of the sediment by producing biogenic structures (van Straaten, 1950; Howard and Frey, 1973; Baumfaulk, 1979), graded bedding by mixing (Warme, 1967) and particle size sorting (Rhoads and Stanley, 1965).

Reworking often results in the deposition of layers of faecal material or pellets at the sediment-water interface. In general, this material has a high water content and low density and is easily eroded by tidal currents. This has been shown for the holothurians Yoldia limulata (Rhoads, 1973) and Molpadia oolitica (Rhoads and Young, 1971; Young and Rhoads, 1971), the polychaete Clymenella torquata (Rhoads, 1967) and the bivalve Nucula proxima (Rhoads, 1967; Rhoads and Young, 1970). Topographical relief of the seafloor by feeding mounds like that of M. oolitica probably contributes to turbulence and tidal current erosion. Rhoads (1970) found that intensive burrowing of subtidal muds produced a granular surface layer 5-10mm thick. This uncompacted zone had a water content of more than 60% and experienced greater resuspension rates than surrounding sediment. Nowell et al (1981), however, showed that free sediment and faecal pellets were more easily entrained than small faecal mounds which were restricted from movement by mucous adhesion between the faecal coils. The same authors also found that animal tracks doubled the boundary roughness of the sediment surface and decreased the critical erosion velocity by 20%.

Tevez et al (1980) found that size-selective feeding by oligochaetes in river sediments produced a layer of faeces at the sediment-water inteface. The high water content of this layer, its irregular surface and the low density of the constituent pellets destabilised the sediment surface and increased its susceptability to erosion. Powell (1977) noted that the feeding activities of the holothurian Leptosynapta tenuis stabilised the upper 3cm of the sediment by compaction.

The effect of burrows and tube-building on sediment stability

Burrows and tubes influence the chemistry of marine sediments and the exchange of ions across the sediment-water interface. This has been studied extensively (Aller and Yingst, 1978; Day, 1978; Aller, 1978, 1980, 1982, 1983; Berner, 1980; McCaffrey et al, 1980; Gust and Harrison, 1981; Hines et al, 1982; Waslenchuk et al, 1983). The effects of tubes and burrows on the physical properties of sediments has not been studied in such depth.

Destabilisation of sediment

Bioturbation of the sediment caused by burrowing crabs can be very extensive (Dillon and Zimmerman, 1970; Ott et al, 1976; Edwards and Frey, 1977; Chackrabarti, 1980; Katz, 1980; Letzch and Frey, 1980; Chackrabarti and Subhashish, 1981). In an experiment by Allen and Curren (1974), 10 specimens of *Uca pugilator* completely reworked an area of sediment $0.5m^2$ within a week, destroying all stratification features in the substrate. Crab burrows diminish the integrity and shear strength of sediments and enhance bed roughness. Ott et al (1976) estimated that the expulsion of sediment from the burrows of *Callianassa stebbingi* and *Upogebia littoralis* caused up to 0.5cm of sediment removal per year. Letzsch and Frey (1980) found that burrows of the crabs *Panopeus herbesti*, *Sesarma reticulatum* and *Uca pugnax* occupied 45% of the sediment surface area. These burrows decreased the shear strength of creek banks causing their subsequent collapse.

In laboratory experiments, Eckman et al (1981) found that tube-building by the polychaete *Owenia fusiformis* decreased the critical erosion velocity of the sediment by causing local scour around the tubes. Sediment was thus more easily eroded. Aller and Dodge (1974) report that the tubes of *Callianassa* sp. elevated above the sediment surface make the sediment prone to erosion by water currents. Luckenbach (1986) found that bioturbation caused by associated fauna, rather than alterations of near-bed flow by animal tubes, were responsible for lowering the critical erosion velocity in natural cohesive sediments. Hecker (1982) reviews the destabilising effects of invertebrates on marine sediment.

Stabilisation

If tubes and burrows of specific invertebrates are present in sufficient numbers they can increase the stability of the sediment by compacting and reducing the water content of the sediment. Invertebrate tubes may also stabilise sediments by projecting above the sediment surface thus reducing turbulence and increasing the boundary layer.

Myers (1972) found that dense colonies of *Corophium insidosum* tubes increased the stability of subtidal sediments. The burrowing sea anemone *Cerianthus* constructs a thick membranous tube. Rowe (1974) found that *Cerianthus* increased shear strength in the surface 5cm of the sediment from 0.98 KPa^2 at distances of >20cm from tubes to about 1.83 KPa^2 beside the tube.

Trask and Rolston (1950) demonstrated large increases in the shear strength of silts and clays associated with only a 5% reduction in sediment water content. Kermack (1955) noted a reduction in moisture content of sediment which had passed through the gut of *Arenicola marina*. The faecal coils were also bound by mucous. Taghon *et al* (1984) and Kraeuter (1976) found that faecal pellets of several species were initially resistant to breakdown but lost this resistence with age due to gradual loss of the mucous binder.

Fager (1964) found that a dense settlement of the polychaete *Owenia fusiformis* stabilised a shifting sand against erosion. The tubes acted as a rigid supporting framework in the sediment. Young and

Rhoads (1971) found that dense mats of the tube-building polychaete Euchone incolor stabilised the faecal mounds of the holothurian Molpadia oolitica. Unconsolidated faecal material between the faecal mounds which did not contain polychaete tubes was easily eroded by water currents. Neuman et al (1970) found that the tubes and burrows of polychaetes, tanaids and harpacticoid copepods in sub-tidal algal mats increased the stability of the sediment. Pamatmat (1968) and Bock and Moore (1968) also noted the stabilisation of sediment by the tubes of tanaids and polychaetes. Laboratory studies by Rhoads et al (1978) showed that fine mucous tubes produced by the capitellid polychaete Heteromastus filiformis increased the critical erosion velocity of the sediment thereby making it more resistant to erosion by water currents.

Three sets of experiments were conducted in an experimental sea water flume to determine the effects of mussels on sediment stability. The first two experiments were conducted on single animals and on groups of animals respectively, in different particle size ranges of sediment. The third experiment was performed on groups of animals in sediment with stones present or not present at different depths.

Most of the results were analysed using two-way and one-way analyses of variance and student's t-tests. Probabilities of $P < 0.05$ (5%) were taken as significant except where stated. An asterisk rating system has been used to show the degree of significance for the t-tests. Except where stated the system is as follows:

Probability	Rating
$0.05 > P > 0.01$	*
$0.01 > P > 0.001$	**
$P < 0.001$	***

MATERIALS AND METHODS

SEA WATER FLUME

The Experimental Sea Water Flume was designed and built by a previous N.E.R.C. Research student (Girling, 1984; N.E.R.C. Award number G74/81/ALS/42) and funded by S.E.R.C. grants GR/B/8872.3 and Z/S T4020 to Mr. P. S. Meadows. The flume is situated in Aquarium 1 of the Zoology Department, Glasgow University.

The flume is a straight trough of rectangular cross-section with a large stilling tank at both ends (figure 1). A 5" diameter pipe is located under the trough and connects the stilling tanks. This completes the circuit. Sea water is circulated through the trough by a 1.5 kwatt pump, situated along part of the pipe (below the upstream end of the trough). A 4" Diaphragm Valve controls the water flow from the pump.

At the upstream end of the trough a Flow Collimator made from 8mm glass tubing reduces turbulence. An adjustable weir is situated at the downstream end. The trough contains a 30cm square box core. Containers with sediment can be placed in this box core. Both walls of the trough are made of 6mm glass for observation of sediment in the box core.

Water velocity in the trough above the box core is measured using a differential pressure measuring device. This consists of a pitot static tube, pressure diaphragm and pressure transducer with digital readout (figure 2). The pitot static tube is composed of an inner tube open to the front, and an outer tube with four holes open to the side and at 90° to each other (figure 2). The inner and outer tubes are connected to opposite sides of a pressure diaphragm. A pressure transducer with digital readout is connected to the diaphragm.

CALIBRATION OF THE DIFFERENTIAL PRESSURE MEASURING DEVICE

The pitot tube and diaphragm are part of an air-free system and this system is bled with sea-water before each experiment. Both

Figure 1. Experimental sea-water flume. UST = upstream stilling tank, DST = downstream stilling tank, P = pump, V = control valve, T = trough (with glass sides), BC = box core and VME = velocity measuring apparatus.

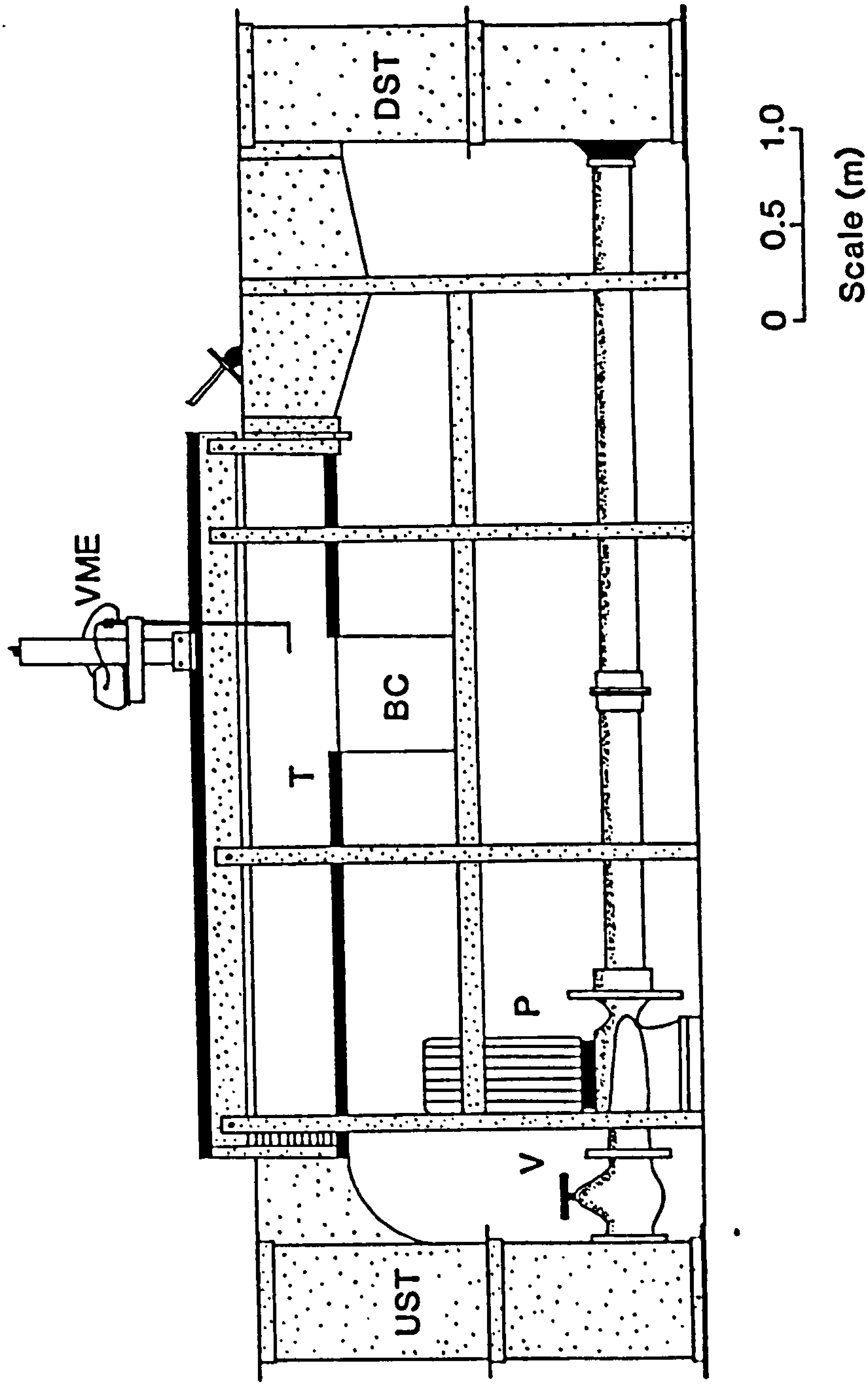
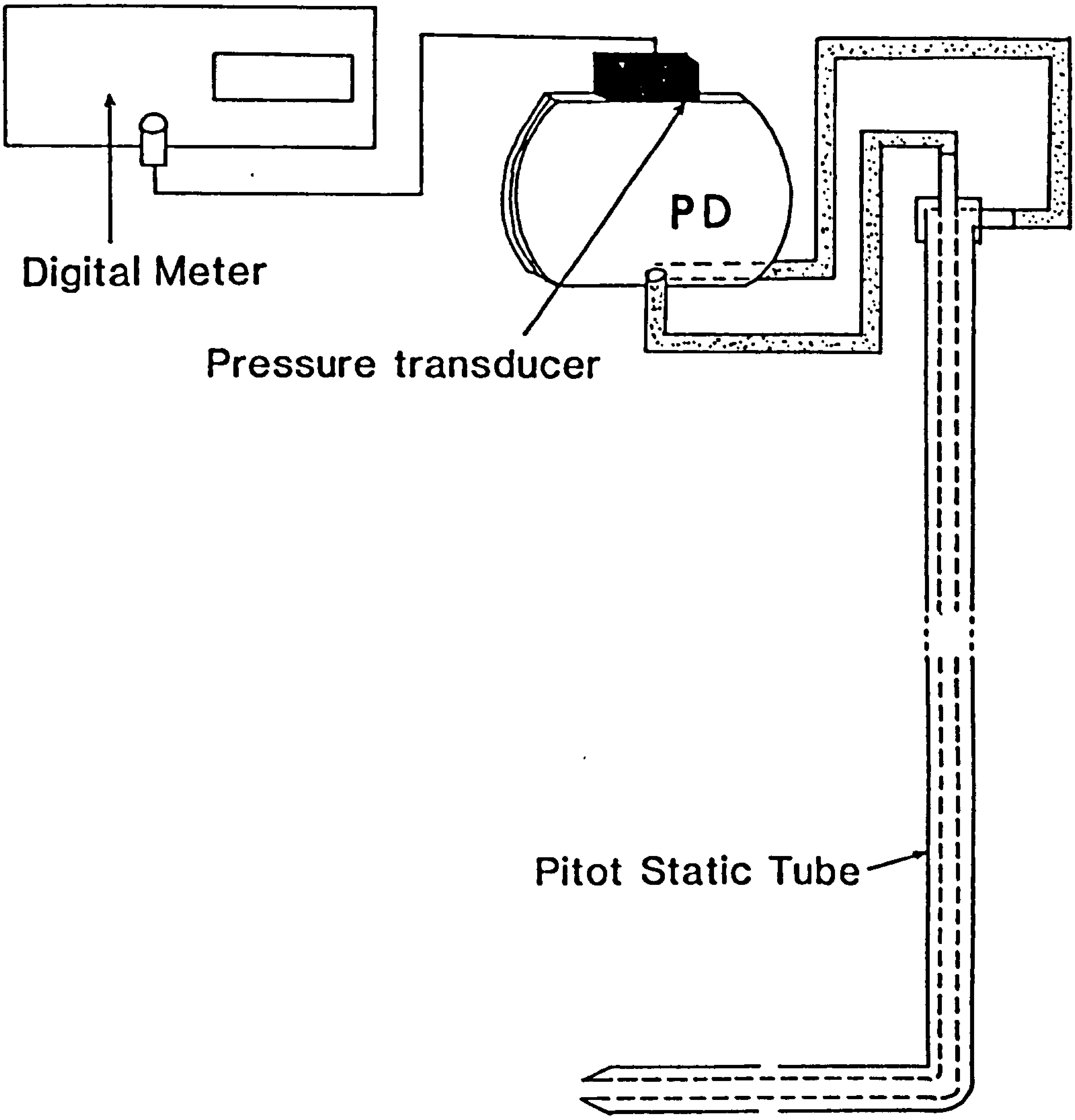

DST
VME
BC
T
P
V
UST
0 0.5 1.0
Scale (m)

Figure 2. Velocity measuring apparatus. The inner and outer tubes of the pitot-static tube are connected to a Pressure diaphragm (PD). The difference in pressure is shown on the pre-calibrated digital meter.


Digital Meter
PD
Pressure transducer
Pitot Static Tube

openings of the pitot tube are kept immersed in a plastic container containing sea water. The front (inner tube) of the pitot tube is connected to a manometer which contained sea water and was inclined at 19.5°. This angle gives a 3x magnification of the vertical pressure head. The other side of the manometer is immersed in the plastic container. The device is calibrated for a pressure head of 0mm H_2O (equal pressure on each side of the diaphragm which equals zero velocity) and 15mm H_2O (45mm on inclined manometer). At 0mm the digital meter is adjusted to 0 units and at 15mm (vertical height) the meter is adjusted to 150 units.

Flow velocity (V) is related to Pressure Head (h) by the equation

$$V^2 = h * 2g \text{ (Massey, 1979)}$$

The meter reading is converted to pressure head (h.cm) by dividing by 100. Then,

$$h = V^2/2g$$

And $\quad V = \sqrt{2gh}$

Similarly, $\quad 1/2mv^2 = mgh$ ie. kinetic energy = potential energy

therefore $\quad V = \sqrt{2gh}$

Velocity can thus be calculated from the figures shown on the digital readout.

COLLECTION OF ANIMALS AND SEDIMENT

Mytilus edulis and *Modiolus modiolus* were collected from Arrochar and Coilessan respectively and sediment from Arrochar (see pp. 64-65).

This part of the materials and methods is divided into two parts. These describe experiments with

A. different particle size ranges of sediment.

B. sediment containing stones at different depth layers.

EXPERIMENTS

A. Animals in different particle size ranges of sediment

Single animals

Two replicate experiments were performed. The following methods were used for each experiment. Sediment was sieved into seven particle size ranges. These were 8-16mm, 4-8mm, 2-4mm, 1-2mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm. Twenty one pneumatic troughs of 30cm diameter and 12.5cm depth were filled with one of the seven particle size ranges. This gave seven sets of troughs, one of each set for M. edulis, one for M. modiolus and one control (no animals present). The troughs were placed in large tanks with a continuous supply of sea water at 10°C. One animal was placed on the sediment surface in the centre of each trough - M. edulis or M. modiolus as appropriate (except the control troughs). The pneumatic troughs were left in the tanks for 12 days. This procedure was performed for each trough at time intervals to ensure that the trough was placed in the flume exactly 12 days after the animal was placed on the sediment surface.

After 12 days each pneumatic trough was removed and placed in the box core of the flume. The animal (if present) was positioned to face the upstream end of the flume. Throughout the transfer from tank to flume the animal and sediment were kept immersed in water with the aid of a plastic cylinder (modified from a small bucket) which fitted tightly around the pneumatic trough. This position was used as a standard for all animals because it gives the shape providing least resistance to the water current. The box core contained an adjustable base which could be raised or lowered depending on the size of container placed in the box core. The height of the pneumatic trough in the box core was therefore adjusted so that the sediment surface was level with the bottom of the flume trough. The flume was filled with sea water to a depth of 24cm above the sediment surface. The cylinder was then removed from around the pneumatic trough. A continuous solid base along the bottom of the flume trough was achieved by placing a 38cm square perspex cover with a 30cm diameter hole into the box core and around the pneumatic trough so that the top of the perspex cover was level with the bottom of the flume trough and the sediment surface. This procedure ensured minimum turbulence around the pneumatic trough when water was circulated in the flume tank.

A video camera with a Betamax video-recorder was used to record the effects of water currents around the animal or across control sediment. The camera was positioned to obtain views from the side of or above the trough at any one particular time. Before the flume pump was switched on, views of the pneumatic trough from above and from the side were recorded on video tape. Colour slides were also taken of the animal/control sediment from above and from the side of the flume trough.

The flume pump was switched on with the Diaphragm valve open at a half turn, and then opened slowly until critical erosion velocity was reached. Critical erosion velocity is the velocity of water at which a few of the sediment particles start moving across the sediment surface (Yalin, 1972; Friedman and Saunders, 1979). Velocity measurements were taken at 0.25cm, 0.5cm, 1.0cm, 2.0cm, 4.0cm and 8.0cm above the sediment surface. Each set of readings at a particular point above the sediment is called a velocity profile. Three readings were taken at each height and the mean of these used for calculations. The velocity of moving water varies with distance away from the base and sides of the trough (the term given to the base or side is a boundary). Viscosity slows down the water in a thin zone adjoining the boundary (Allen 1985). In this zone, the so called boundary layer the velocity of water increases with distance away from the boundary. Outside the boundary layer there is no velocity gradient. Boundary layers occur along the bottom of the flume trough and along the sides of the trough. The flume was designed so that the boundary layers from the sides did not affect the experimental area of the box core (Girling 1985).

The position of velocity profiles above the pneumatic troughs with animals are different from the control troughs. The profiles for troughs with animals and control troughs are described below.

Pneumatic troughs with animals. Velocity profiles were taken at distances of 0.25cm, 0.5cm, 1.0cm, 2.0cm, 4.0cm and 8.0cm from each side at the widest part of the animal. Velocity profiles were also obtained at 6.5cm and 8.0cm in front of the animal. The pitot static tube used to obtain the profiles was 6.5cm long along its base, and must face into the current. Velocity profiles could not therefore be obtained directly in front of the animal.

Control pneumatic troughs. Velocity profiles were obtained at 0.25cm, 0.5cm, 1.0cm, 2.0cm, 4.0cm and at 8.0cm to the front, back and either side of sediment at the centre of the pneumatic trough.

After velocity profiles were obtained the diaphragm valve was opened by a half turn every 3 minutes to a maximum of 11 turns. The effects of increased current velocities were recorded on video tape.

Groups of animals

The procedure is similar to that for the single animals but is given in full for clarity.

Sediment was sieved into five particle size ranges. These were 2-4mm, 1-2mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm. Fifteen pneumatic troughs of 30cm diameter and 12.5cm deep were filled with one of the 5 particle size ranges. This gave five troughs for *M. edulis*, five troughs for *M. modiolus* and five controls. Each trough contained one of five particle size ranges, and ten of the 15 troughs contained animals of one species. The remaining five troughs did not contain animals. The pneumatic troughs were placed in large tanks with a continuous supply of sea water at 10°C. Animals were placed at one of eight orientations on the sediment surface. These orientations were numbered from 1 (0°) to 8 (315°) at 45° intervals. The pneumatic trough was marked at orientation 1 (0°). Animals were given one of these orientations - chosen using random number tables - and then placed on the sediment surface at one animal width from other animals. The times at which the pneumatic troughs were prepared were staggered so that the troughs were placed in the flume exactly 12 days after the animals were placed on the sediment surface. Sea water was drained to expose the upper surface of animals at periods of 1,2,4,8 and 12 days. A clear perspex grid was placed on the animals and the outlines of the trough and animals drawn. The results of these are reported in Section 2 (pages 128-145).

After 12 days the pneumatic trough was removed and placed in the flume in the same manner as for single animals (page 276), with the following difference. The marked position of the pneumatic trough (number 1 orientation) faced the upstream end of the flume. This was used as a standard to avoid subjective positioning of the pneumatic trough in the flume box core.

Before the flume pump was switched on, views of the pneumatic trough from above and from the side were recorded on the video cassette. Colour slides were also taken.

The flume pump was switched on at a half turn, and then opened slowly until the critical erosion velocity was reached. Velocity profiles were taken from left to right across three areas of sediment - the central area of the trough, 8cm in front of the central area and

8cm behind the central area. Seven profiles were obtained for each area. These were at the centre of the sediment, 2,4 and 8cm to the right of the centre and 2,4 and 8cm to the left of the centre To obtain the maximum amount of information from troughs containing animals the exact location of profiles were approximate to the above locations. Profiles were obtained above and around clumps of animals across the centre, 8cm in front of the centre and 8cm behind the centre of the pneumatic trough. As for single animals the profiles were composed of readings at depths of 0.25cm, 0.5cm, 1.0cm, 2.0cm, 4.0cm, 8.0cm and 12.0cm. In addition when velocity profiles were taken above groups of animals the proiles were taken at 0.25cm, 0.5cm, 1.0cm, 2.0cm, 4.0cm, 8.0cm and 12.0cm above the group.

The diaphragm valve was then opened by a half turn every 3 minutes to a maximum of 11 turns. The effects of increased current velocities were recorded on video.

B. Animals in sediment with stones present or absent at different depths

Groups of animals

Sediment was wet-sieved in sea water through a 2mm sieve and sediment between an 8 and 16mm sieve. The procedure is described in Section 2 (pages 144-149). The sediment and stones were added to 9 pneumatic troughs (30cm diameter and 12.5cm deep). Three combinations of stone layers were placed in the sediment at different depths. These depths were 0-1cm (a layer), 3-4cm (b layer), 6-7cm (c layer) and 15-16cm (d layer). The three combinations were stones present at a,b,c and d layers, b,c and d layers and d layer only (tanks 6-8 in figure 11, Section 2, p. 152). This gave 3 sets of tanks, one for M. edulis and one for M. modiolus. The pneumatic troughs were placed in larger tanks with a continuous flow of sea water at $10^{o}C$. Animals were placed at one of eight orientations on the sediment surface. Orientations were numbered from 1 (0°) and at 45° intervals to 8 (315°). Animals were given one of these orientations, chosen using random number tables and then placed on the sediment surface at 1 animal's width from other animals. The troughs were left in the tanks for 12 days.

After 12 days the procedure adopted was exactly as that of the previous experiment (pages 278-280). A brief description is as follows. The pneumatic trough was placed in the box core of the flume. Sea water was added to a depth of 24cm above the sediment surface. The flume pump was switched on with the current control valve open at a half turn. The valve was slowly opened until the critical erosion velocity was reached. Velocity profiles were obtained around and above the animals (tanks with M. edulis or M. modiolus) or across the sediment (control). The current was then increased by opening the flume valve by a half turn every 3 minutes. A video camera and recorder was used to record the effects of increased currents from the valve open at a half turn to 11 turns.

Particle size analysis at the end of each experiment

At the end of the experiments for sediment with groups of animals present I noticed that sediment sorting had occurred around the groups. Samples of sediment were obtained from grooves beside animals, sediment which had built up behind groups and sediment between groups of animals, with the aid of a small spatula. In addition samples were obtained from control tanks which had no animals present.

The length and width of 50 particles from each sample were measured with the aid of a binocular microscope with 1μ graticule. The length plus width of a particle divided by 2 gives a rough estimate of particle size.

RESULTS

The boundary layer thickness is generally defined as the height above the bed at which the water velocity is equal to 99% of the mainstream velocity (Vogel, 1981). A plot of the theoretical boundary layer thickness (y axis) against the main stream velocity (x axis) is shown in figure 3. The equation to this curve is

$$\delta = \frac{0.37.x}{(U_m.x)/V)^{1/5}} \times 100$$

where δ = boundary layer thickness (m), x = distance down flume (m), U_m = mainstream velocity (ms^{-1}) and V = kinematic viscosity (Massey, 1979; Douglas et al 1981). Critical erosion velocities (C.E.V.s) are obtained by superimposing velocity profiles with corresponding scales along the x-axis (velocity) and y-axis (height above the bed) on the theoretical curve. The intersection of the velocity profile with the theoretical curve is the critical erosion velocity.

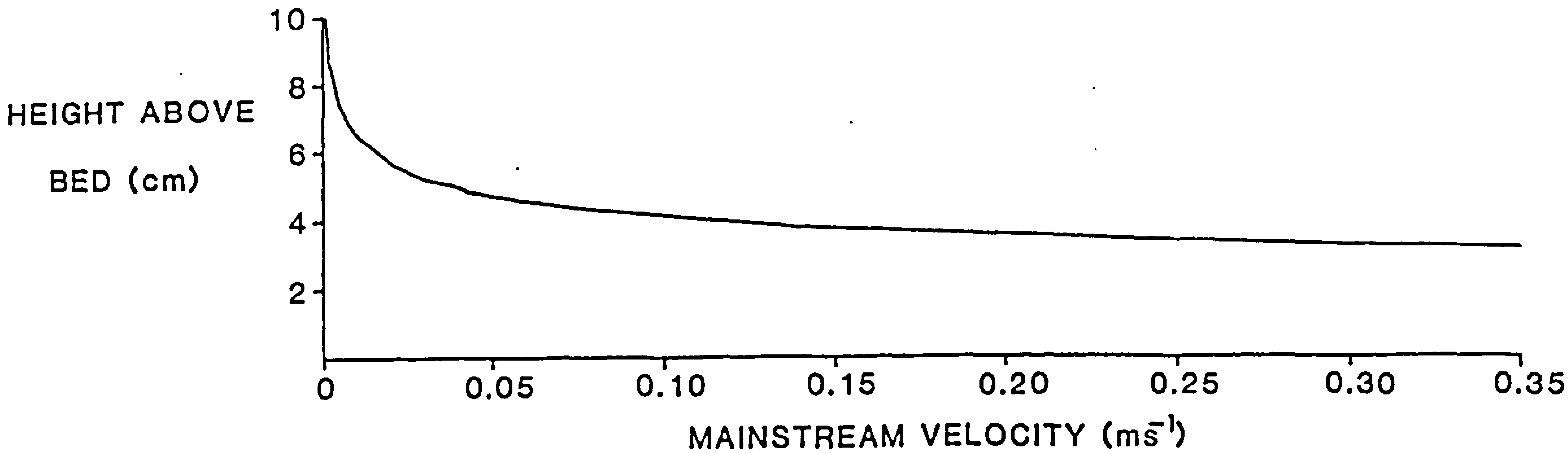
The bed shear stress (B.S.S.) of the sediment was calculated from the following equation:

$$T_o = 0.225 . (\rho . 9.81) . U_m^2 \left(\frac{V}{U_{m2}.\delta}\right)^{1/4} . \frac{1}{1000}$$

where T_o = bed shear stress (KPascals $\equiv$ $KN.m^{-2}$), ρ = seawater density (1025 $Kg.m^{-2}$), U_m = mainstream velocity, V = kinematic viscosity (1.14 x 10^{-6} $m^2.s^{-1}$) and δ = boundary layer thickness (Massey, 1979; Douglas et al, 1981). The seawater density ($Kg.m^{-2}$) is converted to Newtons (since the units of bed shear stress are $N.m^{-2}$) by multiplying by 9.81.

The results in this section are divided into two parts. The first part (pages 284-327) gives the results for tanks containing different

Figure 3. Plot of the theoretical boundary layer above a box core of the experimental sea-water flume.



particle size ranges of sediment. The second part (pages 328-355) gives the results for tanks containing sediment with stones present or absent at different depths. In each part a brief description of the velocity profiles is given, followed by statistical analyses of critical erosion velocities and the bed shear stress of sediments. This is followed by a qualitative description of erosion patterns in the sediment around animals at current velocities greater than critical erosion velocity. In the second part the statistical analyses of sorted sediment obtained from tanks containing animals and of sediment from control tanks are also described.

Different particle size ranges of sediment

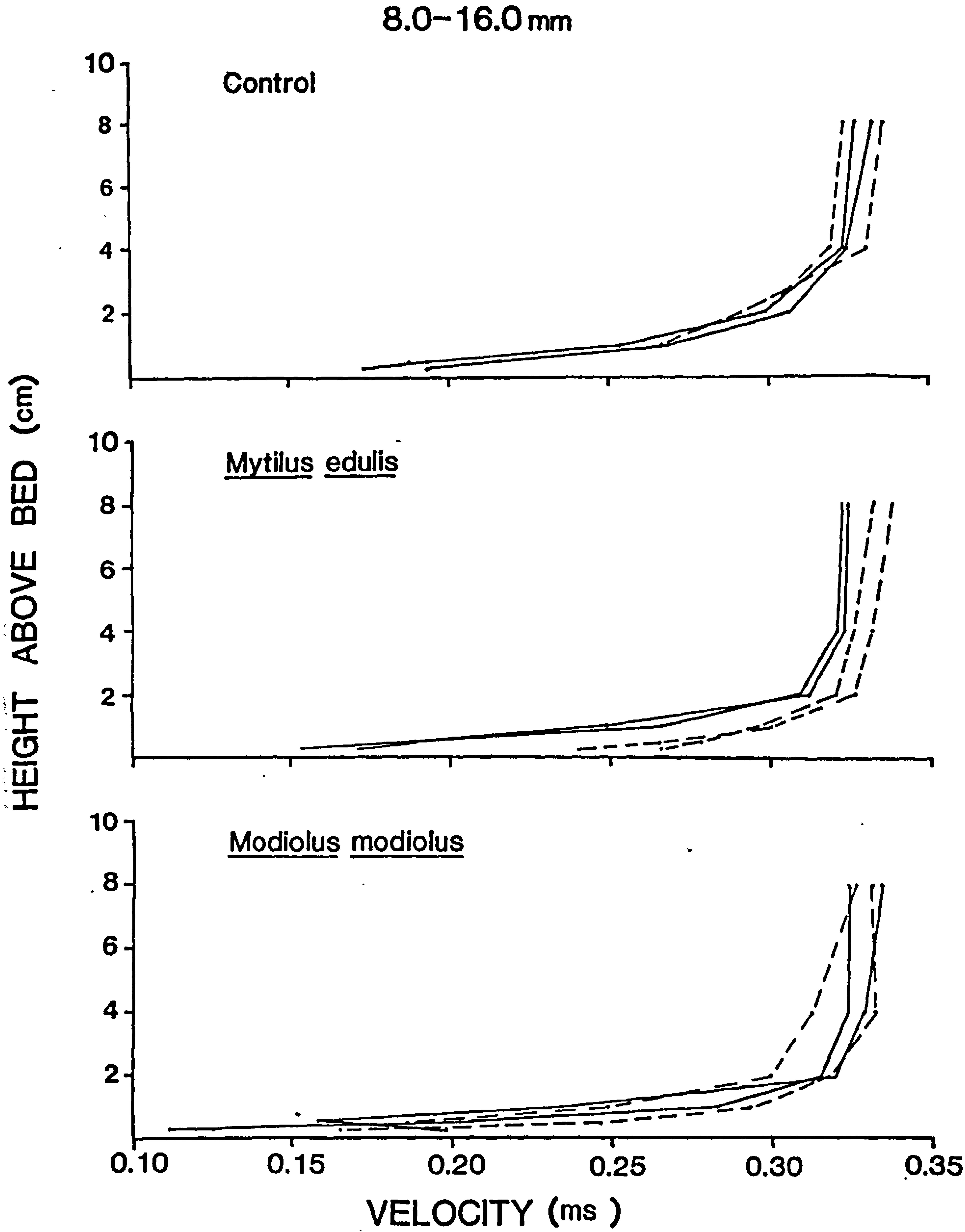
Velocity profiles

Single animals

Twelve velocity profiles were recorded in each tank. The results for each set of two replicate tanks were pooled. This gave twenty four velocity profiles for each treatment (control sediment, sediment with *Mytilus edulis* or for sediment with *Modiolus modiolus*) in each of the seven particle size ranges. Four velocity profiles obtained from each treatment for the seven particle size ranges are shown in figure 4. Graphs for control sediment show profiles at 0.25cm and 6.0cm to the centre of the pneumatic trough. Graphs for sediment containing a single mussel show profiles at 0.25cm and 6cm to the right of the animal.

There was no clear relationship between distance from the animal and water velocity. In some graphs the velocity was greater beside animals but in others the velocity was greater at a distance of 6.0cm from the animal (figure 4). The largest increase in current velocities occur from 0.25 to 2.0cm above the bed. This is due to boundary effects which slows down the current close to the bed but which has a lesser effect with increasing distance away from the bed.

Figure 4. Velocity profiles above the sediment bed for sediment of different particle size ranges. Each particle size range is shown on a separate page. Profiles for control sediment are shown at top, for sediment containing a single Mytilus edulis in the middle and sediment containing a single Modiolus modiolus at the bottom of each page. Velocity profiles were obtained at maximum current velocity (particle size ranges 8.0-16.0mm, 4.0-8.0mm and 2.0-4.0mm) or at critical erosion velocity (particle size ranges 1.0-2.0mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm). / = profiles at 0.25cm to the right of animal/control, ⁄⁄ = profiles at 8.0cm to the right of animal/control.


8.0–16.0 mm
Control
Mytilus edulis
Modiolus modiolus
HEIGHT ABOVE BED (cm)
VELOCITY (ms)
10
8
6
4
2
0.10
0.15
0.20
0.25
0.30
0.35

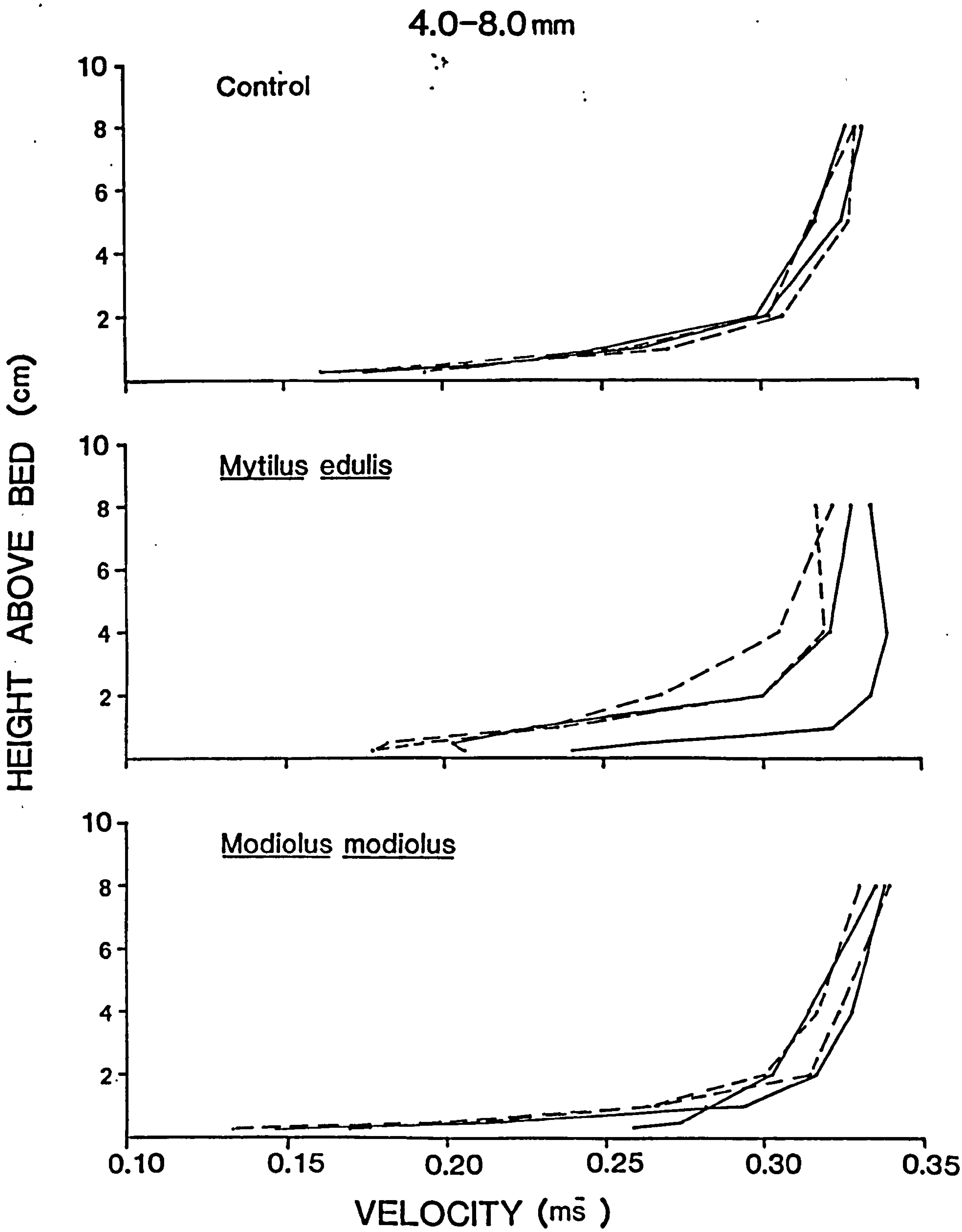


Figure 4. (cont.)

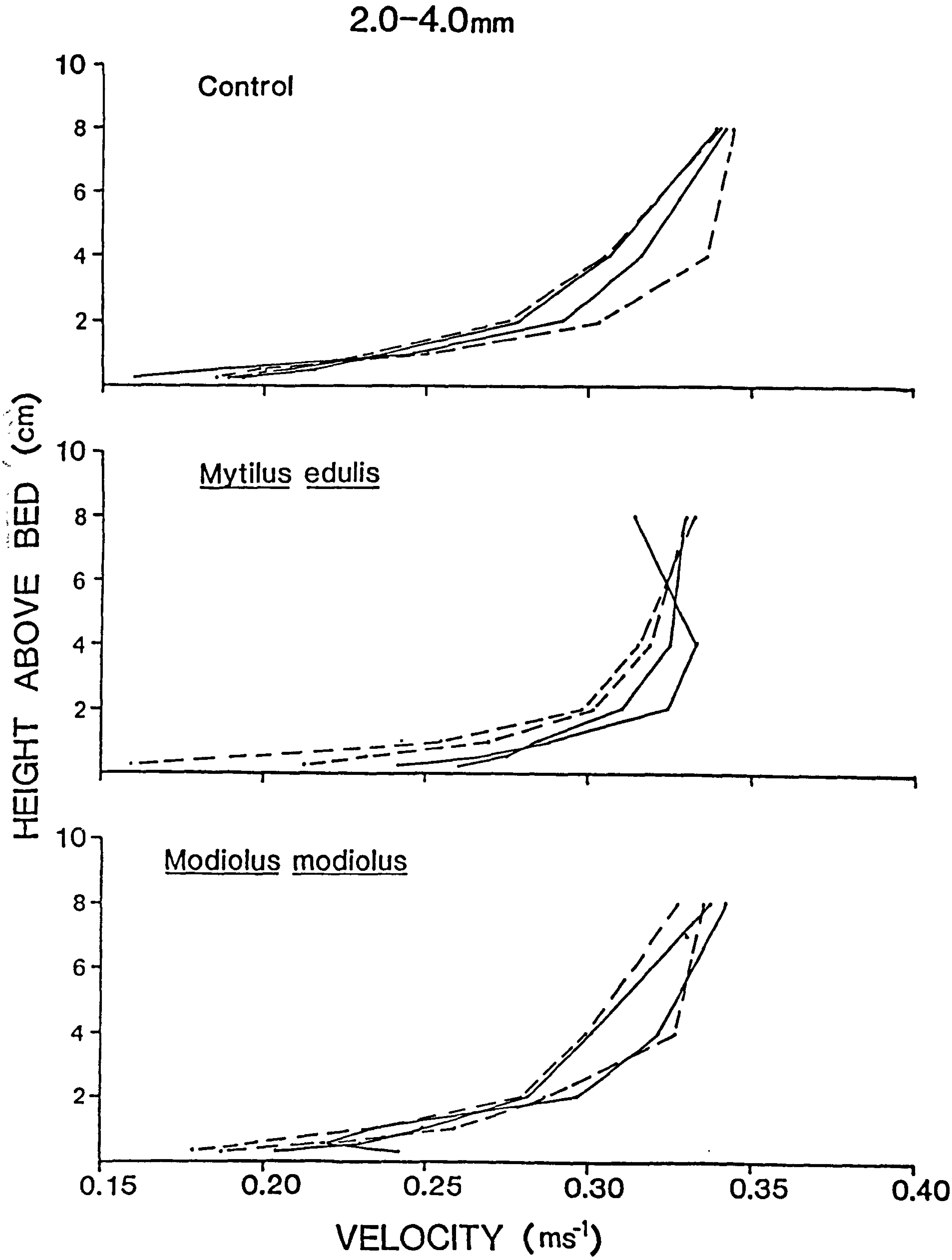


Figure 4. (cont.)

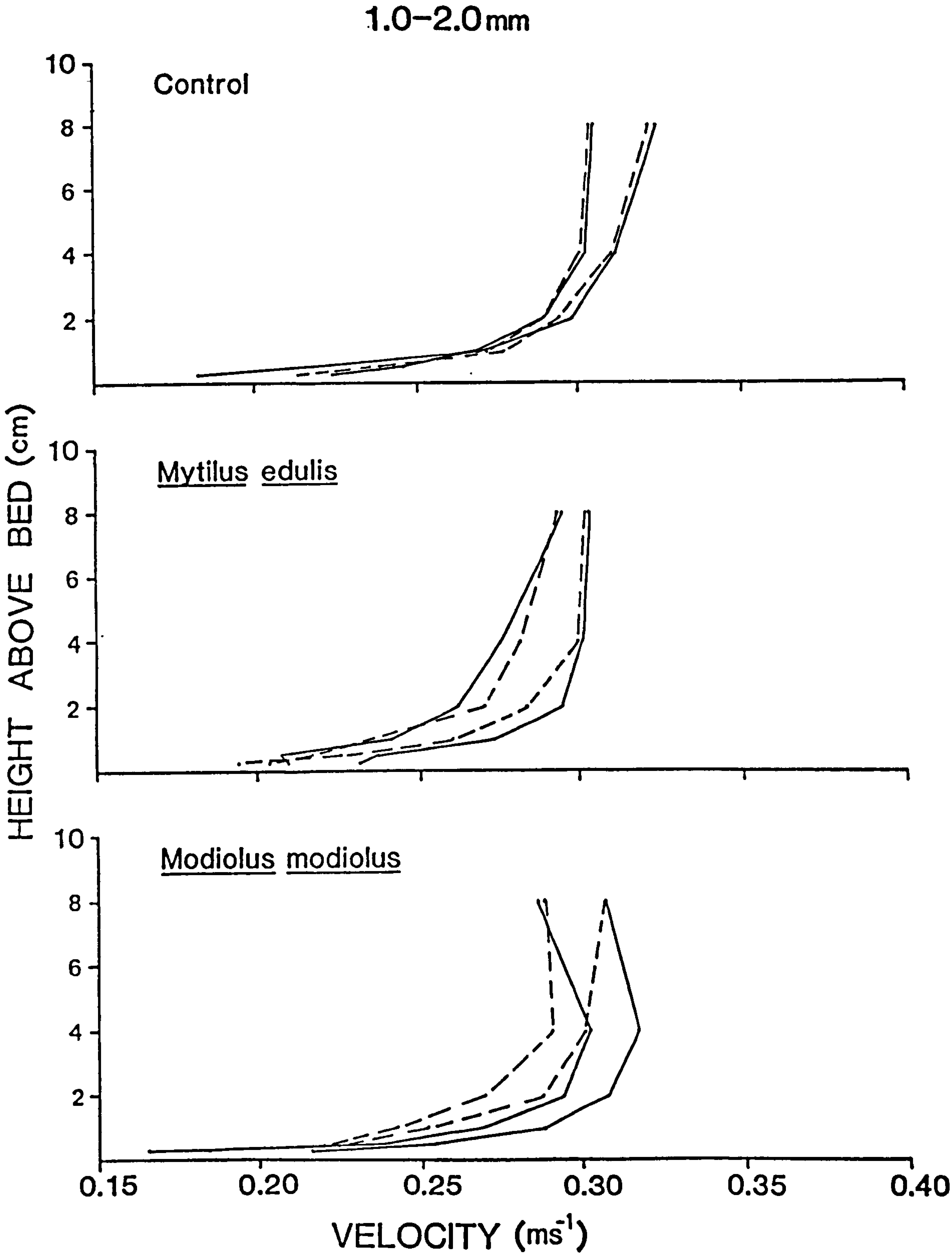


Figure 4. (cont.)

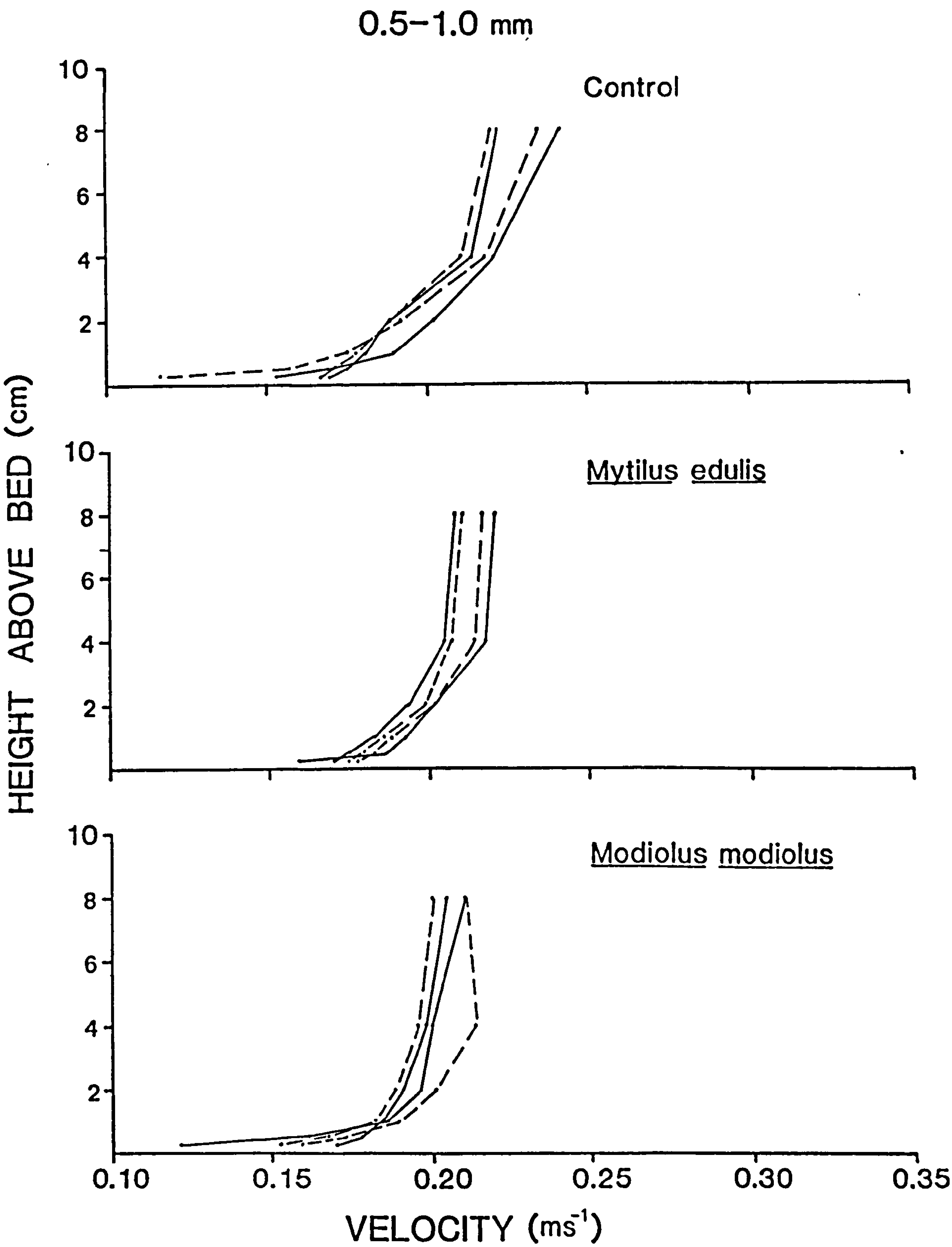


Figure 4. (cont.)

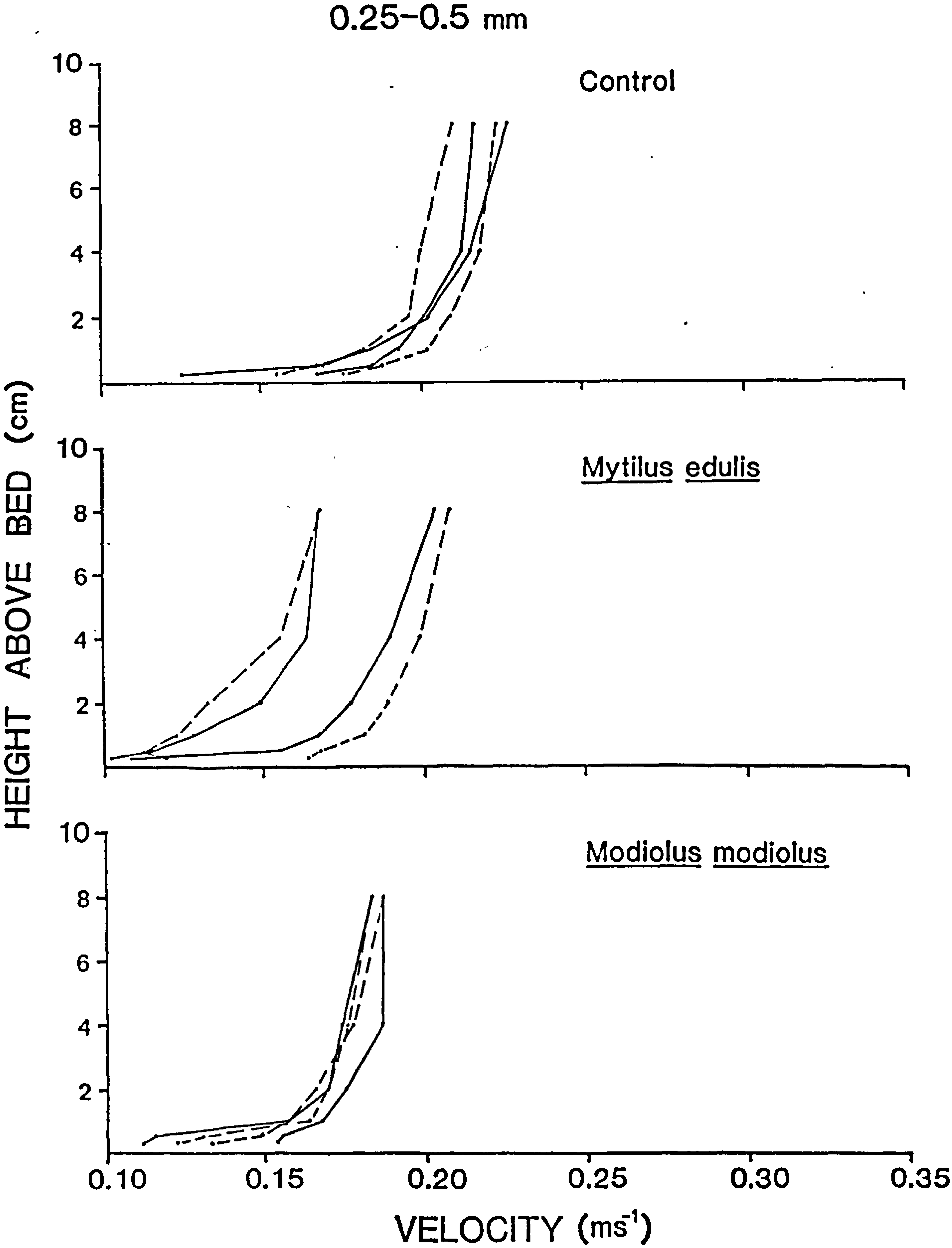


Figure 4. (cont.)

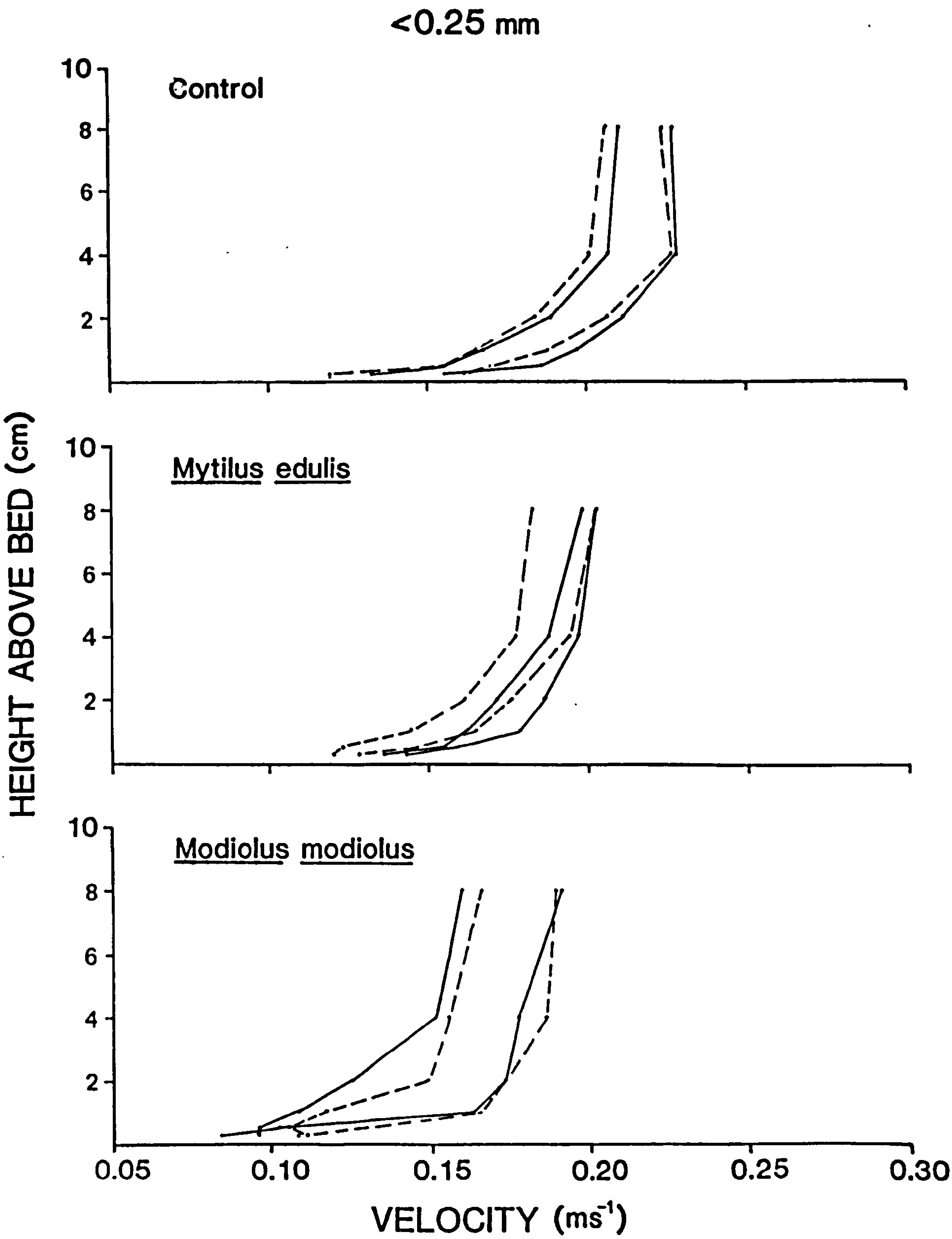


Figure 4. (cont.)

Sediment erosion did not occur in the particle size ranges 2.0-4.0mm, 4.0-8.0mm or 8.0-16.0mm. Velocity profiles for these particle size ranges were therefore taken at the maximum mainstream velocity of about $0.33ms^{-1}$. Sediment erosion occurred in the remaining particle size ranges. In general, sediment erosion occurs at lower velocities when a single M. edulis or M. modiolus was present. This was more pronounced for sediment which contained M. modiolus.

Groups of animals

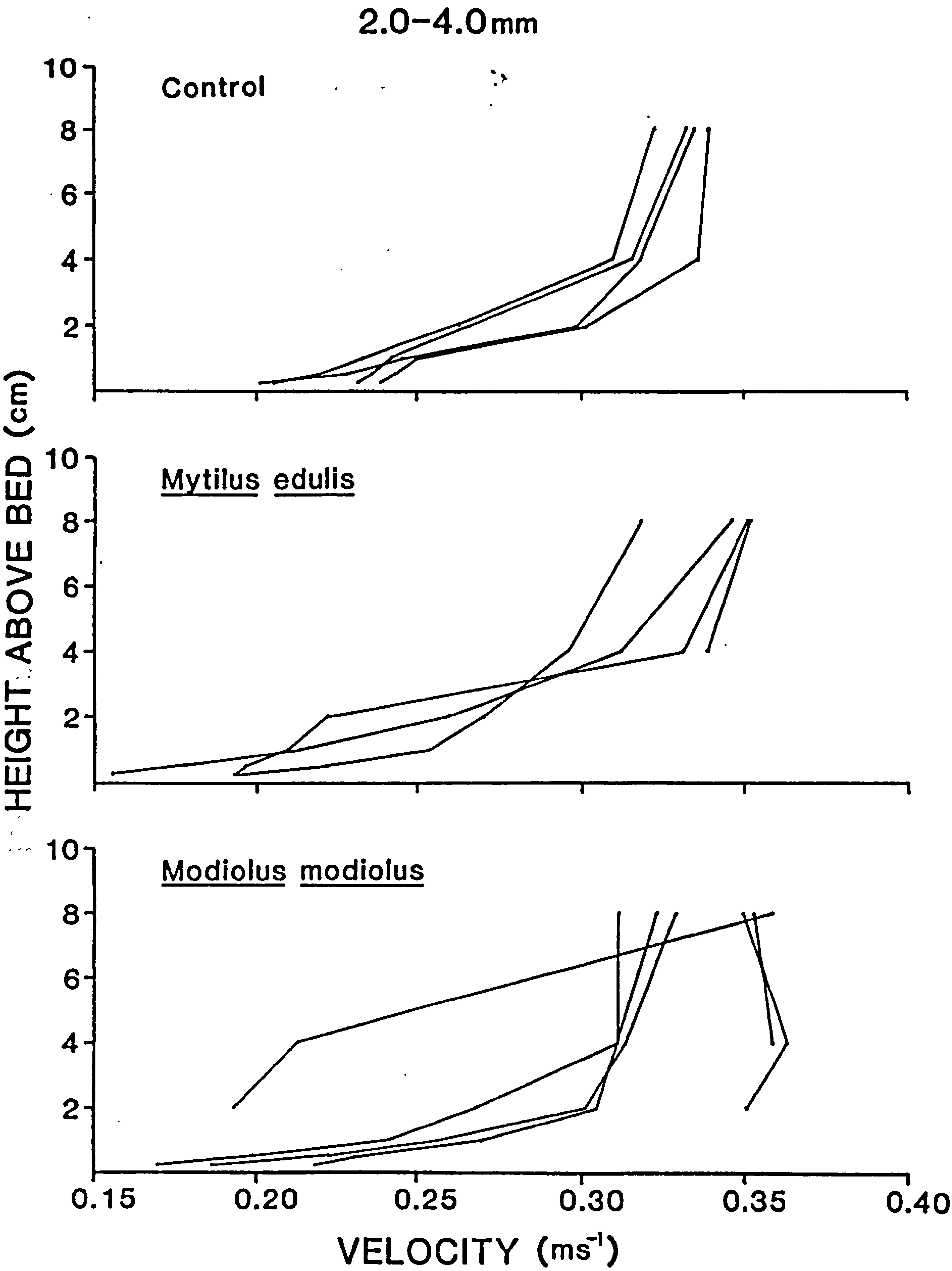
Twelve velocity profiles were obtained for each treatment (control sediment, sediment with M. edulis and sediment with M. modiolus) in each of the five particle size ranges. Four velocity profiles from each treatment for the five particle size ranges are shown in Figure 5. Velocity profiles above animal groups are also shown. Sediment erosion occurred at lower velocities when groups of animals were present. This was more pronounced for sediment which contained groups of M. modiolus.

Several profiles obtained in tanks which included groups of animals were very different in shape from profiles obtained in control tanks. They show that groups of animals appear to slow down current velocities above the bed. The alteration of current flow is very variable and too complicated for any kind of accurate analysis.

Critical erosion velocities and bed shear stress

The critical erosion velocities, obtained from the theoretical curve, and the mainstream velocities are shown in Tables 1 (single animals) and 2 (groups of animals). Each table is in two parts. The first part (I) shows velocities obtained for particle size ranges which do not erode at velocities up to the maximum current velocity ($0.033\ ms^{-1}$). The second part (II) shows critical erosion velocities of particle size ranges which are eroded at current velocities below the maximum current velocity. The theoretical C.E.V.s as a percentage

Figure 5. Velocity profiles above the sediment bed for sediment of different particle size ranges. Each particle size range is shown on a separate page. Profiles for control sediment are shown at top, for sediment containing groups of *Mytilus edulis* in the middle and sediment containing groups of *Modiolus modiolus* at the bottom of each page. Velocity profiles were obtained at maximum current velocity (particle size range 2.0-4.0mm) or at critical erosion velocity (particle size ranges 1.0-2.0mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm).



2.0-4.0mm
Control
Mytilus edulis
Modiolus modiolus
HEIGHT ABOVE BED (cm)
10
8
6
4
2
0.15
0.20
0.25
0.30
0.35
0.40
VELOCITY (ms⁻¹)

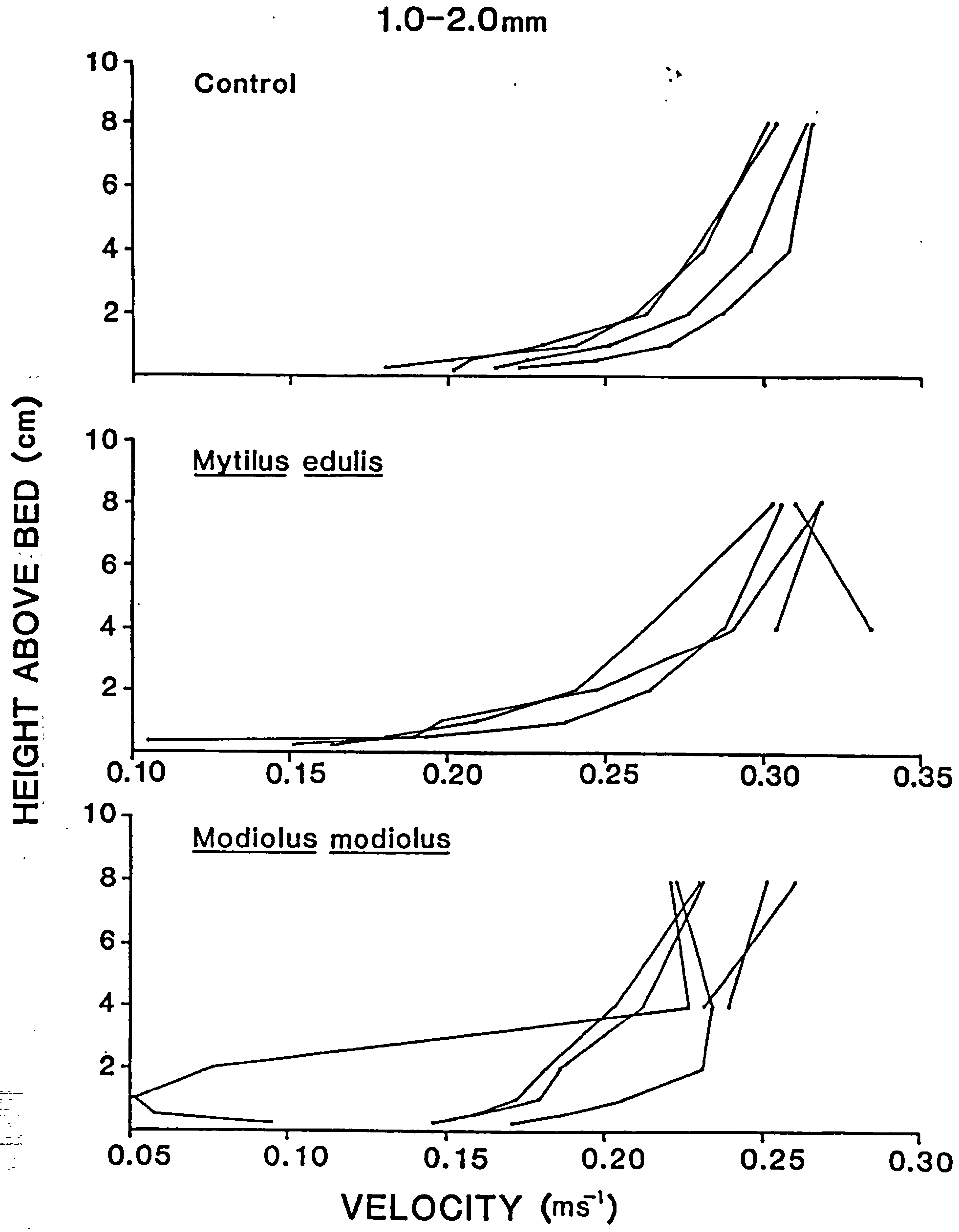


Figure 5. (cont.)

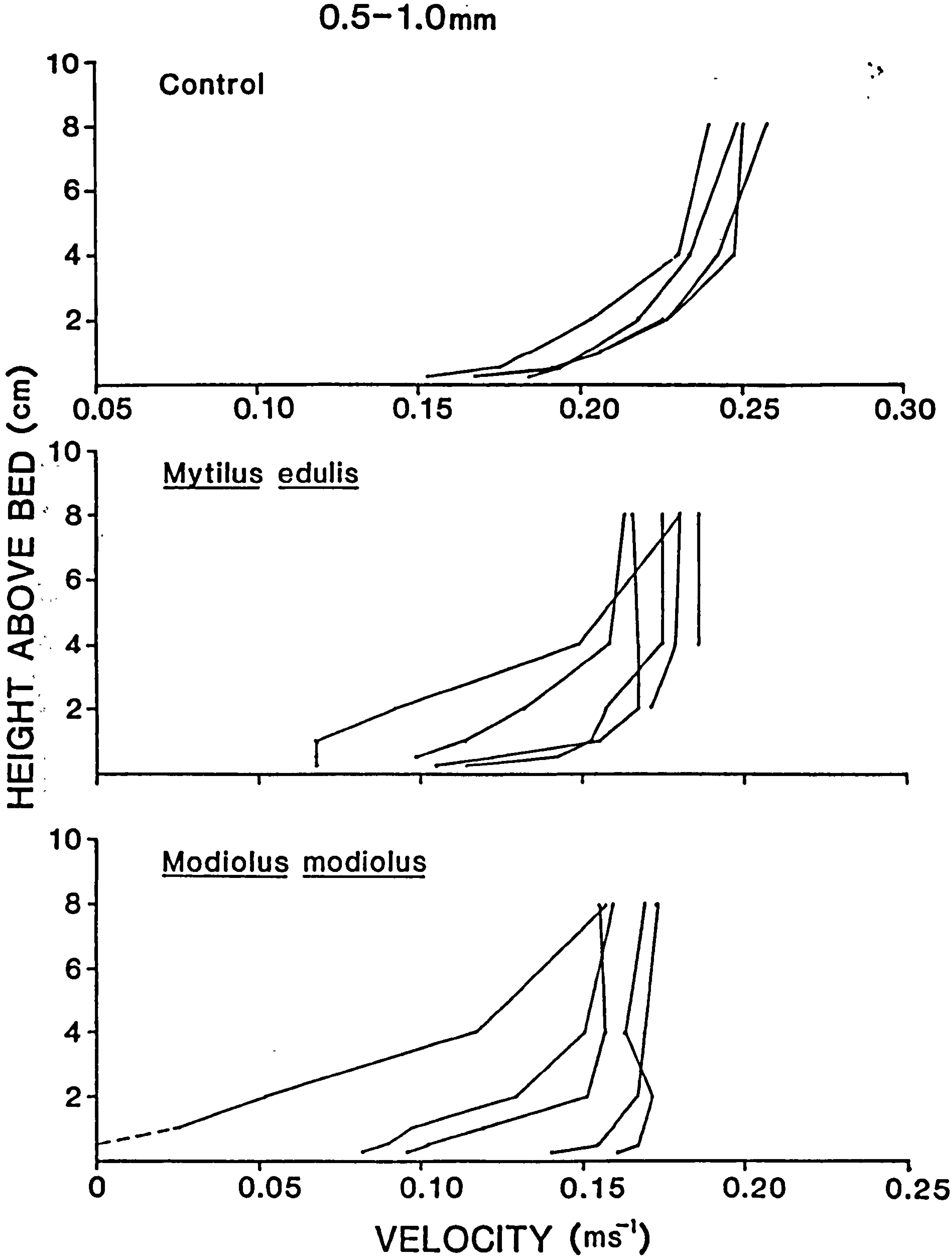


Figure 5. (cont.)

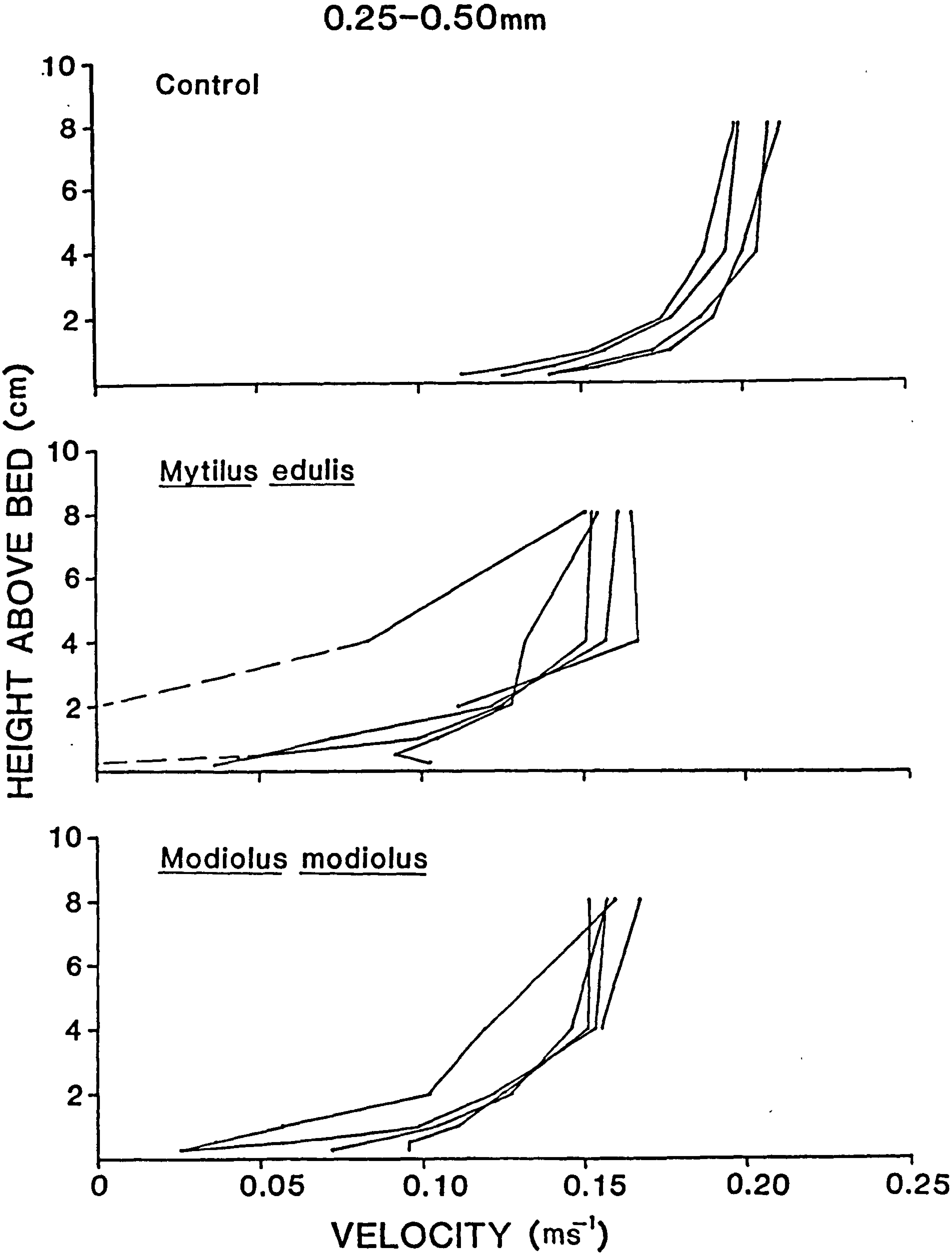


Figure 5. (cont.)

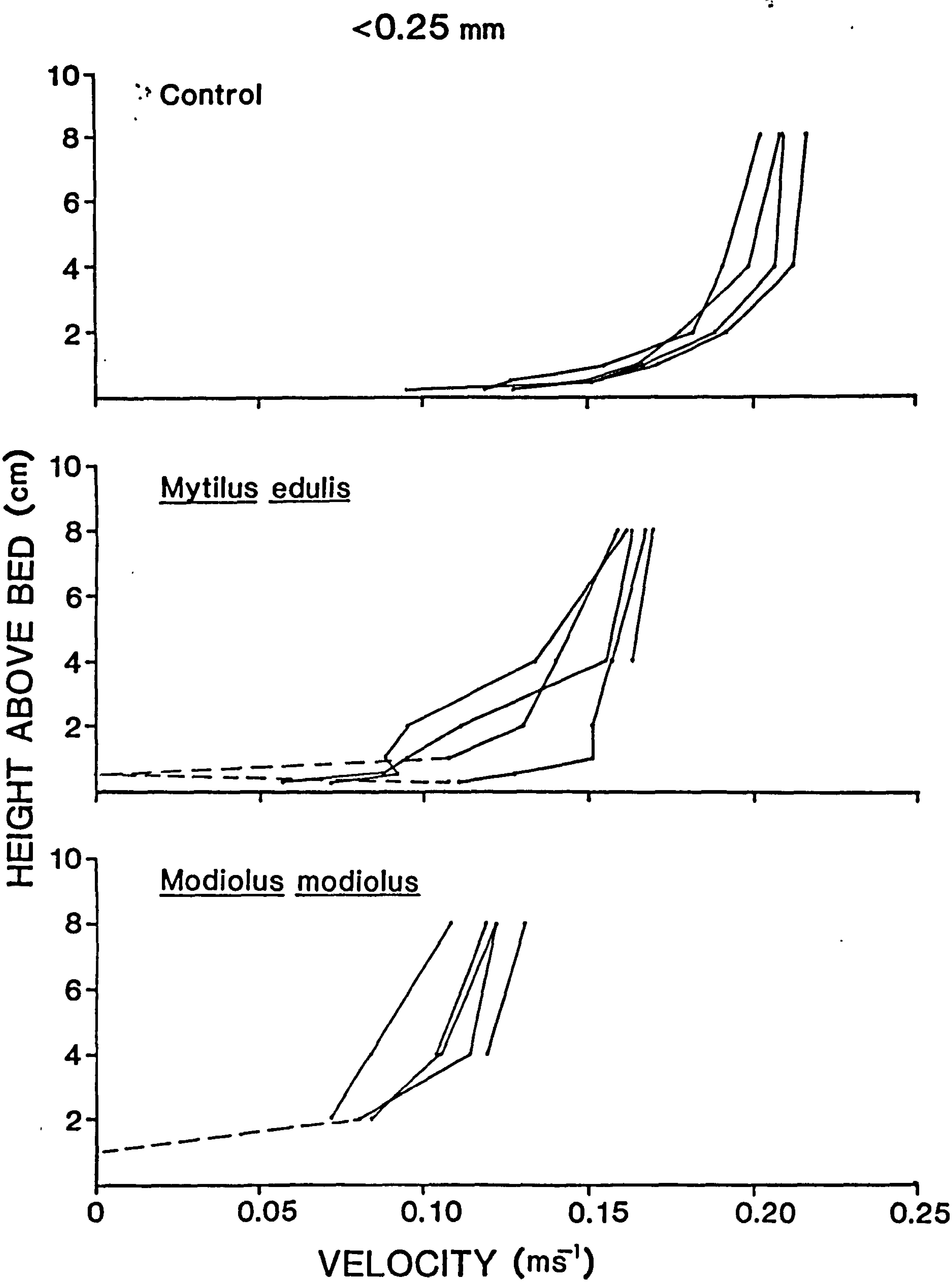


Figure 5. (cont.)

Table 1. Velocities obtained from the theoretical curve of boundary layer thickness, and mainstream velocities (ms^{-1}) for sediment with no animals present (controls), sediment with a single *Mytilus edulis* and sediment with a single *Modiolus modiolus*. A to G represent different particle size ranges of sediment. A = 8.0–16.0mm, B = 4.0–8.0mm, C = 2.0–4.0mm, D = 1.0–2.0mm, E = 0.5–1.0mm, F = 0.25–0.5mm and G = <0.25mm.

	Tank type	Velocity from theoretical curve		mainstream velocity		theoretical mean as a % of the mainstream mean
		mean	std dev	mean	std dev	
I. Particle size ranges in which erosion did not occur						
	Control	0.319	0.004	0.330	0.005	96.6%
A	*M. edulis*	0.322	0.003	0.332	0.005	97.0%
	M. modiolus	0.322	0.004	0.330	0.003	97.6%
	Control	0.313	0.003	0.330	0.002	94.9%
B	*M. edulis*	0.315	0.012	0.329	0.003	95.7%
	M. modiolus	0.315	0.005	0.334	0.003	94.3%
	Control	0.305	0.009	0.335	0.003	91.0%
C	*M. edulis*	0.315	0.005	0.330	0.004	95.5%
	M. modiolus	0.307	0.007	0.336	0.004	91.4%
II Particle size ranges in which critical erosion velocity is reached						
	Control	0.301	0.005	0.314	0.010	95.9%
D	*M. edulis*	0.285	0.010	0.298	0.005	95.6%
	M. modiolus	0.292	0.007	0.297	0.010	98.3%
	Control	0.211	0.003	0.230	0.009	91.7%
E	*M. edulis*	0.205	0.004	0.212	0.005	96.7%
	M. modiolus	0.200	0.005	0.206	0.004	97.1%
	Control	0.209	0.005	0.220	0.006	95.0%
F	*M. edulis*	0.176	0.015	0.187	0.019	94.1%
	M. modiolus	0.177	0.004	0.183	0.010	96.7%
	Control	0.210	0.011	0.217	0.009	96.8%
G	*M. edulis*	0.186	0.007	0.198	0.006	93.9%
	M. modiolus	0.166	0.014	0.177	0.014	93.8%

	Tank type	velocity from theoretical curve		mainstream velocity		theoretical mean as a % of the mainstream mean
		mean	std dev	mean	std dev	
I Particle size ranges in which erosion did not occur						
	Control	0.306	0.009	0.331	0.005	92.4%
A	M. edulis	0.297	0.007	0.333	0.010	89.2%
	M. modiolus	0.299	0.034	0.322	0.017	92.9%
II Particle size ranges in which critical erosion velocity is reached						
	Control	0.290	0.008	0.308	0.004	94.2%
B	M. edulis	0.273	0.007	0.303	0.008	90.1%
	M. modiolus	0.216	0.013	0.237	0.011	91.1%
	Control	0.220	0.010	0.240	0.005	91.7%
C	M. edulis	0.165	0.010	0.176	0.008	93.8%
	M. modiolus	0.160	0.014	0.162	0.006	98.8%
	Control	0.199	0.007	0.205	0.005	97.1%
D	M. edulis	0.154	0.008	0.159	0.005	96.9%
	M. modiolus	0.144	0.008	0.157	0.004	91.7%
	Control	0.203	0.007	0.209	0.004	97.1%
E	M. edulis	0.147	0.007	0.163	0.003	90.2%
	M. modiolus	0.108	0.009	0.119	0.006	90.8%

Table 2. Velocities obtained from the theoretical curve of boundary layer thickness, and mainstream velocities (ms^{-1}) for sediment with no animals present (control), sediment with groups of *Mytilus edulis* and sediment with groups of *Modiolus modiolus*. A to D represent different particle size ranges of sediment. A = 2.0-4.0mm, B = 1.0-2.0mm, C = 0.5-1.0mm, D = 0.25-0.5mm and E = <0.25mm.

of the mainstream velocity are also shown. Theoretical C.E.V.s are in the region of 89.2 to 98.8% of the mainstream velocity. The percentages are greater than 95% in half the tanks and greater than 90% in all but one of the remaining tanks. Vogel (1981) states that defining the boundary layer thickness based on 90% U_m (mainstream velocity) may be more realistic than that based on 99% U_m for the study of marine animals which protrude above the sediment surface. The theoretical C.E.V.s obtained in this study are greater than 90% U_m and up to nearly 98% in some instances. I have used the theoretical C.E.V.s for statistical analysis.

The analysis of C.E.V.s for different particle size ranges is divided into two parts. The first part describes the results for particle size ranges in which critical erosion velocity is not reached (Table 1(I), 2(I)) and the second describes particle size ranges in which critical erosion velocity is reached (Table 1(II), 2.(II)).

<u>Velocities recorded at the maximumum water flow (Tables 1(I), 2(I))</u>

Velocity measurements taken at maximum water flow (particle size ranges 8.0-16.0mm, 4.0-8.0mm and 2.0-4.0mm) should not be significantly different from each other, because the maximum water velocity should always be the same. This was tested statistically as follows. T-tests were performed on the data to test for differences between control sediment, sediment containing <u>M. edulis</u> and sediment containing <u>M. modiolus</u> at each particle size for which no erosion occurred. These showed that in 2 out of 9 cases for single animals (Table 3(I)) and 1 out of 3 cases for groups of animals (Table 4(I), comparisons were significantly different. These differences are probably due to variation in the calibration of the velocity measuring apparatus.

The t values for the comparisons of particle sizes in which no erosion occurred were in the range 0.304 to 4.998 (Table 3(I), 4(I)).

I have been conservative and used t values greater than the highest t values obtained above as a statistical criterion of significance for all other comparisons. Only t values greater than 5 were therefore regarded as not significant in the remaining comparisons.

Critical erosion velocities (Tables 3(II), 4(II))

The critical erosion velocities obtained for the particle size ranges <0.25mm, 0.25-0.5mm, 0.5-1.0mm and 1.0-2.0mm are shown in Tables 3 (II) (single animals) and 4 (II) (groups of animals).

T-tests were performed on the data to determine differences between control sediment, sediment with *M. edulis* and sediment with *M. modiolus* (Tables 3-4). These showed a number of statistically significant results using the conservative criterion outlined above. Single animals and groups of animals significantly decrease the critical erosion velocity of sediments. This was more pronounced for *M. modiolus*. The C.E.V. of sediment containing single *M. modiolus* was significantly lower than sediment containing single *M. edulis* in the particle size range <0.25mm. The C.E.V. of sediment containing groups of *M. modiolus* were significantly lower than sediment containing groups of *M. edulis* in the particle size ranges 0.5-1.0mm and <0.25mm.

T-tests were then performed to determine whether there were any differences between sediment with single animals and sediment with groups of animals using the same conservative statistical criterion. These are shown in Table 5. There was a significant difference between controls in the particle size range 0.25-0.5mm. The C.E.V. of sediment containing groups of *M. edulis* were significantly lower than corresponding sediment containing single animals in the particle size ranges 0.5-1.0mm and <0.25mm. The C.E.V. of sediment containing groups of *M. modiolus* was significantly lower than sediment containing single animals in the particle size range <0.25mm.

Bed shear stress of sediments

The critical bed shear stress for the sediments in which C.E.V. occurred (1.0-2.0mm, 0.5-1.0mm, 0.25-0.5mm and <0.25mm) are shown in Tables 6 (single animals) and 7 (groups of animals).

T-tests were performed on the data to determine differences between control sediment, sediment with *M. edulis* and sediment with *M. modiolus* (Tables 8-9). As is to be expected the t values obtained were similar to those for the same comparisons of C.E.V.s. The conservative criterion of $T > 5.0$ was again used to assess significance. The results showed that single animals and groups of animals significantly decreased the bed shear stress of sediments. The bed shear stress for sediment of the particle size ranges 0.5-1.0mm and <0.25mm was significantly lower for sediment containing a single *Modiolus modiolus* than for corresponding sediment containing a single *M. edulis*. The bed shear stress for sediment of the particle size ranges 0.5-1.0mm, 0.25-0.5mm and <0.25mm was significantly lower for sediment containing groups of *M. modiolus* than corresponding sediment containing groups of *M. edulis*.

T-tests were then performed to determine whether there were any differences between single animals and groups of animals using the same statistical criterion for significance. These are shown in Table 10. There were significant differences between controls for the particle size ranges 0.5-1.0mm and 0.25-0.5mm. The bed shear stress of sediment containing groups of *M. edulis* or *M. modiolus* was significantly lower than corresponding sediment containing a single animal of the same species (all particle size ranges).

Table 3. Students t tests on the maximum current velocity (I) and on critical erosion velocity (II) for sediment with no animals, sediment containing a single Mytilus edulis and sediment containing a single Modiolus modiolus. A to G represent sediment of different particle size ranges. A = 8.0-16.0mm, B = 4.0-8.0mm, C = 2.0-4.0mm, D = 1.0-2.0mm, E = 0.5-1.0mm, F = 0.25-0.5mm and G = <0.25mm. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons t-values >5 are regarded as significant and are denoted by an asterisk (*).

	Comparison	t	d.f.	P
I. Particle size ranges in which erosion did not occur				
	Control to *M. edulis*	2.828	46	0.05> P> 0.01
A	Control to *M. modiolus*	1.819	46	0.70> P> 0.50
	M. edulis to *M. modiolus*	0.203	46	0.90> P> 0.50
	Control to *M. edulis*	1.025	46	0.40> P> 0.20
B	Control to *M. modiolus*	1.368	46	0.20> P> 0.10
	M. edulis to *M. modiolus*	0.304	46	0.90> P> 0.50
	Control to *M. edulis*	4.464	46	P< 0.001
C	Control to *M. modiolus*	0.438	46	0.50> P> 0.40
	M. edulis to *M. modiolus*	4.998	46	P< 0.001
II. Particle size ranges in which critical erosion velocity is reached				
	Control to *M. edulis*	6.502*	46	P< 0.001
D	Control to *. modiolus*	7.174*	46	P< 0.001
	M. edulis to *M. modiolus*	2.551	46	0.02> P> 0.01
	Control to *M. edulis*	5.213*	46	P< 0.001
E	Control to *M. modiolus*	8.511*	46	P< 0.001
	M. edulis to *M. modiolus*	4.212	46	P< 0.001
	Control to *M. edulis*	9.558*	46	P< 0.001
F	Control to *M. modiolus*	23.800*	46	P< 0.001
	M. edulis to *M. modiolus*	0.238	46	0.90> P> 0.50
	Control to *M. edulis*	9.647*	46	P< 0.001
G	Control to *M. modiolus*	12.101*	46	P< 0.001
	M. edulis to *M. modiolus*	5.917*	46	P< 0.001

	Comparison	t	d.f.	P
I. Particle size ranges in which no sediment erosion occurs				
	Control to *M. edulis*	2.970	46	0.01> P> 0.001
A	Control to *M. modiolus*	0.791	46	0.50> P> 0.30
	M. edulis to *M. modiolus*	0.218	46	0.90> P> 0.50
II. Particle size ranges in which critical erosion velocity is reached				
	Control to *M. edulis*	6.112*	46	P< 0.001
B	Control to *M. modiolus*	16.865*	46	P< 0.001
	M. edulis to *M. modiolus*	15.123*	46	P< 0.001
	Control to *M. edulis*	13.512*	46	P< 0.001
C	Control to *M. modiolus*	11.822*	46	P< 0.001
	M. edulis to *M. modiolus*	0.964	46	0.40> P> 0.20
	Control to *M. edulis*	14.539*	46	P< 0.001
D	Control to *M. modiolus*	17.922*	46	P< 0.001
	M. edulis to *M. modiolus*	2.984	46	0.01> P> 0.001
	Control to *M. edulis*	19.451*	46	P< 0.001
E	Control to *M. modiolus*	29.282*	46	P< 0.001
	M. edulis to *M. modiolus*	11.580*	46	P< 0.001

Table 4. Students t tests on the maximumum current velocity (I) and on the critical erosion velocity (II) for sediment containing no animals (control) and sediment containing groups of animals (*Mytilus edulis* or *Modiolus modiolus*). A to G represent sediment of different particle size ranges. A = 2.0-4.0mm, B = 1.0-2.0mm, C = 0.5-1.0mm, D = 0.25-0.5mm and E = <0.25mm. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons t-values >5.00 are regarded as significant and are denoted by an asterisk (*).

Comparison		t	d.f.	P
	Control	4.912	34	P< 0.001
1.0-2.0mm	*M. edulis*	4.219	34	P< 0.001
	M. modiolus	26.468*	34	P< 0.001
	Control	3.770	34	P< 0.001
0.5-1.0mm	*M. edulis*	18.057*	34	P< 0.001
	M. modiolus	12.201*	34	P< 0.001
	Control	5.048*	34	P< 0.001
0.25-0.5mm	*M. edulis*	4.661	34	P< 0.001
	M. modiolus	17.350*	34	P< 0.001
	Control	2.500	34	0.01> P> 0.001
<0.25mm	*M. edulis*	15.529*	34	P< 0.001
	M. modiolus	12.655*	34	P< 0.001

Table 5. Students t tests comparing the critical erosion velocity for sediment with single animals and sediment with groups of animals. Control tanks contained no animals and were therefore identical. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons t values of >5.00 are regarded as significant and are denoted by an asterisk (*).

Particle size range	Tank	mean	std dev
1.0-2.0mm	Control	2.296×10^{-3}	1.25×10^{-4}
	M. edulis	2.090×10^{-3}	5.51×10^{-4}
	M. modiolus	2.075×10^{-3}	1.24×10^{-4}
0.5-1.0mm	Control	1.309×10^{-3}	8.88×10^{-5}
	M. edulis	1.149×10^{-3}	4.87×10^{-5}
	M. modiolus	1.073×10^{-3}	3.59×10^{-5}
0.25-0.5mm	Control	1.210×10^{-3}	5.70×10^{-5}
	M. edulis	8.945×10^{-4}	1.61×10^{-4}
	M. modiolus	8.750×10^{-4}	8.19×10^{-5}
<0.25mm	Control	1.181×10^{-3}	8.07×10^{-5}
	M. edulis	1.005×10^{-3}	5.32×10^{-5}
	M. modiolus	8.161×10^{-4}	1.11×10^{-4}

Table 6. The mean bed shear stress (KPa) for different particle size ranges of sediment with no animals (control) and sediment containing a single mussel (*M. edulis* or *M. modiolus*).

Particle size range	Tank	mean	std dev
1.0-2.0mm	Control	2.185×10^{-3}	5.64×10^{-5}
	M. edulis	2.281×10^{-3}	1.12×10^{-4}
	M. modiolus	1.381×10^{-3}	1.17×10^{-4}
0.5-1.0mm	Control	1.523×10^{-3}	5.72×10^{-5}
	M. edulis	8.216×10^{-4}	6.06×10^{-5}
	M. modiolus	7.114×10^{-4}	4.21×10^{-5}
0.25-0.5mm	Control	1.069×10^{-3}	4.17×10^{-5}
	M. edulis	6.712×10^{-4}	3.64×10^{-5}
	M. modiolus	6.624×10^{-4}	3.14×10^{-5}
<0.25mm	Control	1.092×10^{-3}	4.08×10^{-5}
	M. edulis	7.046×10^{-4}	2.59×10^{-5}
	M. modiolus	4.143×10^{-4}	3.47×10^{-4}

Table 7. The mean bed shear stress (KPa) for different particle size ranges of sediment with no animals (control) and sediment with groups of animals present (*M. edulis* or *M. modiolus*).

	Comparison	t	d.f.	P
	Control to *M. edulis*	7.432*	46	P< 0.001
A	Control to *M. modiolus*	6.301*	46	P< 0.001
	M. edulis to *M. modiolus*	0.698	46	0.50> P> 0.40
	Control to *M. edulis*	7.823*	46	P< 0.001
B	Control to *M. modiolus*	12.104*	46	P< 0.001
	M. edulis to *M. modiolus*	6.080*	46	P< 0.001
	Control to *M. edulis*	8.674*	46	P< 0.001
C	Control to *M. modiolus*	16.386*	46	P< 0.001
	M. edulis to *M. modiolus*	0.781	46	0.50> P> 0.40
	Control to *M. edulis*	9.096*	46	P< 0.001
D	Control to *M. modiolus*	13.041*	46	P< 0.001
	M. edulis to *M. modiolus*	7.378*	46	P< 0.001

Table 8. Students t tests on the bed shear stress for sediment containing no animals (control) and sediment containing single animals (*Mytilus edulis* or *Modiolus modiolus*). A to D represent sediment of different particle size ranges (A = 1.0-2.0mm, B = 0.5-1.0mm, C = 0.25-0.5mm and D = <0.25mm respectively. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons values of t >5.00 are regarded as significant and are denoted by an asterisk (*).

	Comparison	t	d.f.	P
	Control to *M. edulis*	1.487	22	0.20> P> 0.10
A	Control to *M. modiolus*	22.650*	22	P< 0.001
	M. edulis to *M. modiolus*	19.271*	22	P< 0.001
	Control to *M. edulis*	29.799*	22	P< 0.001
B	Control to *M. modiolus*	40.231*	22	P< 0.001
	M. edulis to *M. modiolus*	5.075*	22	P< 0.001
	Control to *M. edulis*	24.924*	22	P< 0.001
C	Control to *M. modiolus*	27.017*	22	P< 0.001
	M. edulis to *M. modiolus*	44.797*	22	P< 0.001
	Control to *M. edulis*	28.992*	22	P< 0.001
D	Control to *M. modiolus*	44.835*	22	P< 0.001
	M. edulis to *M. modiolus*	23.137*	22	P< 0.001

Table 9. Students t tests on the bed shear stress of sediment containing no animals (control) and sediment containing groups of animals (*Mytilus edulis* or *Modiolus modiolus*). A to D represent sediment of different particle size ranges (A = 1.0-2.0mm, B = 0.5-1.0mm, C = 0.25-0.5mm and D = <0.25mm). t = students t, d.f. = degrees of freedom and P = probability. For all comparisons t values >5.00 are regarded as significant and are denoted by an asterisk (*).

Comparison		t	d.f.	P
1.0-2.0mm	Control	1.815	34	0.10> P> 0.05
	M. edulis	6.905*	34	P< 0.001
	M. modiolus	16.151*	34	P< 0.001
0.5-1.0mm	Control	7.518*	34	P< 0.001
	M. edulis	18.369*	34	P< 0.001
	M. modiolus	27.960*	34	P< 0.001
0.25-0.5mm	Control	7.241*	34	P< 0.001
	M. edulis	4.718	34	P< 0.001
	M. modiolus	5.324*	34	P< 0.001
<0.25mm	Control	2.908	34	0.01> P> 0.001
	M. edulis	18.310*	34	P< 0.001
	M. modiolus	12.177*	34	P< 0.001

Table 10. Students t tests comparing the bed shear stress of sediment in experiments with single animals and sediment in experiments with groups of animals. Control tanks contained no animals and were therefore identical. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons values of t >5.00 are regarded as significant and are denoted by an asterisk (*).

Description of erosion patterns

The analysis of notes taken during experiments and subsequent analysis of video tapes enabled me to define an Erosion scale. This scale is a qualitative description of the pattern and severity of sediment erosion in the experimental pneumatic troughs. Characteristic changes in the severity of erosion and the formation of erosion structures were used to differentiate between each level of the scale. A description and corresponding diagrammatic representation of the scale are shown in Table 11 (single animals and groups of animals) and figure 6 (single animals).

Movement of the smallest organic material across the surface begins when the flume pump is switched on and movement of larger organic material occurs as the velocity is increased (stage 1). Critical erosion velocity occurs when some of the sediment particles start to move across the surface (stage 2). The movement of more particles with no erosion patterns (ie. grooves, ridges and ripples) is termed light erosion (stage 3). Moderate (stage 4), heavy (stage 5) and severe (stage 6) erosion describe the pattern and severity of erosion as the velocity is further increased.

A comparison of the Erosion scales for control sediment, sediment containing Mytilus edulis and sediment containing M. modiolus at increasing current velocities are shown in figures 7 (single animals) and 8 (groups of animals). A detailed comparison of the two figures allowed me to make the following statements.

Particle size ranges 2.0-4.0mm, 4.0-8.0mm and 8.0-16.0mm:

Sediment erosion did not occur in control tanks, tanks containing single animals or tanks containing groups of animals.

Particle size range 1.0-2.0mm:

Light erosion occurred in control sediment and sediment containing

SCALE	NAME and DESCRIPTION of EROSION PATTERN
1	Movement of organic material. Small organic material moves across the sediment surface. As the current velocity is increased larger organic material moves across the surface.
2	Critical erosion. A few sediment particles move over the sediment surface. Particles may roll, skim or saltate (small jumps).
3	Light erosion. More particles move across the surface but no erosion patterns are formed.
4	Moderate erosion.
	<u>Control sediment</u>: Large numbers of particles move across the surface of the sediment. Small ripples facing downcurrent start to form.
	<u>Single animals</u>: A small groove forms at the front of the animal and starts to move downstream along the side of the animals shell. The result is a horse-shoe shaped groove. A small ridges starts to form at either side, half way along the animal and downcurrent from the animal. A small groove forms directly behind the animal.
	<u>Groups of animals</u>: A groove forms in front of the group and moves downstream between animals or at the side of groups. Sediment starts to build up behind groups of animals.

Table 11. An Erosion Index describing the patterns of sediment erosion for sediment containing no animals (contol) and sediment containing <u>Mytilus edulis</u> or <u>Modiolus modiolus</u>.

INDEX	NAME and DESCRIPTION of EROSION PATTERN
5	Heavy erosion: Single animals: The horseshoe shaped groove deepens as scouring of sediment occurs at the front and side of animals. Particles from this groove form a ridge at either side of and downcurrent from the animal. The groove directly behind the animal deepens considerably. "Sheets" of particles moving across the surface are very noticeable. Groups of animals: The groove at the front of animal groups continues to deepen. Sediment continues to build up behind groups of animals due to the action of strong eddy currents. In these eddy currents sediment is blown about. The larger particles may settle out as the eddy moves or loses its capacity to provide lift for the particles. Small particles may be carried downstream in the current. In poorly sorted sediments the smaller particles are thus washed downstream leaving regions of coarser particles in the grooves or built up areas of sediment around groups of animals. "Sheets" of particles moving across the surface are very noticeable.

Table 11 (cont.)

INDEX	NAME and DESCRIPTION of EROSION PATTERN
6	**Severe erosion.** Single animals: Sediment particles in the grooves are "thrown" up into the water column. The smallest particles are washed away in the water column and the larger particles move along the side of animals. The groove in front of the animal deepens and widens due to subsidence of the groove walls. Increasing sediment erosion beneath *M. edulis* causes the animal to collapse forwards into the current. Sediment builds up towards to the back of, and downcurrent from the animal. The groove directly behind the animal becomes very deep, particularly close to the animal. Groups of animals: At the side of groups and between animals sediment is "sprayed" erratically up into the water column. Grooves at the side of groups become deeper. Sediment eroded from these grooves form a significant part of the large build up of sediment behind animals or areas between animals where lower current velocities occur (see Plates 21-22). Sediment between animals may have a scooped or trowelled appearance, caused by erosion and build up of sediment in different areas.

Table 11 (cont.)

Figure 6. Diagram of erosion patterns around a single mussel. The numbers 1 to 6 represent the Erosion Index shown in Table 10. 1 = Movement of organic material, 2 = Critical erosion velocity, 3 = Light erosion, 4 = Moderate erosion, 5 = Heavy erosion and 6 = Severe erosion.

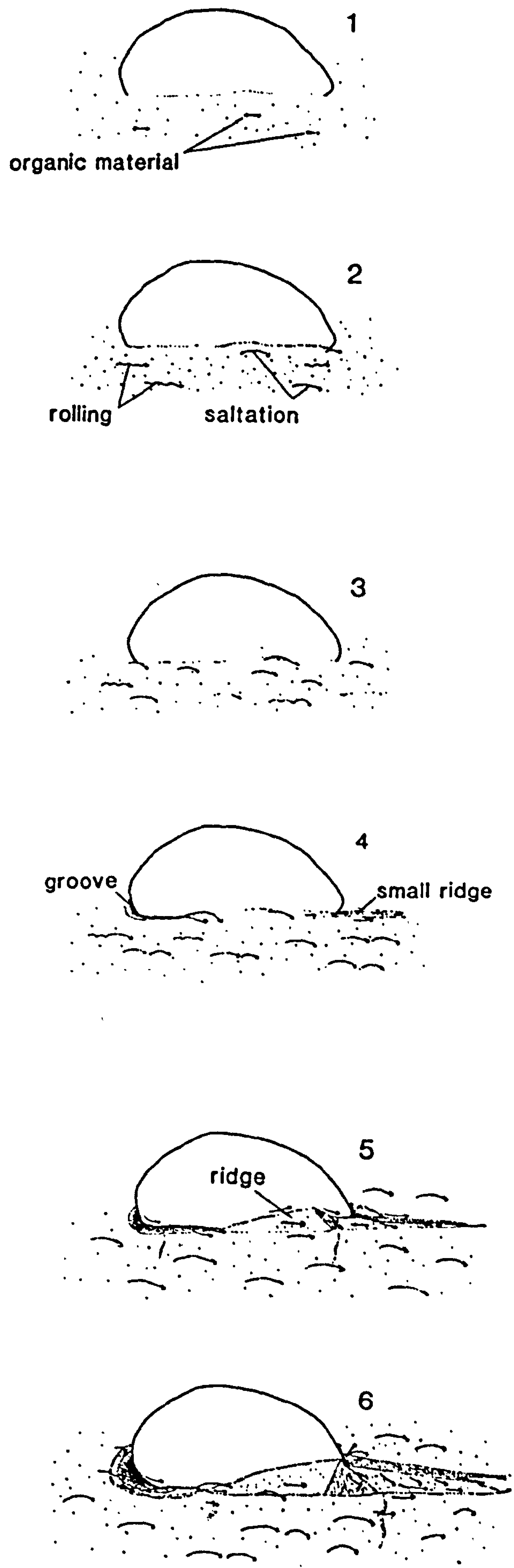
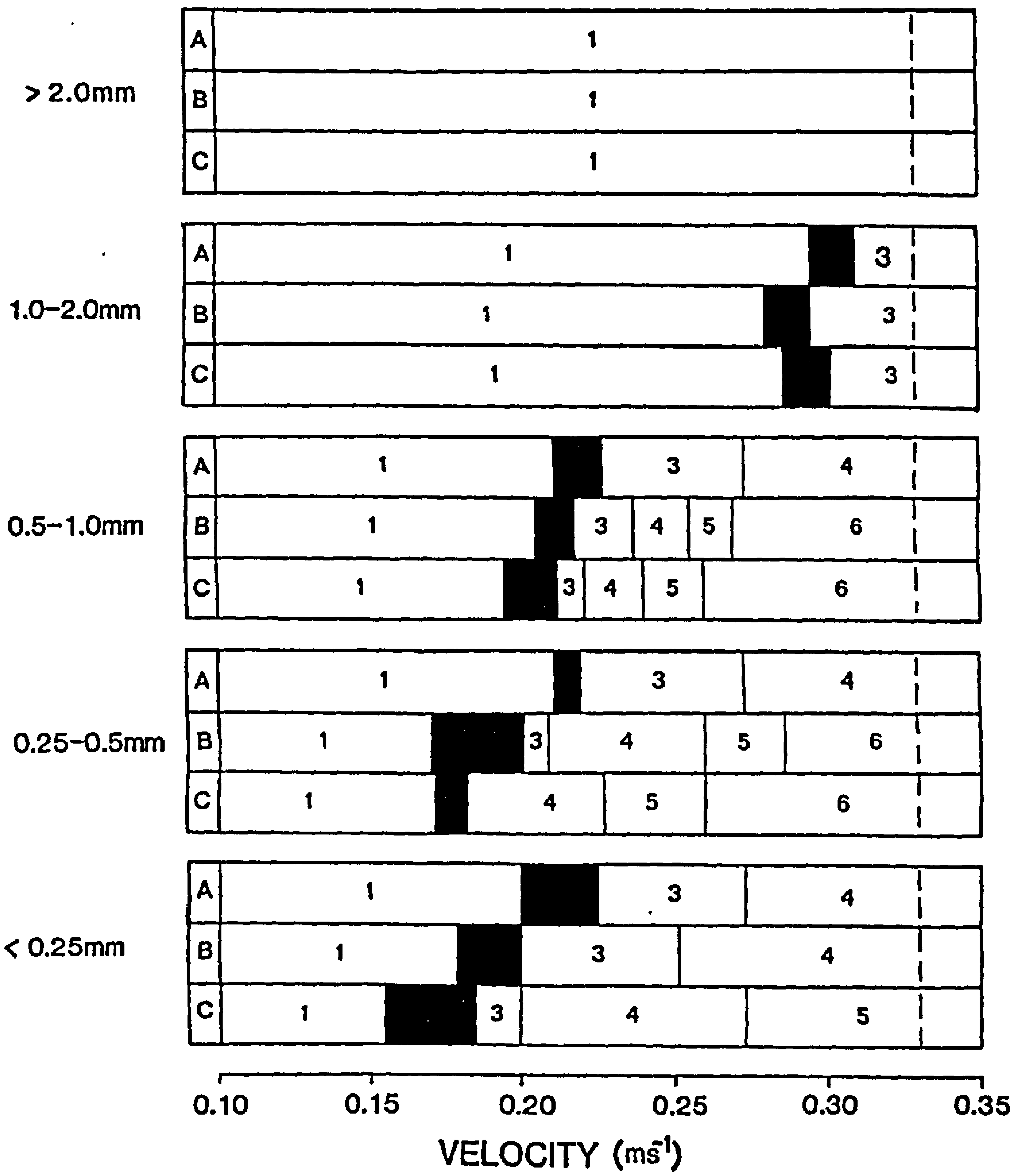
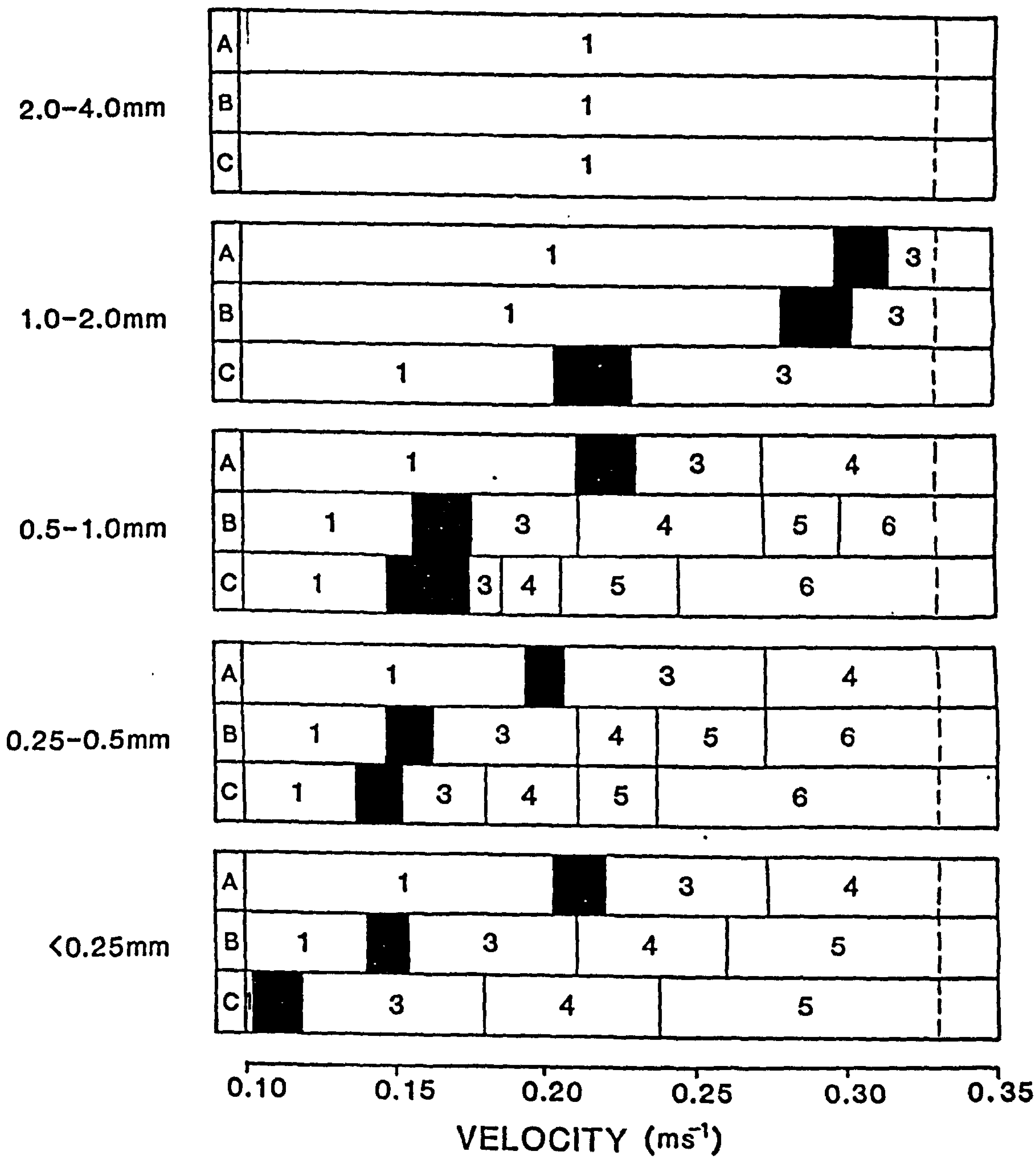

1
organic material
2
rolling
saltation
3
4
groove
small ridge
5
ridge
6

Figure 7. Diagram of Erosion Indices at increasing current velocities for different particle size ranges of sediment. A = control sediment, B = sediment containing a single *Mytilus edulis* and C = sediment containing a single *Modiolus modiolus*.



> 2.0mm
1.0–2.0mm
0.5–1.0mm
0.25–0.5mm
< 0.25mm
A
B
C
1
3
4
5
6
0.10
0.15
0.20
0.25
0.30
0.35
VELOCITY (ms^{-1})

Figure 8. Diagram of Erosion Indices at increasing current velocities for different particle size ranges of sediment. A = control sediment, B = sediment containing groups of *Mytilus edulis* and C = sediment containing groups of *Modiolus modiolus*.


2.0–4.0mm
1.0–2.0mm
0.5–1.0mm
0.25–0.5mm
<0.25mm
A
B
C
1
3
4
5
6
0.10
0.15
0.20
0.25
0.30
0.35
VELOCITY (ms^{-1})

animals at the maximum current velocity of $0.330ms^{-1}$.

Particle size ranges <0.25mm, 0.25-0.5mm and 0.5-1.0mm:

Comparisons between control sediment and sediment with animals present (*M. edulis* and *M. modiolus*).

Moderate sediment erosion occurred in control sediment at the maximum current velocity of $0.330ms^{-1}$. Light (stage 3) and moderate (stage 4) erosion occurred at lower current velocities in sediment containing *M. edulis* and *M. modiolus* than in control sediment. Moderate (stage 5) and severe (stage 6) erosion occurred at lower current velocities in sediment containing *M. modiolus* than in corresponding sediment containing *M. edulis*.

Comparisons between single animals and groups of animals

0.5-1.0mm

At the maximum current velocity ($0.33ms^{-1}$) single animals and groups of animals for both species caused severe sediment erosion.

Heavy (stage 5) and severe (stage 6) erosion occurred at higher current velocities for sediment containing groups of *M. edulis* than for sediment containing single animals. Conversely, heavy and severe erosion occurred at lower current velocities for sediment containing groups of animals than for sediment containing single animals. Figure 7 shows a single *M. modiolus* before erosion occurs (a) and during severe erosion (b).

0.25-0.5mm

At the maximum current velocity ($0.33ms^{-1}$) single animals and groups of animals for both species caused severe sediment erosion.

Moderate erosion (stage 4) occurred at higher current velocities for sediment containing groups of *M. edulis* than for sediment containing single animals. Conversely, moderate erosion occurred for sediment containing groups of *M. modiolus* than for sediment containing single animals. Heavy (stage 5) and severe (stage 6) erosion occurred

Plates 21-22. Group of Modiolus modiolus on sediment of particle size range 0.25-0.50mm. Plate 21 shows animals before the experiment and Plate 22 shows severe erosion around animals.

21.

22.

at lower velocities for sediment containing groups of M. edulis or M. modiolus than for sediment containing single animals of the same species. Plates 21-22 show groups of M. modiolus in sediment of particle size range 0.25-0.5mm at the beginning of the experiment and during the experiment (Erosion scale 6). A deep groove can be seen behind the animal in the foreground. Sediment was built up behind the animal on the right hand side of the photograph.

<0.25mm

At the maximum current velocity ($0.33ms^{-1}$) single M. edulis caused moderate (stage 4) erosion. Groups of M. edulis caused heavy (stage 5) erosion at $0.33ms^{-1}$. Single M. modiolus and groups of animals caused heavy (stage 5) erosion at current velocities of $0.33ms^{-1}$.

Moderate (stage 4) erosion occurred at lower current velocities for sediment containing groups of M. edulis or M. modiolus than for sediment containing single animals of the same species. Lower current velocities occurred for sediment containing groups of M. modiolus than for sediment containing single animals.

Tanks containing sediment with stones present or not present at different depths

Velocity Profiles

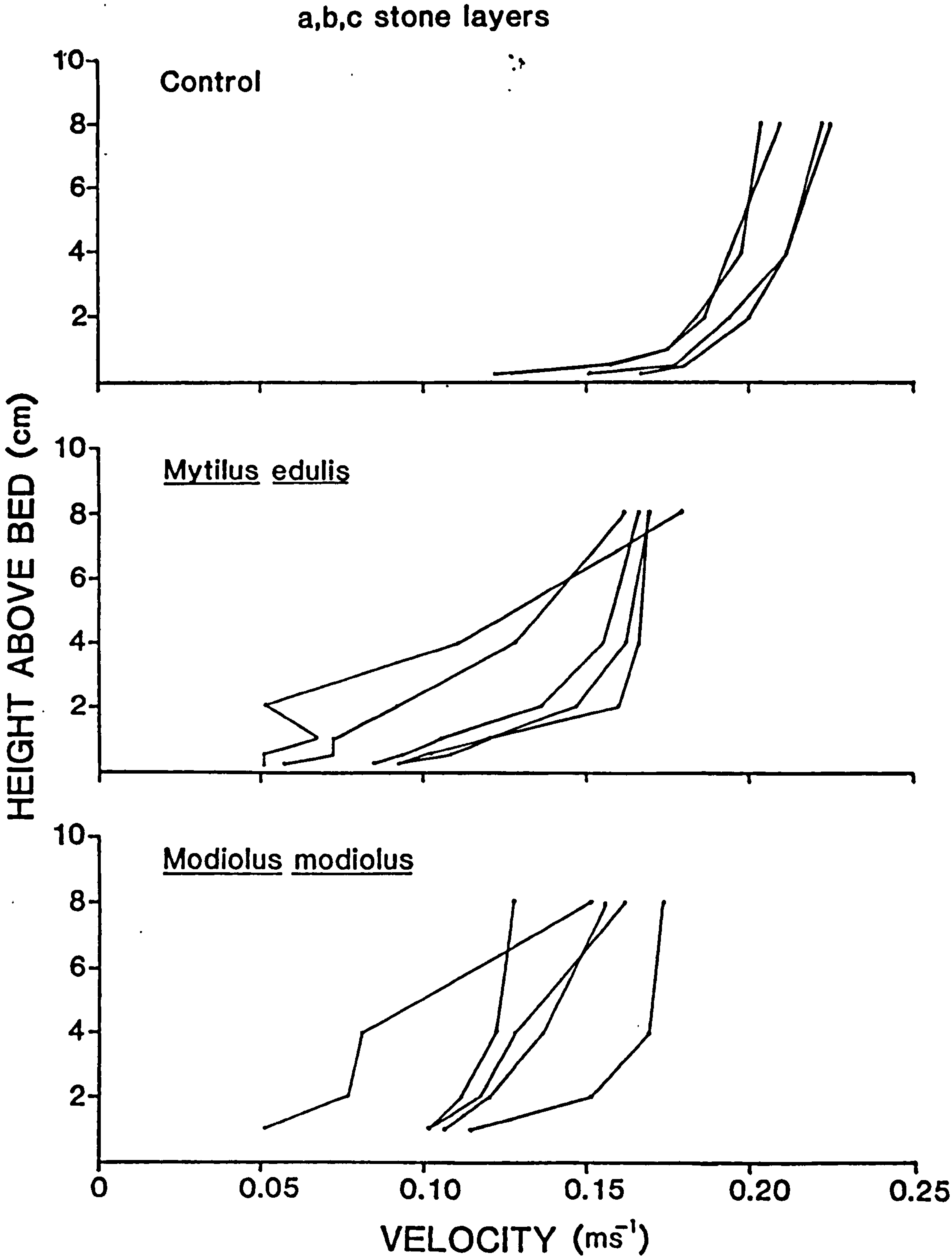
Twelve velocity profiles were recorded in each tank. The results for each set of two replicates were pooled. This gave twenty four velocity profiles for each treatment (control sediment, sediment with M. edulis and sediment with M. modiolus) in each of the three sediment types. Four velocity profiles, obtained from each treatment for each of the sediment types are shown in Figure 9. Velocity profiles above animal groups are also shown. Sediment erosion occurred at lower velocities when animals were present. This seems more pronounced for sediment with M. modiolus.

Critical erosion velocities and bed shear stress

The CEVs, obtained from the theoretical curve, are shown in Table 12. T-tests were performed on the data to determine differences between control sediment, sediment with M. edulis and sediment with M. modiolus (Table 13). The same conservative criterion used for the experiments with different particle size ranges of sediment was applied to the results. These showed that groups of animals significantly decreased the CEV of the sediment. This was more pronounced for sediment containing M. modiolus. The C.E.V. of sediment containing M. modiolus was significantly lower than corresponding sediment containing M. edulis in tanks with stones present in the sediment.

The critical bed shear stress for the different sediment types are shown in Table 14. T-tests were performed on the data to determine differences between control sediment, sediment with M. edulis and sediment with M. modiolus (Table 15). The same conservative criterion used for experiments with different particle size ranges was applied. These showed that the bed shear stress for sediment with animals

Figure 9. Velocity profiles above the sediment bed for sediment of different particle size ranges. Each particle size range is shown on a separate page. Profiles for control sediment are shown at top, for sediment containing groups of Mytilus edulis in the middle and sediment containing groups of Modiolus modiolus at the bottom of each page. Velocity profiles were obtained at critical erosion velocity. The a, b and c stone layers were present at the depths 0-1cm, 3-4cm and 6-7cm respectively.



a,b,c stone layers
Control
Mytilus edulis
Modiolus modiolus
HEIGHT ABOVE BED (cm)
VELOCITY (ms⁻¹)
0
0.05
0.10
0.15
0.20
0.25
2
4
6
8
10

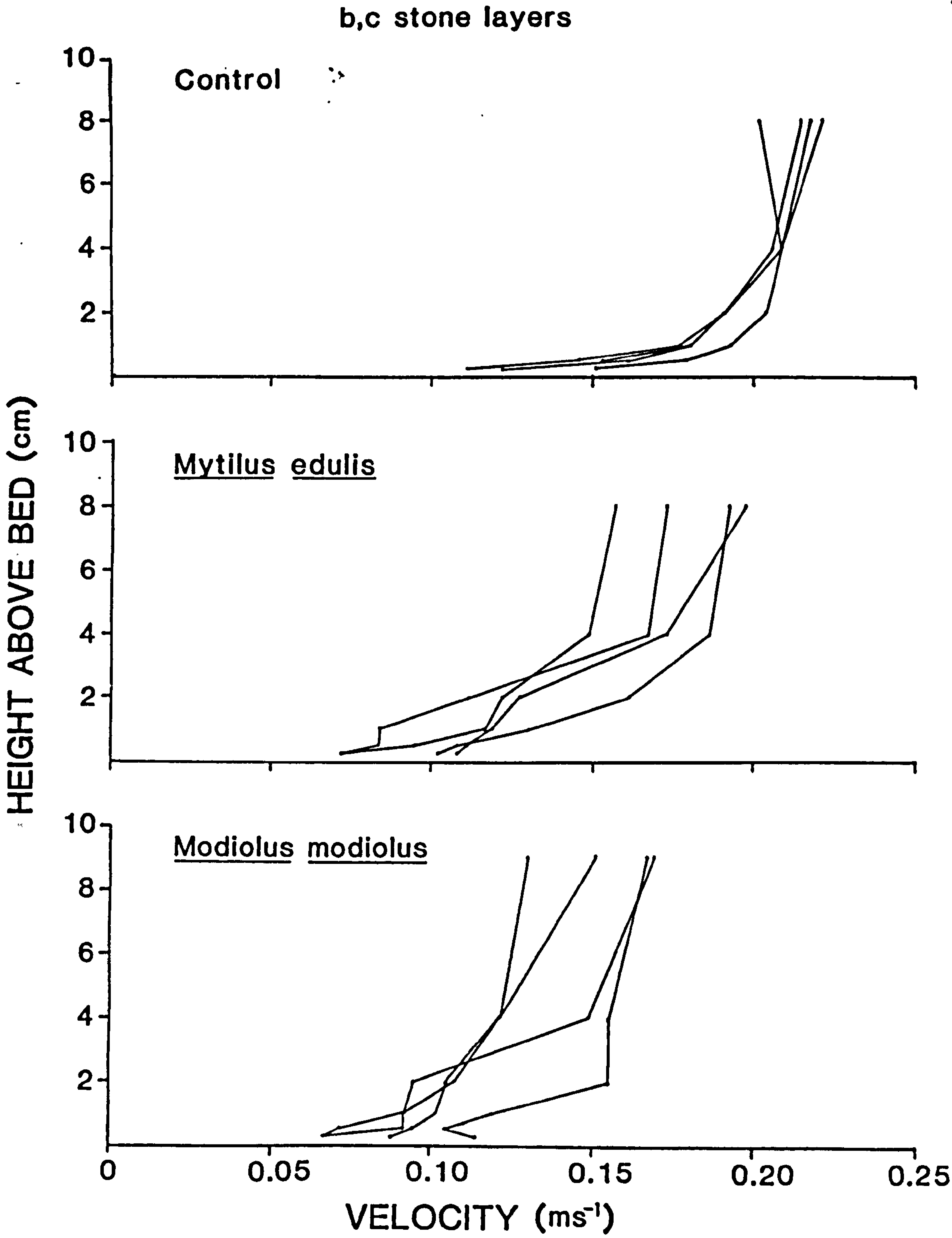


Figure 9. (cont.)

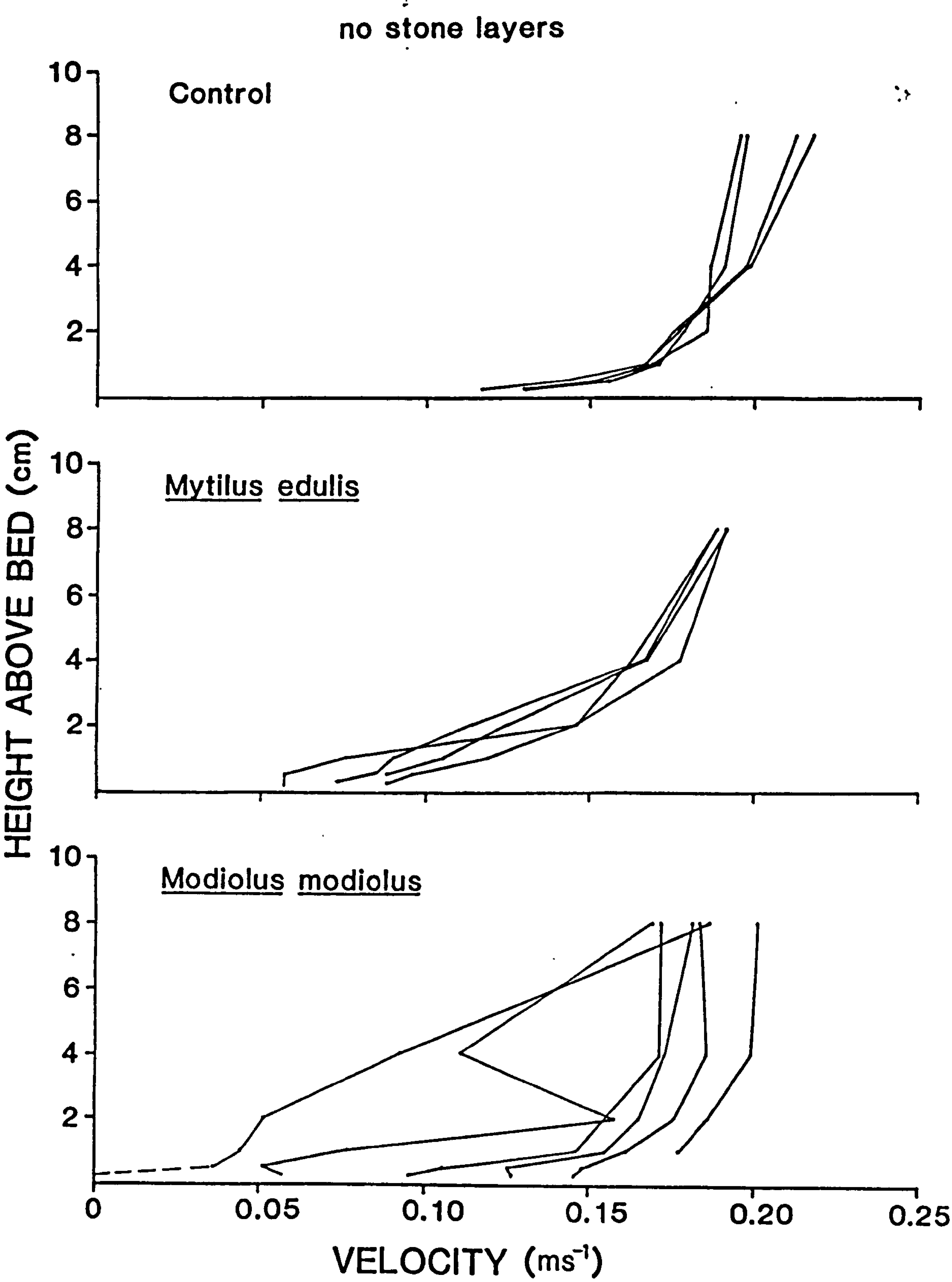


Figure 9. (cont.)

Particle size range	Tank	mean	std dev
a,b,c stone layers	Control	0.214	0.008
	M. edulis	0.167	0.004
	M. modiolus	0.155	0.011
b,c stone layers	Control	0.208	0.007
	M. edulis	0.189	0.002
	M. modiolus	0.181	0.007
no stone layers	Control	0.213	0.005
	M. edulis	0.179	0.010
	M. modiolus	0.155	0.010

Table 12. The mean critical erosion velocity (ms^{-1}) for sediment with stones present or not present at different depths for control tanks and tanks containing groups of animals. Stone layers a, b and c represent the depths 0-1cm, 3-4cm and 6-7cm respectively.

	Comparison	t	d.f.	P
	Control to *M. edulis*	18.799*	46	P< 0.001
A	Control to *M. modiolus*	21.819*	46	P< 0.001
	M. edulis to *M. modiolus*	5.628*	46	P< 0.001
	Control to *M. edulis*	23.106*	46	P< 0.001
B	Control to *M. modiolus*	36.436*	46	P< 0.001
	M. edulis to *M. modiolus*	11.242*	46	P< 0.001
	Control to *M. edulis*	34.669*	46	P< 0.001
C	Control to *M. modiolus*	7.565*	46	P< 0.001
	M. edulis to *M. modiolus*	0.765	46	0.50> P> 0.40

Table13. Students t tests on the critical erosion velocity for sediment containing no animals (control) and sediment containing groups of animals (*Mytilus edulis* or *Modiolus modiolus*). A to G represent sediment with stones present or not present at different depths. A = a,b,c stone layers present, B = b,c stone layers present, C = no stone layers present. t = students t, d.f. = degrees of freedom and P = probability. For all comparisons values of t >5.00 are regarded as significant and are denoted by an asterisk (*).

Particle size range	Tank	mean	std dev
a,b,c stone layers	Control	1.155×10^{-3}	7.46×10^{-5}
	M. edulis	7.388×10^{-4}	3.00×10^{-5}
	M. modiolus	6.470×10^{-4}	7.82×10^{-5}
b,c stone layers	Control	1.117×10^{-3}	6.03×10^{-5}
	M. edulis	9.135×10^{-4}	1.77×10^{-5}
	M. modiolus	6.150×10^{-4}	7.49×10^{-5}
no stone layers	Control	1.217×10^{-3}	4.85×10^{-5}
	M. edulis	8.492×10^{-4}	8.22×10^{-5}
	M. modiolus	6.200×10^{-4}	7.43×10^{-5}

Table 14. The mean bed shear stress (KPa) for sediment with no animals (control) and sediment containing groups of animals (*Mytilus edulis* or *Modiolus modiolus*) in three sediment treatments. Stone layers a, b and c represent the depths 0-1cm, 3-4cm and 6-7cm respectively.

	Comparison	t	d.f.	P
	Control to *M. edulis*	25.342*	44	P< 0.001
A	Control to *M. modiolus*	23.019*	44	P< 0.001
	M. edulis to *M. modiolus*	5.376*	44	P< 0.001
	Control to *M. edulis*	13.272*	44	P< 0.001
B	Control to *M. modiolus*	22.603*	44	P< 0.001
	M. edulis to *M. modiolus*	17.405*	44	P< 0.001
	Control to *M. edulis*	15.704*	44	P< 0.001
C	Control to *M. modiolus*	27.692*	44	P< 0.001
	M. edulis to *M. modiolus*	8.639*	44	P< 0.001

Table 15. Students t tests on the critical shear strength of sediment containing no animals (control) and sediment containing groups of animals (*Mytilus edulis* or *Modiolus modiolus*). A to C represent sediment with stones present or not present at different depths (A = a, b and c stone layers present, B = b and c stone layers present and C = no stone layers present). t = students t, d.f. = degrees of freedom and P = probability. For all comparisons t values >5.00 are regarded as significant and are denoted by an asterisk (*).

present was significantly lower than for control sediment. This was more pronounced for sediment which contained M. modiolus. The bed shear stress for sediments with M. modiolus was significantly lower than for corresponding sediments with M. edulis.

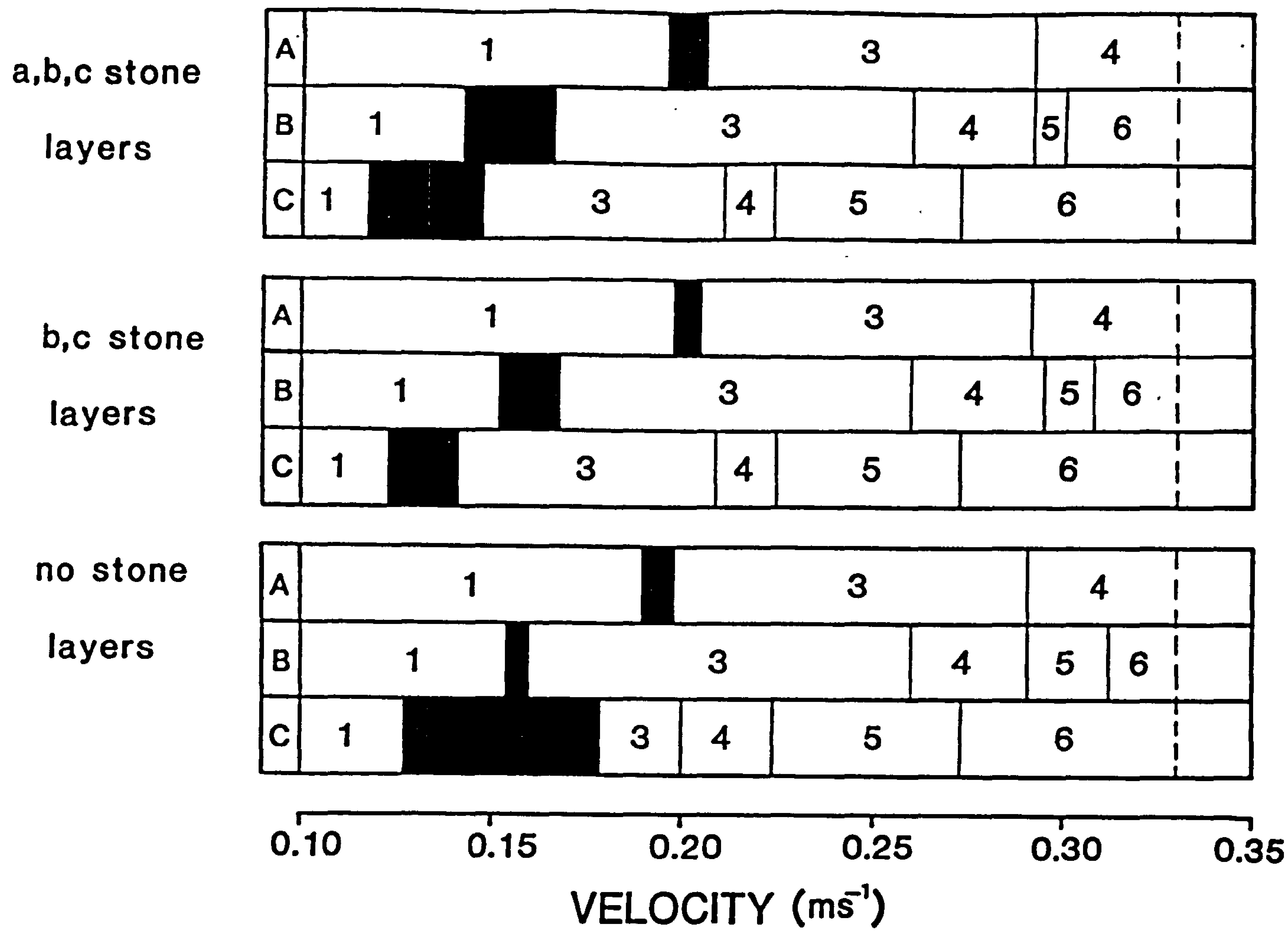
Description of erosion patterns

The Erosion scale described on pages 315-319 was applied to notes taken during the experiment and analysis of video tapes.

A comparison of the erosion scales for control sediment, sediment containing groups of M. edulis and sediment containing M. modiolus, at increasing current velocities is shown in figure10. The following statements can be made from a comparison of control sediment and sediment containing each species.

Moderate erosion occurred in control sediment at the maximum current velocity ($0.33ms^{-1}$). Light (stage 3) and moderate(stage 4) erosion occurred at lower current velocities in sediment containing M. edulis or M. modiolus than in control sediment. Light (stage 3) to severe (stage 6) erosion occurred at lower current velocities in sediment containing M. modiolus than in corresponding sediment containing M. edulis. Light to severe erosion occurred at similar velocities in each of the three sediment types (sediment with stone layers a, b and c, stone layers b and c and sediment with no stone layers) for control sediment, sediment containing M. edulis and sediment containing M. modiolus. Plate 23-24 shows groups of Mytilus edulis on sediment (control sediment, ie. no stones present) at the beginning of the experiment (plate 23) and during the experiment (Erosion Scale 5, Plate 24).

Figure 10. Diagram of Erosion Indices at increasing current velocities for sediment with stones present or not present at different depths. A = control sediment, B = sediment containing groups of *Mytilus edulis* and C = sediment containing groups of *Modiolus modiolus*.


a,b,c stone layers
b,c stone layers
no stone layers
A
B
C
1
3
4
5
6
0.10
0.15
0.20
0.25
0.30
0.35
VELOCITY (ms⁻¹)

Plates 23-24. Groups of *Mytilus edulis* on sediment before erosion occurred (Plate 23) and erosion around animals (Heavy Erosion) during the experiment (Plate 24). Note the scouring of sediment around animals and the build up of sediment behind groups of animals.

23.

24.

FLOW

Particle size analysis

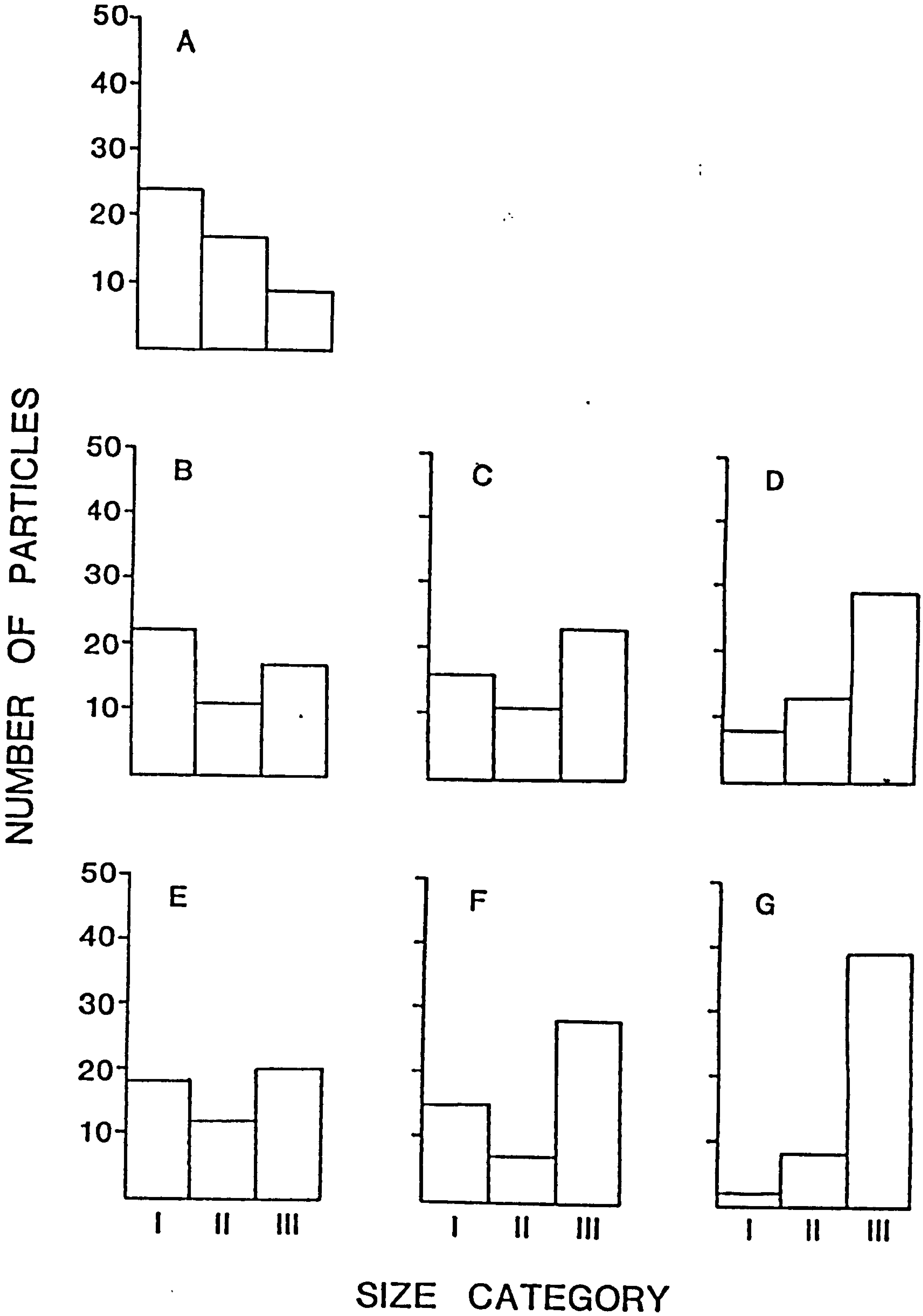
At the end of the experiments using sediment of particle size <2.0mm (with stones present and with stones not present) I noticed changes in the sediment size distribution around groups of animals. Samples of surface sediment were obtained from grooves which had formed around groups, areas of sediment built up behind groups and sediment between groups of animals at the end of the experiment. In addition samples of surface sediment from control tanks (no animals present) were also obtained at the end of the experiment. The length and width of 50 particles from each sample were measured with the aid of a binocular microscope. Particle size was estimated as follows:

$$\text{Particle size} = \frac{\text{length + width}}{2}$$

The number of particles in three size categories for sediment with stones present or not present at different depths in the sediment are shown in figures 11 (tanks with stone layers present at the depths 0-1cm, 3-4cm and 6-7cm) and 12 (tanks with no stone layers present). In each figure A = control tanks (no animals present), B-D = tanks containing M. edulis and E-G = tanks containing M. modiolus. The numbers I, II and III represent the size of particles (I = <0.1mm, II = 0.1-0.2mm and III = >0.2mm). Tanks containing sediment with stones present at the depths 3-4cm and 6-7cm are not included because time did not permit for analysis of the results. The results, however would probably be similar to those obtained for the control tank (no stone layers present). Plate 11 shows groups of M. edulis before erosion (top) and at the end of the experiment (bottom). The build up of sediment behind groups of animals and sediment sorting can clearly be seen.

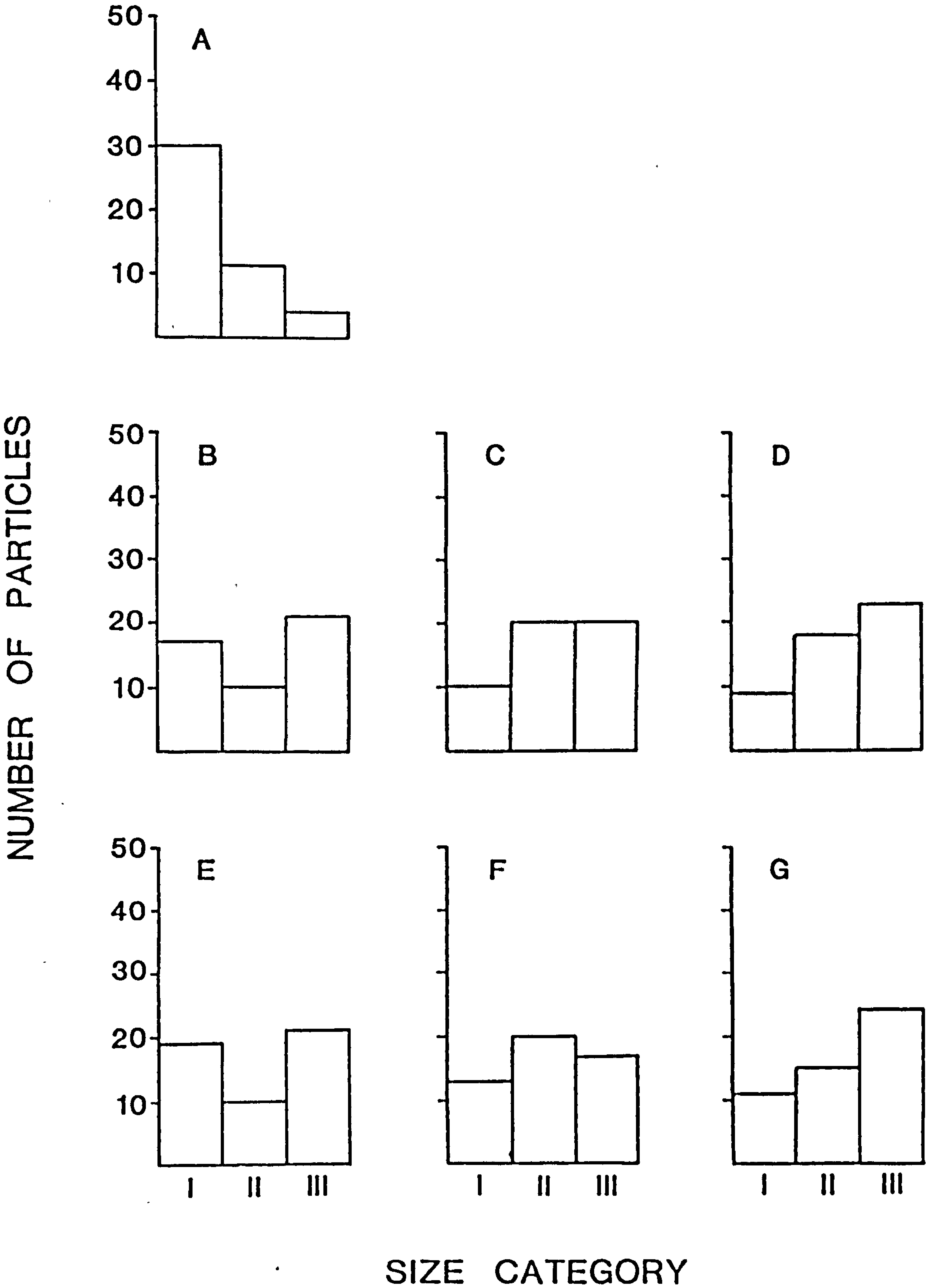
The control sediment contains a greater proportion of small

Figure 11. The number of sediment particles in different size categories from sediment with stones at different depths (0-1cm, 3-4cm and 6-7cm) at the end of experiments in a sea water flume. A = control sediment (no animals present) B to D = sediment containing _M. edulis_ (B to D) and E to F = sediment containing _M. modiolus_ (E to G). B and E represent areas of sediment between groups of animals, C and F represent sediment from grooves at the side of animals and D and F represent samples from areas of sediment built up behind animals. I to III represent particle size ((length $\pm$ width)/2). I = <0.1mm, II = 0.1-0.2mm and III = >0.2mm.



50
40
30
20
10
A
B
C
D
E
F
G
NUMBER OF PARTICLES
I
II
III
SIZE CATEGORY

Figure 12. The number of sediment particles in different size categories from sediment with stones not present at different depths in the sediment (control tank), at the end of experiments in a sea water flume. A = control sediment (no animals present) B to D = sediment containing M. edulis (B to D) and E to F = sediment containing M. modiolus (E to G). B and E represent areas of sediment between groups of animals, C and F represent sediment from grooves at the side of animals and D and F represent samples from areas of sediment built up behind animals. I to III represent particle size ((length + width)/2). I = <0.1mm, II = 0.1-0.2mm and III = >0.2mm.


NUMBER OF PARTICLES
50
40
30
20
10
A
B
C
D
E
F
G
I
II
III
SIZE CATEGORY

particles than the three sample areas from tanks containing animals (between groups of animals, in grooves at the side of animals and from sediment built up behind animals) for both species. This is more pronounced for the areas of sediment build up behind animals.

The results were analysed using X^2 tests to determine whether significant differences occur between

A. Control sediment and 3 sediment samples (between groups of animals, in grooves and from sediment built up behind animals) from tanks containing animals (Tables 16-17)

B. Samples for tanks with animals present (Tables 18-19)

C. Tank 1 (stones present) and tank 2 (stones absent) for each species (Table 20).

D. Species for tanks with stones present and for tanks with stones not present (Table 21)

A. Comparison between control sediment and sediment in tanks with animals present

<u>Tanks with stones present (Table 16)</u>: There was a significantly greater proportion of smaller particles in the control sediment than in sediment from each of the three sample areas (between groups of animals, grooves, and sediment built up behind animals) for both species.

<u>Tanks with no stones present (Table 17)</u>: There was a significantly greater proportion of smaller particles in the control sediment than in sediment from grooves and from sediment built up behind animals. The control sediment was not significantly different from the sediment between groups of animals (both species).

The number of particles in each size category for sediment between animals and in grooves was not significantly different (see below and Table 18). In tank 2 these were therefore pooled and compared to control sediment. There was a significantly greater proportion of

Comparison	Contingency table design R x C	X^2 statistic	d.f.	P
Control to M. e. (B)	2 x 3	17.96	2	$P < 0.001$ ***
Control to M. e. (C)	2 x 3	27.17	2	$P < 0.001$ ***
Control to M. e. (D)	2 x 3	30.42	2	$P < 0.001$ ***
Control to M. m. (E)	2 x 3	16.35	2	$P < 0.001$ ***
Control to M. m. (F)	2 x 3	20.74	2	$P < 0.001$ ***
Control to M. m. (G)	2 x 3	37.28	2	$P < 0.001$ ***

Table 16. Tank 1 (tank with stones present at 0-1cm, 3-4cm and 6-7cm depth in sediment). Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 3. Control = control sediment (no animals present), M. e. = sediment with *Mytilus edulis*, M. m. = sediment with *Modiolus modiolus*, (B) and (E) = area of sediment between groups of animals, (C) and (F) = groove formed at side of group and (D) and (G) = build up of sediment behind group. d.f. = degrees of freedom and P = probability.

Comparison	Contingency table design R x C	X^2 statistic	d.f.	P
Control to *M. e.* (B)	2 x 3	3.83	2	$0.20 > P > 0.10$
Control to *M. e.* (C)	2 x 3	9.01	2	$0.02 > P > 0.01^{*}$
Control to *M. e.* (D)	2 x 3	6.75	2	$0.05 > P > 0.02^{*}$
Control to *M. e.* (B)+(C)	2 x 3	7.59	2	$0.05 > P > 0.02^{*}$
Control to *M. m.* (E)	2 x 3	5.25	2	$0.10 > P > 0.05$
Control to *M. m.* (F)	2 x 3	11.77	2	$0.01 > P > 0.001^{**}$
Control to *M. m.* (G)	2 x 3	23.88	2	$P < 0.001^{***}$
Control to *M. m.* (E)+(F)	2 x 3	12.99	2	$P < 0.001^{***}$

Table 17. Tank 2 (tank with no stones present in the sediment). Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 3. Control = control sediment (no animals present), M. e. = sediment with *Mytilus edulis*, M. m. = sediment with *Modiolus modiolus*, (B) and (E) = area of sediment between groups of animals, (C) and (F) = groove formed at side of group and (D) and (G) = build up of sediment behind group. d.f. = degrees of freedom and P = probability.

Comparison		Contingency table design R x C	X^2 statistic	d.f.	P
Mytilus edulis	(B) to (C)	2 x 3	5.71	2	0.10> P> 0.05
	(B) to (D)	2 x 3	5.31	2	0.10> P> 0.05
	(C) to (D)	2 x 3	0.37	2	0.90> P> 0.80
Modiolus modiolus	(E) to (F)	2 x 3	4.88	2	0.10> P> 0.05
	(E) to (G)	2 x 3	7.54	2	0.20> P> 0.10
	(F) to (G)	2 x 3	5.20	2	0.01> P> 0.001 ***

Table 18. Tank 1 (stones present at 0-1cm, 3-4cm and 6-7cm depth in sediment). Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 3. d.f. = degrees of freedom and P = probability. (B) AND (E) = area of sediment between groups of animals, (C) and (F) = groove formed at front of group and (D) and (G)= build up of sediment behind group.

Comparison		Contingency table design R / C	X^2 statistic	d.f.	P
Mytilus edulis	(B) to (C)	2 x 3	1.85	2	$0.50 > P > 0.30$
	(B) to (D)	2 x 3	9.83	2	$0.01 > P > 0.001^{**}$
	(C) to (D)	2 x 3	3.53	2	$0.20 > P > 0.10$
Modiolus modiolus	(E) to (F)	2 x 3	2.92	2	$0.30 > P > 0.20$
	(E) to (G)	2 x 3	19.71	2	$P < 0.001^{***}$
	(F) to (G)	2 x 3	11.80	2	$P < 0.001^{***}$

Table 19. Tank 2 (tank with no stones present in the sediment). Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 2. d.f. = degrees of freedom and P = probability. (B) and (E) = area of sediment between groups of animals, (C) and (F) = groove formed at side of group and (D) and (G) = build up of sediment behind group.

Comparison		Contingency table design R x C	X^2 statistic	d.f.	P
Control tank		2 x 3	5.26	2	0.10> P> 0.05
Mytilus edulis	(B)	2 x 3	1.09	2	0.70> P> 0.50
	(C)	2 x 3	4.21	2	0.20> P> 0.10
	(D)	2 x 3	1.56	2	0.50> P> 0.30
Modiolus modiolus	(B)	2 x 3	0.23	2	0.90> P> 0.80
	(C)	2 x 3	9.09	2	0.02> P> 0.01*
	(D)	2 x 3	6.70	2	0.01> P> 0.001**

Table 20. Comparison between tank 1 (stones present in sediment at depths 0-1cm, 3-4cm and 6-7cm) and tank 2 (no stones present in sediment). Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 3. (A) = area of sediment between groups of animals, (B) = groove formed at side of group and (C) = build up of sediment behind group. d.f. = degrees of freedom and P = probability.

	Comparison	Contingency table design R x C	X^2 statistic	d.f.	P
	Area (B) to (E)	2 x 3	0.05	2	$0.90 > P > 0.80$
I	Area (C) to (F)	2 x 3	0.63	2	$0.50 > P > 0.30$
	Area (D) to (G)	2 x 3	1.01	2	$0.70 > P > 0.50$
	Area (B) to (E)	2 x 3	0.69	2	$0.50 > P > 0.30$
II	Area (C) to (F)	2 x 3	1.41	2	$0.50 > P > 0.30$
	Area (D) to (G)	2 x 3	6.25	2	$0.05 > P > 0.02^{*}$

Table 21. Comparison between species. Statistical analyses on the number of particles in three size categories for sediment at the end of flume experiment 3. I = tank 1 (stones present at 0-1cm, 3-4cm and 6-7cm), II = tank 2 (no stones present), Areas (B) and (E) = sediment between groups of animals, Areas (C) and (F) = groove formed at side of animal and Areas (D) and (G) = build up of sediment behind animal.

smaller particles in control sediment than there was in the pooled sample from tanks containing animals (both species).

B. Comparison between areas of sediment for tanks with animals present

Tanks with stones present (Table 18): There was a significantly greater proportion of larger particles in the area of sediment built up behind animals than there was in sediment between groups of animals for Modiolus modiolus.

Tanks with no stones present (Table 19): There was a significantly greater proportion of larger particles in sediment from the areas of sediment built up behind animals than there was in sediment between groups of animals (both species) and a significantly greater proportion in the groove at the side of animals than in sediment between groups for Modiolus modiolus.

There were no significant differences between sediment in grooves at the side of animals and sediment between groups of animals for both species in tanks with stones present and tanks with stones not present (Tables 18-19).

C. Comparison between tanks with stones present and tanks with no stones present for Mytilus edulis and for Modiolus modiolus

Mytilus edulis: There were no significant differences between tanks with stones present and tanks with stones not present for sediment between groups of animals, in grooves at the side of animals for areas of sediment built behind animals (Table 20).

Modiolus modiolus: There was a significantly greater proportion of larger particles in the grooves at the side of animals and areas of sediment built up behind animals in tanks with stones not present than there were in tanks with stones present. (Table 20).

D. Comparison between species for tanks with stones present and for tanks with stones not present

There was a significantly greater proportion of larger particles in the areas of sediment built up behind animals for Modiolus modiolus than there was for Mytilus edulis in tanks with no stones present. No other comparisons were significant (Table 21).

DISCUSSION

This discussion is concerned with two main aspects of sediment stability and erosion. The first is a critical appraisal of the curves concerned with the initial movement of sediment. The second is a discussion of the importance of mussels and other invertebrates in relation to sediment stability.

Critical appraisal of the curves concerned with the initial movement of sediment

Miller et al (1977) reviewed and discussed the literature for critical velocities of sediment in relation to the initial work by Shields (1936) and Hjulstrom (1935, 1939). They incorporated the relevant literature into several curves. Among these were graphs of grain diameter against mainstream velocity and grain diameter against critical shear stress (Miller et al, 1977, pp 518 and 519 respectively). The authors stated that determining a threshold θ_t (Shield criterion) or T_t (bed shear stress) was inherently preferable over relating grain diameter to U_{100} (mainstream velocity at 100cm above the bed). The critical erosion velocity for sediment of mean particle diameters 16.0mm, 8.0mm, 4.0mm, 2.0mm, 1.0mm, 0.5mm and 0.25mm from Hjulstrom (1935, figure 1, p.10) and Miller et al (1977, Figure 6, p.518) are shown in Table 22 at the end of this discussion. These are compared to each particle size range in the present study.

My work agrees very well with Hjulstrom (1935) but not with Miller et al (1977). The values taken from the figure in Miller et al (1977) were two to three times that for this study and the values taken from Hjulstrom (1935). The critical shear stress for abiotic sediment of mean diameters 2.0, 1.0, 0.5 and 0.25mm taken from the curve in Miller et al (1977, figure 7, p.519), are shown in Table 23 at the end of this discussion. The authors present the critical shear stress in dynes/cm^2. One dyne is equal to 10^{-5}N and so 1 dyne/cm^2 = 10^{-8} KN/cm^2

$= 10^{-4}$ KN/m^2. The critical shear stress for particles of diameter 16.0mm, 8.0mm, 4.0mm, 2.0mm, 1.0mm, 0.5mm and 0.25mm is compared with the data I have obtained for the different particle size ranges (controls). The values obtained in my experiments were about double that predicted from the curve in Miller et al (1977) for the particle size ranges of 1.0-2.0mm and 0.5-1.0mm, and about a quarter that for the particle size range 0.25-0.5mm.

A combination of factors may be responsible for the differences in critical erosion velocity and bed shear stress between my own work and that of Miller et al, 1977). These include differences in bed roughness, density of particles (since the curves in Miller et al (1977) were based on particles of quartz density). In addition, there were probably differences in the point at which measurements were taken and in the apparatus used for taking the measurements. I have taken measurements when a few particles were observed by eye moving over the surface. Other workers have used some form of magnification over a part of the sediment bed to determine when the first few particles move. Any differences between observation with the naked eye and with some form of magnification would be more pronounced for smaller particle sizes because movement would be more difficult to see with the naked eye. In addition, there may have been differences in sediment binding caused by small invertebrates and micro-organisms.

The importance of mussels and other invertebrates in relation to sediment stability

Mytilus edulis and *Modiolus modiolus* initially destabilise sediments by decreasing the critical bed shear stress. Sediment erosion therfore occurs at lower current velocities. Animals cause local scour around their shells. This is shown by the small horseshoe-shaped grooves which occur at current velocities greater than critical erosion velocity. The activities of an animal, as it searches for a suitable attachment with its foot, destroys the integrity of sediment and will inevitably increases the water content. This is interesting because it has been known for some time that sediment stability decreases with an increase in water content (Trask and Rolston, 1950).

Both species of mussel increase the bed roughness of sediments and this in turn lowers the critical erosion velocity of the sediment. M. edulis searches for stones in the surface sediment and readily moves across the sediment in search of a more suitable site. In a series of field experiments Kuenen (1942) found that M. edulis placed on sand were moved by water currents. My own observations suggest that M. modiolus does not move readily in the laboratory, and in the field I have noticed that animals which had been left in groups were found in the same area on subsequent dives. Animals attach byssus threads to stones deeper in the sediment and an animal will displace sediment with its foot to burrow into the sediment. The displacement of sediment produces a long narrow mound around each sides of the shell which undergoes erosion at velocities greater than critical erosion velocity.

The experiments with M. edulis and M. modiolus have been performed in controlled laboratory conditions. These showed that groups of mussels destabilise sediment. In the field areas of M. edulis beds, including those at Arrochar appear to stabilise sediments by protecting the underlying sediment and increasing the boundary layer. The apparent contradiction between my laboratory experiments and field observations can be explained by differences in density. Eckman et al (1981) found that tube-building by the polychaete Owenia fusiformis decreased the critical erosion velocity by causing local scour around the tubes. Fager (1964), however found that a dense settlement of the same species stabilised a shifting sand against erosion. In a similar manner, the dense beds of M. edulis found at Arrochar and other areas in the Clyde Sea area are likely to protect the underlying sediment and increase the thickness of the boundary layer. Sediment scour would still occur around the edges of such beds but the area beneath the animals will be protected as long as the bed remains intact. The dense network of threads attached to stones and to other animals will further protect the sediment. Animals and threads may cause sedimentation. In addition to the animals own faecal material, the local sedimentary environment is rendered more attractive to other invertebrates. Tsuchiya and Nishirira (1985) found that clusters of M. edulis on rocky shores were attractive to other species through the creation of more microhabitats. In addition, small algae (Fucus sp.) found attached to animals in established groups attracted more species. M. modiolus is not found in Loch Long at high densities. Small groups of up to 4 individuals were sometimes found. It is very unlikely that this species stabilises sediment in the field. Animals used for the majority of laboratory experiments were not given enough time to burrow very deep into the sediment. When animals were left for periods of up to 100 days they gradually buried deeper into the sediment. Thus, although M. modiolus was shown to decrease sediment stability, this effect becomes less pronounced as the animal makes its way deeper into the sediment. Sediment erosion around M. modiolus may have the effect of ensuring the siphons are kept above the bed by causing local scour around the animal.

Some invertebrate species cause local destabilision which benefits that animal whereas others stabilise sediments. The hypothesis of different species in a single sediment community producing areas of stability and instability is an interesting one. The burrowing sea anemone Cerianthus lloydii is the most numerous benthic species at the subtidal site containing M. modiolus. It occurs at very high densities in the sediment. Rowe (1974) found that Cerianthus doubled the shear strength in the surface 5cm of the sediment. Although M. modiolus destabilised sediments the effects of other species which stabilise sediment must be taken into account. It is therefore necessary to determine the effects of each species in a community and the net effect of the whole community on sediment stability.

Sediment sorting around animals is very important in relation to initial settlement of larvae and the interpretation of modified depositional sedimentary environments. The feeding activities of Arenicola marina results in a heterogeneous distribution of several grain size fractions (Baumfaulk, 1979). Van Straaten (1952, 1954) found an almost ubiquitous thin layer of course shell debris, particularly the shells of Hydrobia ulvae at a depth of 20 to 30cm in the subsurface of the tidal flats of the Dutch Wadden Sea. He ascribed this to the feeding activities of A. marina. Rhoads and Stanley (1965) found that selective size feeding by the polychaete Clymenella torquata produced a positive gradation of particles from homogenised sand within a period of about one month. In sediment cores from Cape Cod, Mass. they found a gradual coarsening of deposit from top to bottom, caused by this species. Warme (1967) also reported this phenomenon, called biogenic graded bedding, caused by Callianassa spp. for a lagoon in California. Thus feeding by deposit feeders is known to cause partial sorting of sediment. The sorting of sediments in high currents by M. edulis and M. modiolus is the first record of sediment sorting caused by the modification of currents around any species. Particle size influences the distribution of many intertidal species including Corophium volutator (Meadows, 1964c). This species is common in the mid to high tide shore at Arrochar, close to mussel beds. It is not clear how M. edulis affects the local distribution of other species. Tube-building invertebrates such as C. volutator and Nereis virens are important in modifying the sediment and sediment stability. The activity of M. edulis is likely to destroy tubes and inhibit tube-building.

It would seem obvious to classify bottom living invertebrates into species which stabilise sediments and species which destabilise sediments. The density of a species, however, is an important determinant of whether a particular species has a stabilising or destabilising effect on sediment. Most papers report observations or the shear strength of sediments in support of statements about sediment stability (Rhoads, 1970; Rhoads and Young, 1970; Southward, 1974; Yinghst and Aller, 1982; Twitchell et al, 1985). Detailed field and laboratory studies of communities are essential to determine the role of species in sediment transport. Controlled experiments on the interaction of different species will probably give the most significant results (Rowe, 1974; Young and Southward, 1978). Careful interpretation of experimental studies will give a better insight into the role of animal and plant communities in sedimentation and sediment transport in estuaries.

Particle size	Hjulstrom (1939)	Miller et al (1977)	Particle size range	Present study
16.0mm	1.04-1.07	2.10		
			16.0 to 8.0mm	———
8.0mm	0.80-1.02	1.20		
			8.0 to 4.0mm	———
4.0mm	0.48-0.70	1.00		
			4.0 to 2.0mm	———
2.0mm	0.26-0.45	0.81		
			2.0 to 1.0mm	0.301
1.0mm	0.16-0.25	0.61		
			1.0 to 0.5mm	0.221
0.5mm	0.13-0.22	0.51		
			0.5 to 0.25mm	0.209
0.25mm	0.15-0.25	0.46		
			< 0.25mm	0.210

Table 22. A comparison of the critical erosion velocities (m/s^{-1}) for sediment of different particle sizes obtained by different workers and those obtained in the present study.

Particle size	Miller et al (1977)	Particle size range	Present study
16.0mm	1.34×10^{-2}		
		16.0 to 8.0mm	———
8.0mm	7.00×10^{-3}		
		8.0 to 4.0mm	———
4.0mm	2.4×10^{-3}		
		4.0 to 2.0mm	———
2.0mm	1.05×10^{-3}		
		2.0 to 1.0mm	2.296×10^{-3}
1.0mm	5.3×10^{-4}		
		1.0 to 0.5mm	1.309×10^{-3}
0.5mm	2.7×10^{-4}		
		0.5 to 0.25mm	1.210×10^{-3}
0.25mm	1.7×10^{-4}		
		< 0.25mm	1.181×10^{-3}

Table 23. A comparison of the critical shear stress (KN/m^2) for sediment of different particle sizes obtained by Miller et al (1977) and that obtained in the present study.

APPENDICES

APPENDIX 1

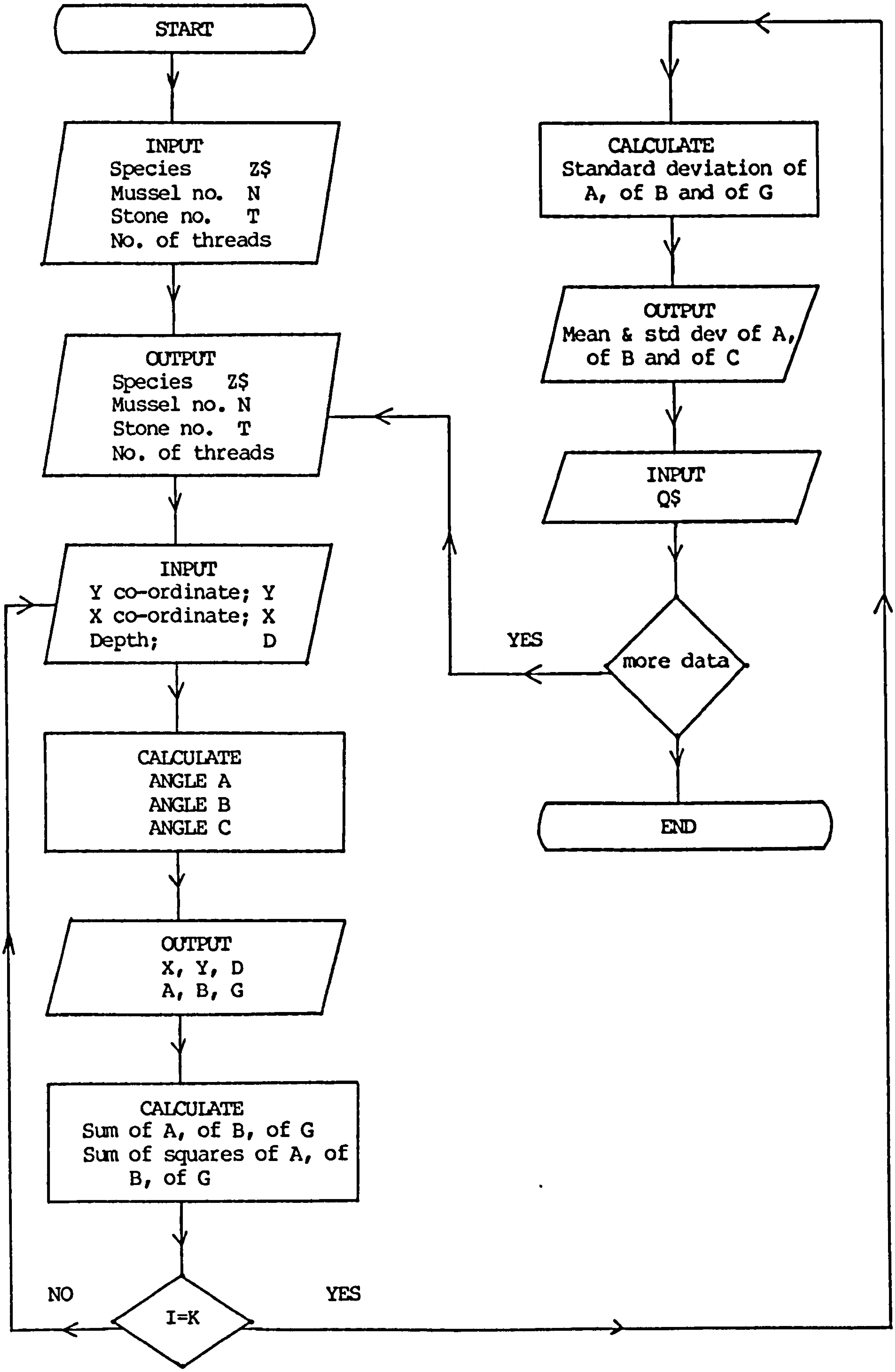
Computer program to calculate angles of byssus threads in sediment

```
5 REM ** MEAN AND STANDARD DEVIATION OF ANGLES CALCULATED FROM THREE
10 REM ** DIMENSIONAL CO-ORDINATES **
20 PRINT "THIS PROGRAMME CALCULATES ANGLES (IN DEGREES) FOR THREE ANGLES"
30 PRINT
40 PRINT "EACH ANGLE IS THAT OF A SINGLE BYSSUS THREAD FROM THE"
50 PRINT "INSERTION AT THE SHELL TO THE BYSSUS PAD"
60 PRINT
70 PRINT "ANGLE A IS THE PLAN VIEW ANGLE OF THE THREAD VIEWED FROM ABOVE"
80 PRINT
90 PRINT "ANGLE B IS THE SIDE VIEW ANGLE OF THE THREAD VIEWED FROM THE"
100 PRINT "RIGHT SIDE"
110 PRINT
120PRINT"ANGLEC IS THE END VIEW ANGLE OF THE THREADVIEWEDFROM THE FRONT"
130 PRINT
140 CLEAR
150 INPUT "ENTER MUSSEL SPECIES" ; Z$
160 INPUT "ENTER MUSSEL NUMBER"  ; N
170 INPUT "ENTER STONE NUMBER"   ; T
180 INPUT "ENTER NUMBER OF THREADS" ; K
190 INPUT "ENTERDEPTH OF MUSSEL IN SEDIMENT"; M
200 LPRINT "SPECIES",,"MUSSEL","STONE"
210 LPRINT Z$,N,T
220 LPRINT "DEPTH OF MUSSEL IN SEDIMENT="M
230 LPRINT "NUMBER OF THREADS ON STONE"T"="K
240 LPRINT
250 REM **CALCULATION OF ANGLES IN DEGREES**
260 FOR I = 1 TO K
270 INPUT "ENTER X CO-ORDINATE" ; X
280 INPUT "ENTER Y CO-ORDINATE" ; Y
290 INPUT "ENTER DEPTH"         ; D
300 D=D+M
310 INPUT "ENTER LENGTH OF THREAD" ; L
320 INPUT "IS THE BYSSUS THREAD ATTACHED TO A STONE OR TO SEDIMENT ?" ;A$
330 PRINT "IS THE BYSSUS THREAD ATTACHED AT THE RIGHT OR THE LEFT SIDE"
340 INPUT "OF THE ANIMAL" ; B$
350 REM **CALCULATION OF ANGLE A**
360 A=ATN(Y/X)
370 A=(360*A)/6.28318
380 A=SQR(A*A)
390 IF X<0 THEN 410
400 A=180-A
410 IF Y>0 THEN 430
420 A=360-A
430 REM **CALCULATION OF ANGLE B**
440 B=ATN(D/X)
450 B=(360*B)/6.28318
460 B=SQR(B*B)
470 IF X<0 THEN 490
480 B=180-B
490 IF D>0 THEN 510
500 B=360-B
510 REM **CALCULATION OF ANGLE C**
520 C=ATN(D/Y)
530 C=(360*C)/6.28318
540 C=SQR(C*C)
```

Computer program (cont.)

```
550 IF Y<0 THEN 570
560 C=180-C
570 IF D>0 THEN 600
580 C=360-C
590 REM **LENGTH OF VECTORS A, B AND C**
600 AA=SQR(X^2+Y^2)
610 BB=SQR(X^2+D^2)
620 CC=SQR(Y^2+D^2)
630 LPRINT "X CO-ORDINATE(cm)="X, "ANGLE A (degrees)="A
640 LPRINT "Y CO-ORDINATE(cm)="Y, "ANGLE B (degrees)="B
650 LPRINT "DEPTH(cm)="         D, "ANGLE C (degrees)="C
660 LPRINT "LENGTH OF THREAD(cm)="L
670 LPRINT "LENGTH OF VECTOR A="AA
680 LPRINT "LENGTH OF VECTOR B="BB
690 LPRINT "LENGTH OF VECTOR C="CC
700 LPRINT "THE BYSSUS THREAD IS ATTACHED TO" A$ "ON THE" B$ "SIDE"
710 LPRINT "OF THE ANIMAL"
720 LPRINT
730 REM **SUM AND SUM OF SQUARES OF A, B AND C VALUES**
740 S=S+A
750 R=R+A*A
760 P=P+B
770 Q=Q+B*B
780 V=V+C*C
790 REM **SUM AND SUM OF SQUARES OF THREAD LENGTHS**
800 W=W+L
810 E=E+L^2
820 REM **SUM AND SUM OF SQUARES OF AA, BB AND CC VALUES**
830 SS=SS+AA
840 RR=RR+AA^2
850 PP=PP+BB
860 QQ=QQ+BB^2
870 UU=UU+CC
880 VV=VV+CC^2
890 NEXT I
900 REM **STANDARD DEVIATION OF A, B AND C VALUES AND THREAD LENGTHS**
910 F=SQR(R-S*S/K)/(K-1)
920 G=SQR(Q-P*P/K)/(K-1)
930 H=SQR(V-U*U/K)/(K-1)
940 J=SQR(E-W*W/K)/(K-1)
950 LPRINT "MEAN OF A="S/K, "STD DEV OF A="F
960 LPRINT "MEAN OF B="P/K, "STD DEV OF B="G
970 LPRINT "MEAN OF C="U/K, "STD DEV OF C="H
980 LPRINT "MEAN OF THREAD LENGTH="W/K,"STD DEV OF THREAD LENGTH="J
990 LPRINT
1000 REM **STANDARD DEVIATION OF AA, BB AND CC VECTORS**
1010 FF=SQR(RR-SS^2/K)/(K-1)
1020 GG=SQR(QQ-PP^2/K)/(K-1)
1030 HH=SQR(EE-WW^2/K)/(K-1)
1040 LPRINT "MEAN OF AA VECTORS="SS/K, "STD DEV OF AA="FF
1050 LPRINT "MEAN OF BB VECTORS="PP/K, "STD DEV OF BB="GG
1060 LPRINT "MEAN OF CC VECTORS="UU/K, "STD DEV OF CC="HH
1070 LPRINT
1080 LPRINT
1090 INPUT "PRESS Y TO CONTINUE, RETURN TO FINISH";Y$
1100 IF Y$=Y THEN 140
1110 END
```

Flow diagram for computer program to calculate angles of byssus threads in sediment


START
INPUT
Species Z$
Mussel no. N
Stone no. T
No. of threads
OUTPUT
Species Z$
Mussel no. N
Stone no. T
No. of threads
INPUT
Y co-ordinate; Y
X co-ordinate; X
Depth; D
CALCULATE
ANGLE A
ANGLE B
ANGLE C
OUTPUT
X, Y, D
A, B, G
CALCULATE
Sum of A, of B, of G
Sum of squares of A, of B, of G
NO
I=K
YES
CALCULATE
Standard deviation of A, of B and of G
OUTPUT
Mean & std dev of A, of B and of C
INPUT
Q$
YES
more data
END

APPENDIX 2

Three of the tests I considered for a comparison of the data in Tables 4 and 5 (pp 202-203 respectively) were found to be unsuitable. These were the X^2 test, Kruskal-Wallis one-way analysis of variance and Mann-Whitney U test. The Kendall coefficient of concordance and Sign test were less powerful than the Wilcoxon matched-pairs signed-ranks test.

The X^2 test can only be used to compare between tanks if the number of threads/animal at a particular depth is not significantly different within tanks. X^2 tests showed significant differences within tanks for the majority of tanks and the test was therefore unsuitable.

The Kruskal-Wallis one way analysis of variance and Mann-Whitney U tests are non-parametric equivalents of the One-way analysis of variance and t-test respectively. The Kruskal-Wallis test makes use of two tables of probability, dependent on sample size and/or number of samples. X^2 tables are of use only with sample sizes > 5. Table O in Siegel (1956) is used for comparisons of 3 samples but does not give enough detail of probabilities for a sample size of 2. Tables for the Mann-Whitney U test can only be used when the sample size of at least one sample is 3 (Table J in Siegal (1956). Therefore these tests were not used.

The Kendall coeffeicient of concordance can be used to show whether animals show a preference for attaching byssus threads to the same depths in different experimental tanks. The main advantage is that the test compares the three depths together(as opposed to two for the Wilcoxon matched-pairs signed-ranks test), but has a disadvantage in that only ranks are considered (not magnitude of the difference). Depths were ranked from 1 (largest number of threads) to 3 (smallest number of threads). If one depth is consistently ranked low or high but the other two depths have a mixture of ranks the test frequenty gives a significant result for similarity. The depth 5-8cm is frequently ranked high (small number of threads) and all 7 comparisons shown on page 1 were found to be significantly similar. Thus the overall correlation was too strong to pick up significant differences between 0-2cm and 5-8cm.

The Sign test gives similar results to the Wilcoxon matched-pairs signed-ranks test but is a less powerful test.

APPENDIX 3

Appendix 3; Table 1. _Mytilus edulis_. The mean, plan and side view angles for groups of byssus threads attached to stones and to sediment. A is the plan view angle, B is the side view angle and C is the end view angle. AA, BB and CC are the corresponding vector lengths for each group of threads. The data for three of the animals are shown in Section 2, Table 54 (p. 175).

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 1 (a stone layer); animal 1							
stone 1 (a layer)	2	A	172.63	225.53	AA	0.351	0.048
		B	314.73	0.13	BB	0.460	0.031
		C	277.38	28.82	CC	0.353	0.047
stone 2 (a layer)	5	A	149.52	18.01	AA	0.431	0.047
		B	194.29	6.02	BB	0.377	0.111
		C	207.28	22.99	CC	0.237	0.066
stone 3 (a layer)	12	A	189.51	23.60	AA	1.499	0.488
		B	197.82	10.16	BB	1.398	0.380
		C	285.61	37.74	CC	0.667	0.596
stone 4 (a layer)	1	A	156.15	——	AA	0.208	——
		B	212.28	——	BB	0.225	——
		C	235.00	——	CC	0.146	——
stone 5 (a layer)	13	A	140.00	15.49	AA	1.142	0.295
		B	206.00	19.86	BB	0.991	0.265
		C	208.84	14.65	CC	0.805	0.156
Tank 1 (cont.); animal 2							
stone 1 (a layer)	7	A	226.19	7.96	AA	2.054	0.264
		B	195.27	7.94	BB	1.480	0.374
		C	344.98	6.47	CC	1.511	0.092
stone 2 (a layer)	2	A	215.20	2.50	AA	0.940	0.013
		B	155.73	12.03	BB	0.858	0.119
		C	32.42	16.77	CC	0.664	0.094
stone 3 (a layer)	3	A	195.39	5.61	AA	1.542	0.185
		B	168.77	4.79	BB	1.512	0.148
		C	35.75	14.82	CC	0.523	0.212
stone 4 (a layer)	1	A	209.10	——	AA	1.662	——
		B	174.10	——	BB	1.460	——
		C	10.52	——	CC	0.822	——
stone 5 (a layer)	11	A	232.29	17.64	AA	1.378	0.247
		B	196.63	15.63	BB	0.861	0.400
		C	284.10	137.76	CC	1.067	0.236
stone 6 (a layer)	3	A	227.92	19.39	AA	0.936	0.293
		B	213.43	12.45	BB	0.758	0.396
		C	330.47	6.76	CC	0.730	0.119
stone 7 (a layer)	8	A	166.41	9.29	AA	1.057	0.222
		B	190.78	26.39	BB	1.128	0.130
		C	211.05	58.02	CC	0.574	0.186

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
stone 8 (a layer)	2	A	138.37	26.15	AA	0.344	0.127
		B	217.84	31.88	BB	0.340	0.138
		C	218.96	8.97	CC	0.327	0.294
Tank 2 (b stone layer); animal 1							
No threads attached							
Tank 2 (cont.); animal 2							
No threads attached							
Tank 3 (c layer only); animal 1							
No threads produced							
Tank 3 (c layer only); animal 2							
sediment	4	A	146.11	22.21	AA	0.078	0.015
		B	266.18	0.74	BB	0.962	0.395
		C	267.13	2.03	CC	0.961	0.393
Tank 4 (a,b stone layers); animal 1							
stone 1 (a layer)	3	A	292.13	14.53	AA	0.939	0.310
		B	309.41	15.67	BB	0.557	0.348
		C	329.26	25.60	CC	1.056	0.178
stone 2 (a layer)	7	A	314.80	29.60	AA	0.618	0.404
		B	296.06	23.16	BB	0.664	0.256
		C	304.30	29.04	CC	0.806	0.288
stone 3 (a layer)	5	A	287.85	14.97	AA	0.574	0.283
		B	286.07	19.06	BB	0.610	0.166
		C	313.13	19.81	CC	0.809	0.110
Tank 4 (a,b stone layers); animal 2 (threads from animal to stones)							
stone 1 (a layer)	1	A	287.35	——	AA	1.978	——
		B	319.72	——	BB	0.773	——
		C	345.17	——	CC	1.953	——
stone 2 (a layer)	1	A	219.11	——	AA	1.281	——
		B	210.44	——	BB	1.153	——
		C	324.14	——	CC	0.997	——
stone 3 (a layer)	1	A	4.22	——	AA	0.951	——
		B	43.26	——	BB	1.301	——
		C	94.49	——	CC	0.895	——

Appendix 3; Table 1 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 4 (cont.)							
stone 4 (a layer)	2	A	203.10	——	AA	1.315	——
		B	181.89	——	BB	1.211	——
		C	355.57	——	CC	0.518	——
stone 5 (a layer)	5	A	234.26	15.82	AA	0.400	0.146
		B	226.36	22.71	BB	0.350	0.099
		C	322.79	14.92	CC	0.389	0.046
stone 6 (a layer)	2	A	197.32	169.88	AA	0.211	0.170
		B	297.46	29.00	BB	0.247	0.115
		C	278.65	52.14	CC	0.250	0.090
stone 7 (a layer)	1	A	224.01	——	AA	0.245	——
		B	247.74	——	BB	0.247	——
		C	291.57	——	CC	0.462	——
Tank 4 (cont) animal 2 (threads from shed byssus complex to stones)							
stone 3 (a layer)	3	A	31.27	6.29	AA	0.806	0.797
		B	17.16	12.27	BB	0.731	0.097
		C	152.75	18.24	CC	0.496	0.135
stone 5 (a layer)	5	A	224.40	11.52	AA	0.697	0.107
		B	151.25	16.72	BB	0.576	0.085
		C	27.13	7.87	CC	0.566	0.232
stone 6 (a layer)	9	A	311.81	20.45	AA	0.722	0.148
		B	30.82	27.70	BB	0.602	0.177
		C	25.25	20.92	CC	0.604	0.226
stone 7 (a layer)	4	A	309.07	14.54	AA	1.088	0.209
		B	332.98	15.82	BB	0.744	0.188
		C	337.26	17.08	CC	0.930	0.257
stone 8 (a layer)	5	A	259.81	14.31	AA	1.120	0.249
		B	129.83	47.03	BB	0.479	0.091
		C	89.81	149.09	CC	1.147	0.219
stone 9 (a layer)	3	A	326.31	25.33	AA	1.177	0.330
		B	330.84	12.23	BB	1.048	0.410
		C	318.68	20.02	CC	0.781	0.266
Tank 5 (a,c stone layers); animal 1							
stone 1 (layer a)	5	A	36.32	4.11	AA	1.374	0.121
		B	350.44	2.45	BB	1.122	0.125
		C	192.72	1.87	CC	0.831	0.085

Appendix 3; Table 1 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 5, animal 1(cont.)							
stone 2 (a layer)	13	A	181.29	23.07	AA	0.722	0.146
		B	204.60	12.06	BB	0.752	0.151
		C	261.88	39.06	CC	0.371	0.156
stone 3 (a layer)	20	A	148.43	26.29	AA	0.506	0.249
		B	236.67	22.36	BB	0.812	0.310
		C	248.06	21.55	CC	0.749	0.367
Tank 5 (a,c stone layers) ; animal 2							
stone 1 (a layer)	5	A	146.42	187.27	AA	0.956	0.061
		B	133.83	171.56	BB	1.046	0.098
		C	193.09	83.24	CC	0.437	0.264
stone 2 (a layer)	9	A	36.56	19.72	AA	0.704	0.122
		B	62.29	15.66	BB	1.290	0.180
		C	107.71	4.33	CC	1.188	0.344
stone 3 (a layer)	9	A	133.46	13.12	AA	0.941	0.153
		B	144.11	14.95	BB	0.851	0.375
		C	145.12	21.27	CC	0.903	0.237
stone 4 (a layer)	8	A	62.11	8.12	AA	0.790	0.170
		B	61.24	7.26	BB	0.763	0.168
		C	136.35	5.16	CC	0.967	0.230
Tank 6 (b,c stone layers); animal 2							
stone 1 (b layer)	4	A	15.86	5.92	AA	0.400	0.112
		B	278.30	2.25	BB	2.651	0.112
		C	267.79	0.38	CC	2.623	0.098
Tank 7 (a,b,c stone layers) animal 2							
stone 1 (a layer)	2	A	142.75	15.83	AA	1.092	0.251
		B	153.33	8.12	BB	0.938	0.051
		C	144.44	23.81	CC	0.831	0.243
stone 2 (a layer)	1	A	222.85	——	AA	1.017	——
		B	146.17	——	BB	0.898	——
		C	35.85	——	CC	0.854	——
stone 3 (a layer)	3	A	153.04	15.05	AA	0.928	0.388
		B	186.46	26.70	BB	0.851	0.315
		C	181.12	53.56	CC	0.563	0.317
stone 4 (a layer)	1	A	156.50	——	AA	0.100	——
		B	110.97	——	BB	0.257	——
		C	99.46	——	CC	0.243	——

Appendix 3; Table 1 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 7, animal 2 (cont.)							
stone 5 (a layer)	2	A	308.87	11.65	AA	0.533	0.156
		B	311.42	39.37	BB	0.451	0.200
		C	338.74	28.94	CC	0.515	0.321
stone 6 (a layer)	2	A	304.97	1.35	AA	1.524	0.203
		B	339.65	5.89	BB	0.939	0.192
		C	345.32	5.09	CC	1.294	0.181
stone 7 (a layer)	3	A	313.65	5.46	AA	0.939	0.061
		B	20.87	19.61	BB	0.725	0.100
		C	20.94	18.52	CC	0.752	0.047
Tank 8 (control) ; animal 2							
No threads produced							
Tank 9 (stones in each 1cm layer); animal 1							
stone 1 (a layer)	2	A	12.67	4.24	AA	1.293	0.142
		B	7.17	5.20	BB	1.273	0.147
		C	152.96	10.32	CC	0.319	0.100
stone 2 (a layer)	1	A	320.97	——	AA	1.578	——
		B	0.75	——	BB	1.226	——
		C	0.92	——	CC	0.994	——
stone 3 (a layer)	6	A	293.52	8.71	AA	1.069	0.300
		B	240.68	172.01	BB	0.418	0.151
		C	241.62	177.92	CC	0.987	0.305
stone 4 (a layer)	3	A	334.09	8.61	AA	0.775	0.156
		B	231.78	193.88	BB	0.723	0.093
		C	228.41	179.55	CC	0.406	0.099
stone 5 (a layer)	15	A	223.25	45.80	AA	0.668	0.285
		B	151.95	67.28	BB	0.665	0.306
		C	95.42	121.56	CC	0.409	0.227
stone 6 (a layer)	6	A	264.11	24.09	AA	0.597	0.284
		B	257.83	17.48	BB	0.573	0.133
		C	314.10	19.01	CC	0.812	0.185
stone 7 (a layer)	5	A	160.93	30.61	AA	1.100	0.290
		B	161.57	11.32	BB	1.000	0.351
		C	99.96	69.45	CC	0.559	0.170

Appendix 3; Table 1 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 9 (cont.); animal 2							
stone 1 (a layer)	2	A	356.65	0.33	AA	1.397	0.089
		B	4.86	0.99	BB	1.400	0.091
		C	55.01	8.35	CC	0.145	0.024
stone 2 (a layer)	2	A	84.69	3.03	AA	0.728	0.048
		B	298.27	27.92	BB	0.202	0.115
		C	193.47	9.55	CC	0.751	0.083
stone 3 (a layer)	1	A	304.58	——	AA	1.040	——
		B	344.29	——	BB	0.613	——
		C	349.03	——	CC	0.872	——
stone 4 (a layer)	6	A	308.78	1.01	AA	0.801	0.084
		B	300.81	3.44	BB	0.982	0.068
		C	306.57	4.60	CC	1.052	0.065
stone 5 (a layer)	12	A	246.31	13.18	AA	0.674	0.111
		B	235.16	18.29	BB	0.440	0.108
		C	330.20	10.27	CC	0.706	0.111
stone 6 (a layer)	1	A	75.36	——	AA	0.277	——
		B	279.83	——	BB	0.410	——
		C	236.44	——	CC	0.485	——

Appendix 3; Table 1 (cont.)

Appendix 3; Table 2. Modiolus modiolus. The mean, plan and side view angles for groups of byssus threads attached to stones and to sediment. A is the plan view angle, B is the side view angle and C is the end view angle. AA, BB and CC are the corresponding vector lengths for each group of threads. The data for three of the animals are shown in Section 2, Table 55 (pp. 177-179).

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 1 (a stone layer); animal 1							
stone 1 (a layer)	5	A	168.26	4.79	AA	1.730	0.115
		B	183.81	1.93	BB	1.693	0.091
		C	200.95	17.04	CC	0.384	0.131
stone 2 (a layer)	4	A	7.55	3.30	AA	1.887	0.232
		B	345.52	1.22	BB	1.930	0.240
		C	243.22	11.22	CC	0.547	0.031
sediment	25	A	157.47	10.91	AA	1.653	0.287
		B	184.27	7.73	BB	1.523	0.319
		C	190.96	17.14	CC	0.671	0.343
sediment	14	A	138.62	1.88	AA	2.992	0.808
		B	195.99	2.78	BB	2.320	0.546
		C	198.12	3.79	CC	2.089	0.594
sediment	27	A	126.11	5.17	AA	2.696	0.476
		B	224.55	2.66	BB	2.186	0.203
		C	215.59	3.29	CC	2.682	0.544
sediment	2	A	159.23	4.54	AA	2.602	0.530
		B	208.30	2.29	BB	2.757	0.539
		C	235.04	3.89	CC	1.620	0.507
sediment	4	A	151.25	8.61	AA	1.414	0.154
		B	226.16	2.30	BB	1.765	0.069
		C	242.22	8.21	CC	1.455	0.124
Tank 1 (a stone layer); animal 2							
stone 1 (a layer)	6	A	356.17	1.56	AA	1.504	0.377
		B	3.47	0.92	BB	1.503	0.373
		C	43.43	19.74	CC	0.144	0.043
stone 2 (a layer)	1	A	328.94	——	AA	2.760	——
		B	340.27	——	BB	2.511	——
		C	329.23	——	CC	0.144	——
stone 3 (a layer)	5	A	350.91	6.47	AA	1.044	0.302
		B	334.99	8.13	BB	1.130	0.268
		C	287.71	11.76	CC	0.479	0.042
stone 4 (a layer)	3	A	340.65	1.56	AA	1.638	0.219
		B	343.32	2.07	BB	1.164	0.213
		C	319.61	1.58	CC	0.708	0.032
sediment	2	A	320.56	0.72	AA	2.111	0.262
		B	322.27	3.69	BB	2.059	0.132
		C	316.77	4.53	CC	1.840	0.120

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 1, animal 2(cont.)							
sediment	2	A	328.28	28.69	AA	0.938	0.314
		B	329.45	4.12	BB	0.824	0.025
		C	312.38	35.87	CC	0.736	0.355
sediment	35	A	134.30	11.13	AA	1.956	1.046
		B	221.63	19.03	BB	1.839	0.702
		C	222.11	12.84	CC	1.687	0.570
sediment	15	A	328.74	15.10	AA	2.314	0.828
		B	328.69	1.92	BB	2.133	0.466
		C	312.94	18.57	CC	1.779	0.807
sediment	35	A	317.07	6.66	AA	1.412	0.897
		B	301.88	11.60	BB	1.839	0.738
		C	299.44	8.70	CC	1.748	0.637
Tank 2 (b stone layer); animal 1							
sediment	2	A	318.56	2.34	AA	3.466	0.075
		B	357.08	1.06	BB	2.602	0.148
		C	356.74	0.93	CC	2.296	0.059
sediment	97	A	319.93	18.45	AA	2.340	0.973
		B	295.63	70.08	BB	2.674	1.328
		C	292.52	68.86	CC	2.335	1.078
sediment	22	A	54.12	21.02	AA	0.538	0.206
		B	280.77	3.73	BB	1.421	0.307
		C	253.45	6.77	CC	1.476	0.376
sediment	15	A	137.79	6.61	AA	1.843	0.721
		B	237.36	7.09	BB	2.586	1.018
		C	239.90	7.15	CC	2.464	0.857
Tank 2 (b stone layer); animal 2							
stone 1 (b layer)	4	A	283.60	0.15	AA	2.337	0.148
		B	282.46	8.48	BB	2.533	0.190
		C	312.52	0.59	CC	3.322	0.102
stone 2 (b layer)	12	A	52.71	4.35	AA	4.269	0.108
		B	330.35	2.75	BB	3.603	0.230
		C	211.62	1.16	CC	3.358	0.180
sediment	15	A	297.40	2.98	AA	2.417	0.139
		B	297.65	2.94	BB	2.399	0.182
		C	315.31	1.32	CC	3.013	0.135

Appendix 3; Table 2. (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 2, animal 2(cont.)							
sediment	1	A	187.31	----	AA	3.034	----
		B	221.23	----	BB	4.002	----
		C	278.33	----	CC	2.666	----
sediment	1	A	339.84	----	AA	0.714	----
		B	281.64	----	BB	3.320	----
		C	274.33	----	CC	3.261	----
sediment	79	A	41.88	4.48	AA	2.895	0.693
		B	333.07	15.37	BB	2.567	0.761
		C	209.10	16.33	CC	2.410	0.853
sediment	30	A	43.69	0.77	AA	4.812	0.318
		B	316.70	0.75	BB	4.800	0.291
		C	224.62	0.95	CC	4.667	0.276
Tank 3 (c stone layer); animal 1							
sediment	4	A	292.58	0.18	AA	4.708	0.011
		B	325.58	0.50	BB	2.191	0.014
		C	344.10	0.25	CC	4.520	0.001
sediment	13	A	302.79	4.57	AA	1.484	0.420
		B	296.74	1.49	BB	1.738	0.349
		C	308.21	3.88	CC	2.005	0.510
sediment	6	A	120.66	1.90	AA	1.389	0.160
		B	229.83	7.09	BB	1.108	0.026
		C	215.32	5.04	CC	1.464	0.056
sediment	24	A	5.44	2.48	AA	2.517	0.267
		B	328.51	2.59	BB	2.946	0.359
		C	261.40	3.59	CC	1.570	0.297
sediment	75	A	194.83	7.96	AA	2.266	0.380
		B	222.02	6.97	BB	3.044	0.865
		C	288.22	13.79	CC	2.206	0.702
Tank 3 (c stone layer); animal 2							
sediment	9	A	353.18	0.40	AA	1.833	0.023
		B	323.97	5.73	BB	2.273	0.195
		C	279.48	1.52	CC	1.363	0.297
sediment	1	A	319.75	----	AA	2.817	----
		B	323.97	----	BB	4.683	----
		C	293.62	----	CC	4.541	----

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
sediment	18	A	321.93	2.44	AA	1.722	0.092
		B	289.78	6.96	BB	4.265	0.835
		C	286.02	7.79	CC	4.185	0.828
sediment	2	A	298.01	0.66	AA	1.863	0.004
		B	284.87	0.74	BB	3.412	0.081
		C	296.52	0.53	CC	3.685	0.084
sediment	1	A	279.89	——	AA	0.873	——
		B	273.93	——	BB	2.190	——
		C	291.89	——	CC	2.348	——
sediment	2	A	257.02	0.34	AA	1.301	——
		B	264.43	1.05	BB	1.371	——
		C	292.93	0.54	CC	1.238	——
sediment	60	A	158.12	8.99	AA	3.917	0.837
		B	198.93	2.05	BB	3.786	0.772
		C	222.45	20.44	CC	2.001	0.475
Tank 4 (a,b layers); animal 1							
stone 1 (a layer)	2	A	135.12	0.30	AA	4.918	0.016
		B	168.88	0.01	BB	3.552	0.007
		C	168.83	0.17	CC	3.537	0.027
stone 2 (a layer)	15	A	134.93	2.59	AA	6.311	0.328
		B	174.21	1.93	BB	3.979	0.009
		C	174.63	0.51	CC	3.950	0.021
stone 3 (a layer)	7	A	142.66	1.99	AA	3.687	1.167
		B	174.31	0.42	BB	2.947	0.208
		C	172.58	0.07	CC	2.250	0.011
stone 4 (a layer)	7	A	149.02	0.77	AA	4.772	0.192
		B	183.96	2.92	BB	4.104	0.128
		C	186.62	4.95	CC	2.481	0.124
stone 5 (a layer)	1	A	113.59	——	AA	3.099	——
		B	174.93	——	BB	1.245	——
		C	177.78	——	CC	2.842	——
stone 6 (a layer)	10	A	200.10	0.84	AA	2.405	0.084
		B	201.72	0.61	BB	2.430	0.083
		C	312.57	0.87	CC	1.221	0.022
stone 7 (a layer)	2	A	154.22	1.88	AA	6.916	0.180
		B	173.89	1.36	BB	6.261	0.048
		C	167.39	3.72	CC	3.086	0.245

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 4, animal 1 (cont.)							
stone 8 (a layer)	10	A	147.61	17.40	AA	2.549	0.319
		B	199.93	3.17	BB	2.192	0.468
		C	215.74	20.64	CC	1.547	0.529
stone 9 (a layer)	7	A	172.20	1.28	AA	2.410	0.150
		B	215.16	4.88	BB	2.943	0.314
		C	258.95	1.74	CC	1.740	0.376
stone 10 (a layer)	10	A	169.29	1.33	AA	1.759	0.168
		B	215.91	1.27	BB	2.136	0.215
		C	255.40	1.53	CC	1.297	0.160
stone 11 (b layer)	3	A	154.39	3.37	AA	1.984	0.007
		B	228.03	1.36	BB	2.672	0.029
		C	246.72	2.24	CC	2.165	0.084
stone 12 (b layer)	2	A	95.77	0.10	AA	4.960	0.065
		B	256.95	1.69	BB	2.230	0.349
		C	203.70	3.17	CC	5.400	0.201
sediment	3	A	112.48	0.51	AA	6.800	0.090
		B	214.02	1.03	BB	3.136	0.070
		C	195.60	0.21	CC	6.524	0.056
sediment	2	A	170.49	1.95	AA	3.717	0.057
		B	191.95	0.09	BB	3.746	0.035
		C	231.84	6.03	CC	0.992	0.085
sediment	28	A	50.12	1.01	AA	1.349	0.147
		B	320.13	0.15	BB	1.310	0.359
		C	214.83	0.25	CC	1.043	0.319
Tank 4 (a,b layers); animal 2							
stone 1 (a layer)	2	A	207.66	1.01	AA	2.704	0.015
		B	205.90	0.85	BB	2.663	0.020
		C	317.18	0.13	CC	1.711	0.044
stone 2 (a layer)	1	A	143.73	——	AA	3.076	——
		B	164.45	——	BB	2.574	——
		C	159.24	——	CC	1.946	——
stone 3 (b layer)	3	A	211.88	7.66	AA	0.647	0.136
		B	257.50	1.45	BB	2.494	0.017
		C	278.16	3.38	CC	2.463	0.025
stone 4 (b layer)	1	A	53.20	——	AA	1.536	——
		B	291.78	——	BB	2.479	——
		C	241.88	——	CC	2.610	——

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 4, animal 2 (cont.)							
stone 5 (b layer)	2	A	116.24	0.46	AA	1.900	0.079
		B	222.39	0.40	BB	1.130	0.021
		C	204.22	0.74	CC	1.858	0.074
sediment	64	A	231.66	10.23	AA	1.656	0.367
		B	208.17	22.16	BB	1.263	0.438
		C	338.01	12.09	CC	1.459	0.522
sediment	9	A	125.99	4.94	AA	2.005	0.174
		B	252.21	1.65	BB	3.826	0.228
		C	246.09	1.92	CC	3.991	0.321
sediment	9	A	115.64	0.51	AA	1.866	0.037
		B	253.66	3.78	BB	3.021	0.736
		C	238.78	6.66	CC	3.375	0.660
Tank 5 (a,c stone layers); animal 1							
stone 1 (a layer)	1	A	208.49	——	AA	5.753	——
		B	176.38	——	BB	5.066	——
		C	6.65	——	CC	2.763	——
stone 2 (a layer)	9	A	163.06	33.50	AA	1.087	0.384
		B	244.08	13.05	BB	2.234	0.234
		C	267.00	7.23	CC	1.962	0.033
stone 3 (a layer)	2	A	302.18	3.44	AA	1.230	0.221
		B	294.43	0.17	BB	1.569	0.143
		C	305.92	3.43	CC	0.177	0.239
stone 4 (a layer)	3	A	344.93	5.40	AA	1.308	0.022
		B	301.64	1.16	BB	2.403	0.090
		C	279.53	3.74	CC	2.077	0.085
stone 5 (a layer)	2	A	273.78	5.84	AA	1.286	0.945
		B	271.02	1.89	BB	2.110	0.057
		C	299.38	18.23	CC	2.531	0.529
sediment	56	A	317.01	3.83	AA	3.532	1.223
		B	322.41	5.56	BB	4.934	1.064
		C	320.58	2.38	CC	4.622	0.591
sediment	15	A	296.25	1.70	AA	1.603	0.116
		B	282.74	1.31	BB	3.276	0.624
		C	294.71	3.38	CC	3.511	0.599
sediment	40	A	225.94	8.94	AA	4.848	1.342
		B	212.82	14.08	BB	4.068	1.167
		C	329.04	7.52	CC	3.858	0.451

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 5, animal 1 (cont.)							
sediment	2	A B C	24.99 326.44 234.91	0.15 0.38 0.58	AA BB CC	2.233 2.429 1.641	0.160 0.160 0.103
Tank 5 (a,c stone layers); animal 2							
stone 1 (a layer)	2	A B C	329.21 353.24 347.77	10.99 0.63 6.15	AA BB CC	2.564 2.179 1.359	0.371 0.063 0.594
stone 2 (a layer)	5	A B C	198.02 189.34 331.22	8.66 2.99 11.71	AA BB CC	1.125 1.089 0.356	0.378 0.409 0.035
stone 3 (a layer)	6	A B C	165.96 219.83 253.32	5.71 4.12 6.93	AA BB CC	1.268 1.604 1.076	0.105 0.164 0.134
stone 4 (a layer)	5	A B C	28.53 341.19 211.11	2.88 7.39 7.98	AA BB CC	2.343 2.188 1.333	0.116 0.097 0.242
stone 5 (a layer)	1	A B C	159.85 197.30 220.31	—— —— ——	AA BB CC	4.214 4.143 1.904	—— —— ——
stone 6 (a layer)	6	A B C	136.67 182.33 182.35	4.99 1.53 1.49	AA BB CC	6.442 4.665 4.425	0.449 0.325 0.625
stone 7 (a layer)	11	A B C	144.67 191.10 198.32	9.96 2.70 15.20	AA BB CC	4.703 3.842 2.855	0.276 0.189 0.647
sediment	2	A B C	318.52 348.81 347.38	0.60 0.40 0.72	AA BB CC	4.499 3.436 3.053	0.065 0.086 0.016
sediment	3	A B C	324.73 340.22 333.06	4.16 2.13 1.17	AA BB CC	1.987 1.724 1.279	0.150 0.189 0.051
sediment	10	A B C	349.70 338.38 292.67	8.04 2.84 17.25	AA BB CC	2.624 2.754 1.155	0.314 0.321 0.212
sediment	1	A B C	174.64 212.76 261.71	—— —— ——	AA BB CC	2.366 2.801 1.532	—— —— ——

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 5, animal 2 (cont.)							
sediment	2	A	144.62	4.94	AA	4.336	0.178
		B	198.89	0.27	BB	3.734	0.376
		C	205.89	3.76	CC	2.779	0.136
sediment	1	A	35.27	——	AA	5.024	——
		B	351.95	——	BB	4.143	——
		C	191.31	——	CC	2.958	——
sediment	11	A	6.74	1.72	AA	2.301	0.050
		B	306.99	2.06	BB	3.808	0.236
		C	264.97	1.01	CC	3.057	0.273
Tank 6 (b,c layers); animal 2							
stone 1 (b layer)	3	A	15.15	1.11	AA	3.682	0.107
		B	2.78	0.05	BB	3.558	0.085
		C	169.78	0.93	CC	0.979	0.096
stone 2 (b layer)	6	A	17.61	1.21	AA	2.573	0.812
		B	310.59	0.87	BB	3.768	0.053
		C	254.78	1.13	CC	2.965	0.020
stone 3 (b layer)	2	A	3.33	0.34	AA	5.509	0.069
		B	345.43	0.22	BB	5.683	0.069
		C	257.39	1.14	CC	1.466	0.003
stone 4 (b layer)	2	A	336.73	0.83	AA	1.416	0.087
		B	295.16	0.95	BB	3.056	0.058
		C	281.44	1.03	CC	2.822	0.417
stone 5 (b layer)	5	A	125.85	5.18	AA	0.952	0.068
		B	253.29	3.81	BB	1.983	0.337
		C	247.70	2.00	CC	2.053	0.366
stone 6 (b layer)	16	A	45.99	1.91	AA	1.360	0.171
		B	292.15	2.59	BB	2.503	0.050
		C	247.16	2.62	CC	2.515	0.052
stone 7 (b layer)	5	A	151.08	13.80	AA	0.321	0.053
		B	263.00	0.55	BB	2.211	0.005
		C	265.84	2.31	CC	2.202	0.010
stone 8 (b layer)	3	A	25.43	2.12	AA	1.514	0.248
		B	334.32	0.21	BB	1.749	0.280
		C	225.01	0.35	CC	2.029	0.264
stone 9 (b layer)	6	A	98.78	0.95	AA	2.456	0.022
		B	262.45	0.82	BB	2.852	0.011
		C	229.36	0.11	CC	3.726	0.014

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 6, animal 2 (cont.)							
stone 10 (c layer)	24	A	137.07	4.80	AA	0.901	0.029
		B	264.25	0.45	BB	6.550	0.006
		C	264.63	0.63	CC	6.546	0.006
stone 11 (c layer)	9	A	138.43	3.41	AA	1.427	0.447
		B	254.48	0.47	BB	3.979	0.009
		C	256.14	1.26	CC	3.950	0.021
sediment	8	A	2.13	0.43	AA	2.054	0.247
		B	295.35	0.48	BB	4.494	0.067
		C	268.99	0.21	CC	4.333	0.073
Tank 7 (a,b,c stone layers); animal 2							
stone 1 (a layer)	1	A	202.96	——	AA	1.564	——
		B	196.70	——	BB	1.503	——
		C	324.69	——	CC	0.747	——
stone 2 (a layer)	4	A	224.32	1.79	AA	2.053	0.063
		B	219.80	0.26	BB	1.910	0.135
		C	319.53	1.70	CC	1.886	0.069
stone 3 (a layer)	1	A	220.44	——	AA	1.156	——
		B	224.42	——	BB	2.038	——
		C	292.20	——	CC	1.985	——
stone 4 (a layer)	6	A	303.51	1.01	AA	1.750	0.124
		B	305.34	0.03	BB	1.667	0.033
		C	316.96	2.24	CC	1.996	0.085
stone 5 (a layer)	9	A	138.61	2.05	AA	3.323	0.039
		B	158.89	10.13	BB	2.739	0.369
		C	156.49	10.77	CC	2.471	0.400
stone 6 (a layer)	1	A	151.00	——	AA	3.796	——
		B	152.13	——	BB	3.756	——
		C	136.34	——	CC	2.543	——
stone 7 (a layer)	14	A	148.73	7.09	AA	1.981	0.472
		B	134.85	6.50	BB	2.348	0.251
		C	121.87	9.89	CC	1.972	0.183
stone 8 (b layer)	10	A	318.87	3.62	AA	1.644	0.132
		B	300.69	3.34	BB	2.428	0.089
		C	297.28	0.44	CC	2.343	0.008
stone 9 (b layer)	6	A	198.60	1.39	AA	2.174	0.046
		B	216.79	0.53	BB	2.572	0.336
		C	294.22	1.74	CC	1.690	0.234

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 7, animal 2 (cont.)							
stone 10 (b layer)	10	A	239.43	3.83	AA	1.514	0.248
		B	243.89	3.27	BB	1.749	0.280
		C	309.67	0.91	CC	2.029	0.264
stone 11 (c layer)	6	A	321.70	5.45	AA	2.036	0.110
		B	290.71	0.51	BB	4.486	0.017
		C	286.73	2.69	CC	4.386	0.635
stone 12 (c layer)	5	A	303.94	1.89	AA	1.081	0.052
		B	277.52	0.58	BB	4.616	0.008
		C	281.08	0.33	CC	4.663	0.009
sediment	13	A	314.26	1.24	AA	2.272	0.103
		B	305.39	0.52	BB	2.736	0.085
		C	306.09	1.03	CC	2.761	0.114
sediment	4	A	112.93	0.97	AA	1.156	0.075
		B	265.48	0.29	BB	5.715	0.006
		C	259.41	0.70	CC	5.796	0.018
sediment	6	A	18.16	0.34	AA	1.435	0.116
		B	280.29	0.48	BB	7.625	0.300
		C	266.60	0.08	CC	7.515	0.286
Tank 8 (control); animal 1							
No threads produced							
Tank 9 (stones at each 1cm layer); animal 1							
stone 1 (a layer)	1	A	97.10	——	AA	4.545	——
		B	122.86	——	BB	1.036	——
		C	169.08	——	CC	4.593	——
stone 2 (a layer)	4	A	204.86	0.58	AA	6.025	0.236
		B	174.61	0.67	BB	5.491	0.225
		C	11.51	1.38	CC	2.585	0.109
stone 3 (a layer)	3	A	213.14	1.33	AA	4.061	0.047
		B	181.29	2.37	BB	3.402	0.013
		C	238.14	204.80	CC	2.224	0.109
stone 4 (a layer)	9	A	235.51	3.38	AA	4.394	0.124
		B	171.37	2.48	BB	2.514	0.202
		C	6.04	2.09	CC	3.640	0.202
stone 5 (a layer)	2	A	117.68	27.36	AA	1.043	0.458
		B	140.83	5.53	BB	0.481	0.338
		C	154.49	27.72	CC	1.027	0.470

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 9, animal 1 (cont.)							
stone 6 (a layer)	4	A	345.63	1.90	AA	3.249	0.231
		B	4.30	3.38	BB	3.160	0.237
		C	15.12	9.44	CC	0.842	0.096
stone 7 (b layer)	9	A	131.14	3.15	AA	2.830	0.176
		B	231.21	3.88	BB	2.975	0.104
		C	227.40	4.28	CC	3.153	0.065
stone 8 (b layer)	21	A	64.14	12.83	AA	1.602	0.209
		B	287.26	5.50	BB	2.189	0.200
		C	235.80	7.55	CC	2.541	0.155
stone 9 (unmarked)	32	A	32.69	15.92	AA	1.641	0.313
		B	318.81	11.70	BB	1.789	0.293
		C	234.36	10.78	CC	1.416	0.189
stone 10 (unmarked)	11	A	178.16	0.67	AA	4.511	0.110
		B	177.85	1.52	BB	4.513	0.110
		C	135.53	29.23	CC	0.251	0.057
stone 11 (unmarked)	9	A	308.65	19.12	AA	0.924	0.189
		B	303.61	15.59	BB	1.008	0.198
		C	309.85	5.89	CC	1.034	0.062
stone 12 (unmarked)	2	A	27.23	2.69	AA	1.502	0.032
		B	319.77	1.52	BB	4.513	0.110
		C	238.73	29.23	CC	1.321	0.041
stone 13 (unmarked)	2	A	305.95	5.45	AA	2.873	0.197
		B	311.89	0.52	BB	2.509	0.132
		C	321.08	5.10	CC	2.989	0.197
stone 14 (unmarked)	10	A	160.81	6.47	AA	1.978	0.190
		B	172.71	3.53	BB	1.876	0.187
		C	158.65	9.49	CC	0.689	0.209
stone 15 (unmarked)	9	A	143.43	3.79	AA	3.074	0.256
		B	197.94	5.02	BB	2.598	0.225
		C	203.51	6.41	CC	2.000	0.115
stone 16 (a layer)	4	A	221.09	7.81	AA	4.857	1.567
		B	181.91	5.27	BB	3.677	1.318
		C	267.74	175.72	CC	3.150	1.060
stone 17 (a layer)	5	A	229.56	1.42	AA	3.071	0.041
		B	308.98	2.75	BB	2.411	0.011
		C	324.97	1.10	CC	3.262	0.046

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 9 (stones at each 1cm layer); animal 2							
stone 1 (a layer)	7	A	243.29	3.39	AA	2.384	0.188
		B	155.32	1.49	BB	1.169	0.051
		C	13.07	2.11	CC	2.187	0.220
stone 2 (a layer)	4	A	198.79	5.79	AA	2.945	0.020
		B	162.71	7.93	BB	2.936	0.219
		C	42.82	21.90	CC	1.369	0.038
stone 3 (a layer)	9	A	194.36	8.89	AA	2.727	0.151
		B	178.07	14.32	BB	2.691	0.199
		C	190.59	147.98	CC	0.857	0.440
stone 4 (a layer)	10	A	296.10	2.02	AA	3.913	0.318
		B	284.12	148.15	BB	1.741	0.275
		C	285.90	149.98	CC	3.514	0.230
stone 5 (a layer)	11	A	310.97	36.08	AA	1.153	0.877
		B	310.49	28.40	BB	1.161	0.400
		C	309.08	38.95	CC	1.154	0.412
stone 6 (a layer)	6	A	11.48	6.28	AA	2.666	0.196
		B	343.25	3.42	BB	2.723	0.259
		C	237.39	17.00	CC	0.979	0.075
stone 7 (a layer)	4	A	47.92	3.32	AA	3.071	0.089
		B	352.83	3.61	BB	2.079	0.206
		C	186.77	3.91	CC	2.294	0.035
stone 8 (b layer)	7	A	292.67	1.55	AA	4.863	0.317
		B	309.37	3.30	BB	2.957	0.156
		C	333.02	1.12	CC	5.030	0.235
stone 9 (b layer)	2	A	232.49	1.06	AA	3.922	0.163
		B	227.73	1.82	BB	3.551	0.109
		C	319.82	0.71	CC	4.070	0.068
stone 10 (unmarked)	26	A	306.64	11.78	AA	1.626	0.301
		B	306.79	13.28	BB	1.629	0.085
		C	314.78	9.54	CC	1.830	0.217
stone 11 (unmarked)	11	A	329.85	1.33	AA	2.948	0.008
		B	331.49	1.11	BB	2.901	0.064
		C	316.90	2.84	CC	2.030	0.011
stone 12 (unmarked)	14	A	34.51	16.14	AA	1.305	0.282
		B	328.93	2.89	BB	1.204	0.323
		C	223.13	18.66	CC	0.988	0.193

Appendix 3; Table 2 (cont.)

Substrate	number of threads	Angle	mean	s.d.	Vector	mean	s.d.
Tank 9, animal 2 (cont.)							
stone 13 (unmarked)	13	A	233.86	7.01	AA	1.652	0.232
		B	243.15	6.42	BB	2.166	0.234
		C	304.49	3.35	CC	2.346	0.362
stone 14 (unmarked)	17	A	189.64	175.12	AA	1.703	0.132
		B	297.13	1.54	BB	3.669	0.156
		C	270.36	5.79	CC	3.280	0.132
sediment	2	A	356.58	0.78	AA	4.560	0.194
		B	358.70	0.22	BB	4.553	0.190
		C	339.11	0.51	CC	0.293	0.078
sediment	1	A	220.20	——	AA	2.612	——
		B	177.07	——	BB	1.998	——
		C	3.46	——	CC	3.462	——
sediment	1	A	204.46	——	AA	2.971	——
		B	184.99	——	BB	2.714	——
		C	349.14	——	CC	1.252	——
sediment	10	A	215.34	0.24	AA	3.245	0.070
		B	214.62	0.48	BB	3.217	0.081
		C	315.77	0.36	CC	2.620	0.082
sediment	9	A	337.91	1.27	AA	1.897	0.084
		B	317.55	2.47	BB	2.390	0.179
		C	293.91	0.64	CC	1.768	0.208
sediment	7	A	7.98	2.22	AA	3.040	0.100
		B	316.46	2.34	BB	4.164	0.306
		C	261.44	3.01	CC	2.908	0.311

Appendix 3; Table 2 (cont.)

REFERENCES

ALLEN, E. A. and H. A. CURRAN (1974). Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. Journal of Sedimentary Petrology 44: 538-548.

ALLEN, J. A., M. COOK, D. J. JACKSON, S. PRESTON and E. M. WORTH (1976). Observations on the rate of production and mechanical properties of the byssus threads of Mytilus edulis L. Journal of Molluscan Studies 42: 279-289.

ALLEN, J. A., P. R. O. BARNETT, J. M. BOYD, R. C. KIRKWOOD, D. W. MACKAY and J. C. SMYTY (Editors, 1986). The Environment of the Estuary and Firth of Clyde. Proceedings of the Symposium held at Glasgow, 1-2 October, 1985. Proceedings of the Royal Society of Edinburgh B 90.

ALLEN, J. R. L. (1985). Principles of Physical Sedimentology. George Allen and Unwin: London, Boston and New York.

ALLER, R. C. (1978). The effects of animal-sediment interactions on geochemical processes near the sediment-water interface. pp. 157-172. In: Estuarine Interactions (Ed. M. L. Wiley). Academic Press.

ALLER, R. C. (1980). Diagenetic processes near the sediment-water interface of Long Island South.I. Decomposition and nutrient element geochemistry (S.N.P.). Advanced Geophysics 22: 237-350.

ALLER, R. C. (1982). The effects of macrobenthos on chemical properties of marine sediment and overlying water. pp. 53-102. In: Animal-sediment Relations (Ed. P. L. McCall and M. J. S. Tevesz). Plenum Press: New York.

ALLER, R. C. (1983). The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. Journal of Marine Research 41: 299-322.

ALLER, R. C. and R. DODGE (1974). Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. Journal of Marine Research 32 209-232.

ALLER, R. C. and J. Y. YINGST (1980). Relationships between microbial distribution and the anaerobic decomposition of organic matter in surface sediments of Long Island Sound, U.S.A. Marine Biology 56: 29-42.

ANDERSON, F. E., L. BLANK, L. E. WATLING, W. MOOK and L. M. MAYER (1981). A temporal and spatial study of mudflat erosion and deposition. Journal of Sedimentary Petrology 51: 729-736.

ASPIRAS, R. B., O. N. ALLEN, R. F. HARRIS and G. CHESTERS (1971). Aggregate stabilisation by filamentous micro-organisms. Soil Science 112: 282-284.

BAAS BECKING, G. M., I. R. CAPLAN and D. MOORE (1960). Limits of the natural environment in terms of pH and oxidation-reduction potentials. Journal of Geology 68: 243-284.

BAIRATI, A. and L. VITELLARO ZUCCARELLO (1974a). Ultrastructure of the byssal apparatus of Mytilus galloprovincialis. III. Analysis of the byssal characteristics by polarised light microscopy. Journal of Submicroscopic Cytology, 6: 367-369.

BAIRATI, A. and L. VITELLARO ZUCCARELLO (1974b). The ultrastructure of the byssal apparatus of Mytilus galloprovincialis. II Observations by microdissections and scanning electron microscopy. Marine Biology 28: 145-158.

BATHURST, R. G. C. (1967). Subtidal gelatinous mat, sand stabiliser and food, Great Bahama Bank. Journal of Geology 75: 736-738.

BAUMFAULK, Y. A. (1979). Heterogeneous grain size distributions in tidal flat sediments, caused by the bioturbation activity of Arenicola marina (polychaete). Netherlands Journal of Sea Research 13(3/4): 428-440.

BAYNE, B. L. (1964). Primary and secondary settlement in Mytilus edulis L. Journal of Animal Ecology 28: 513-523.

BAYNE, B. L. (1965). Growth and delay of metamorphosis of the larvae of Mytilus edulis L. Ophelia 2: 513-523.

BAYNE, B. L. (1975). Aspects of the physiological condition in Mytilus edulis L., with special reference to the effects of oxygen tension and salinity. pp. 213-218. In: Proceedings of the Ninth European Marine Biology Symposium (Ed. H. Barnes), Aberdeen University Press: Aberdeen.

BAYNE, B. L. (1976). Aspects of reproduction in bivalve molluscs. pp. 432-448. In: Estuarine Processes, volume 1 (Ed. M. Wiley). Academic Press: New York.

BAYNE, B. L., D. L. HOLLAND, M. N. MOORE, D. M. LOWE and J. WIDDOWS (1978). Further studies on the effects of stress in the adult on the eggs of Mytilus edulis. Journal of the Marine Biological Association of the U.K. 58: 825-841.

BAYNE, B. L., J. WIDDOWS and R. J. THOMPSON (1976). Physiological Integrations. pp. 261-299. In: Marine Mussels (Ed. B. L. Bayne). Cambridge University Press: Cambridge.

BEAUMONT, A. R., and M. D. BUDD (1982). Delayed growth of mussel (Mytilus edulis) and scallop (Pecten maximus) veligers at low temperatures. Marine Biology 71: 97-100.

BERNER, R. A. (1980). Early Diagenesis: A Theoretical Approach. Princeton University Press, Princeton, New Jersey.

BIERNBAUM, C. K. (1979). Influence of sedimentary factors on the distribution of benthic amphipods of Fishers Island Sound, Connecticut. Journal of Experimental Marine Biology and Ecology 38: 201-223.

BLACK, M. (1933). The algal sediments of Andros Island, Bahamas. Philosophical Transactions of the Royal Society, Lond. 22(B): 165-192.

BLOK, J. W. de and H. J. F. GEELEN (1958). The substratum required for the settling of mussels (Mytilus edulis L.). Les Archives Neerlandaises de Zoologie 13: 446-460.

BLOK, J. W. de and M. TAN MASS (1977). Function of byssus threads in young post-larval Mytilus edulis. Nature, London 267: 558.

BLOOM, S. A., J. L. SIMON and V. D. HUNTER (1972). Animal-sediment relations and Community analysis for a Florida Estuary. Marine Biology 13: 43-56.

BOADEN, P. J. S. (1962). Colonisation of graded sand by an interstitial fauna. Cahiers de Biologie Marine 3: 245-248.

BOADEN, P. J. S. (1963). The interstitial fauna of some North Wales beaches. Journal of the Marine Biological Association of the United Kingdom 43: 79-96.

BOCK, W. D. and D. F. MOORE (1968). A commensal relationship between a foraminifer and a bivalve mollusc. Gulf Research Report 2: 273-279.

BOWDEN, K. F. (1967). Circulation and Diffusion. pp. 15-36. In: Estuaries (Ed. G. H. Lauff). American Association for the Advancement of Science, Washington.

BOWDEN, K. F. (1978). Estuary circulation and diffusion problems. pp. 141-150. In: Tidal Power and Management (Eds. R. T. Severn, D. L. Dinely and L. E. Hawker). 30th Symposium of the Colston Research Society, University of Bristol, 1978. John Wright & Sons, Dorchester.

BRANSON, F. A. and J. B. OWEN (1970). Plant cover, run-off and sediment yield relationships on Mancos Shale in W. Colorado. Water Research 6: 783-790.

BRAYSHAW, A. C., L. E. FROSTICK and I REID (1983). The hydrodynamics of particle clusters and sediment entrainment in coarse alluvial channels. Sedimentology 30: 137-143.

BRIGGS, D. (1977). Sources and Methods in Geography: Sediments. Butterworths, London.

BROWN, C. H. (1952). Some structural proteins of Mytilus edulis. Quarterly Journal of Microscopic Science 93: 487-502.

BROWN, B. (1982). Spatial and temporal distribution of a deposit feeding polychaete on a heterogeneous tidal flat. Journal of Experimental Marine Biology and Ecology 65: 213-227.

BUBNOVA, N. P. (1971). Diet and assimilation of food by the detritus-feeding mollusc Portlandia arctica. Oceanology 11: 248-251.

CADEE, G. C. (1976). Sediment reworking by Arenicola marina on tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Reserch 10: 440-460.

CAMERON, W. M. and D. W. PRITCHARD (1963). Estuaries. pp. 306-324. In: The Sea, 2 (Ed. M. N. Hill). Interscience Publishers, New York.

CAPPER, P. L. and W. F. CASSIE (1976). The Mechanics of Engineering Soils. 6th Edition Spon Engineering Series. John Wiley & Sons.

CARR, R. S. and D. J. REISH (1978). Influence of water-soluble petroleum hydrocarbons on byssal thread formation. Veliger 21: 283-287.

CASSIE, R. M. and A. D. MICHAEL (1968). Fauna and sediments of an intertidal mud flat: A multivariate analysis. Journal of Experimental Marine Biology and Ecology 2: 1-23.

CHACKRABARTI, A. (1980). Influence of biogenic activity of Ghost crabs on the size parameters of beach sediments. Senkenbergiana marina 12: 183-199.

CHACKRABARTI, A. and D. SUBHASHISH (1981). Burrow patterns of Macrophthalmus telescopicus (Owen) and their environmental significance. Senkenbergiana marina 15: 43-53.

CHANNON, R. D. and D. HAMILTON (1976). Wave and tidal sorting of shell sediments southwest of England. Sedimentology 23: 17-42.

CHAPMAN, A. R. O. (1974). The ecology of macroscopic marine algae. Annual Review of Ecology and Systematics 5: 65-80.

CHAPMAN, G. and G. E. NEWELL (1949). The distribution of lugworms (Arenicola marine L.) over the flats at Whitstable. Journal of the Marine Biological Association of the United Kingdom 28: 627-634.

CHARACKLIS, W. G. (1981). Fouling biofilm development: A process analysis. Biotechnology and Bioengineering 23: 1923-1960.

CHIPPERFIELD, P. N. J. (1953). Observations on the breeding and settlement of Mytilus edulis (L.) in British waters. Journal of the Marine Biological Association of the United Kingdom 32: 449-476.

CLARK, P. J. and F. C. EVANS (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 4: 444-453.

COLLAR, R. H. F. (1974). The River Clyde Estuary: Current knowledge of water and sediment movement. In: The Clyde Estuary and Firth. Natural Environment Research Council Publications, Series C, 11: 10-13.

COLMAN, J. (1940). On faunas inhabiting intertidal seaweeds. Journal of the Marine Biological Association of the United Kingdom 24: 129-183.

COLEMAN, N. and E. K. TRUEMAN (1971). The effect of aerial exposure on the activity of the mussels Mytilus edulis L. and Modiolus modiolus (L.). Journal of Experimental Marine Biology and Ecology 7: 295-304.

COMELY, C. A. (1978). Modiolus modiolus (L.) from the Scottish west coast. I. Biology. Ophelia 17: 167-193.

COOK, M. (1970). Composition of mussel and barnacle deposits at the attachment interface. pp. 139-150. In: Adhesion in Biological Systems (Ed. R. S. Manly). Academic Press, New York.

CRISP, D. J. (1955). The behaviour of barnacle cyprids in relation to water movement over a surface. Journal of Experimental Biology 32: 569-590.

CRISP, D. J. and H. BARNES (1954). The orientation and distribution of barnacles at settlement with particular reference to surface contour. Journal of Animal Ecology 23: 142-162.

CRISP, D. J. and H. G. STUBBINGS (1957). The orientation of barnacles to water currents. Journal of Animal Ecology 26: 179-196.

CULLEN, D. J. (1973). Bioturbation of superficial marine sediments by interstitial meiobenthos. Nature, London 242: 323-324.

DARE, D. P. (1976). Settlement, growth and production of the mussel, Mytilus edulis L., in Morecombe Bay, England. Fishery Investigations. Ministery of Agriculture, Fisheries and Food (ser. 2), 28(1), 25pp.

DAVENPORT, J. and J. DAVENPORT (1984). A preliminary assesment of growth rates of mussels from the Falkland Islands (Mytilus chilensis Hupe and Aulacomya ater (Molina)). Journal du Conseil 41: 154-158.

DAVIS, R. A. Jnr. (1983). Depositional Systems: A genetic approach to sedimentary geology. Prentice-Hall. 667pp..

DAY, J. H. (1978). The effects of plants and animals on estuarine chemistry. pp. 216-221. In: Biogeochemistry of Estuarine Sediments. Proceedings of a UNESCO/SCOR Workshop, 1976. UNESCO, Paris.

DAY, J. H. and D. P. WILSON (1934). On the relation of the substratum to the metamorphosis of Scololepis fuliginosa (Claparede). Journal of the Marine Biological Association of the United Kingdom 19: 655-662.

DEEGAN, C. E. (1974). Geological investigations in the Firth of Clyde made by the Institute of Geological Sciences. In: The Clyde Estuary and Firth. Natural Environment Research Council Publications, Series C, 11: 6-9.

DENNY, M. (1980). The role of gastropod pedal mucus in locomotion. Nature, London 285: 160.

DILLON, W. P. and H. B. ZIMMERMAN (1970). Erosion by biological activity in two New England submarine canyons. Journal of Sedimentary Petrology 40: 542-547.

DONAHUE, J. (1971). Burrow morphologies in north-central Pacific sediments. Marine Geology 11: M1-M7.

DORSETT, D. A. (1961). The behaviour of Polydora ciliata (Johnst.). Tube building and burrowing. Journal of the Marine Biological Association of the United Kingdom 41: 577-590.

DOUGLAS, J. F., J. M. GASIORECK and J. A. SWAFFIELD (1981). Fluid Mechanics. Pitman: London.

DYER, K. R. (1979). Estuarine Hydrography and Sedimentation. Cambridge University Press: London and New York.

EDGAR, W. D. and P. S. MEADOWS (1969). Case construction, movement, spatial distribution and substrate selection in the larva of Chironomus riparius Meigen. Journal of Experimental Biology 50: 247-253.

ECKMAN, J. E., A. R. M. NOWELL and P. A. JUMARS (1981). Sediment destabalisation by animal tubes. Journal of Marine Research 39: 339-372.

EDWARDS, J. M. and R. W. FREY (1977). Substrate characteristics within a Holocene Salt Marsh Sapelo Island, Georgia. Senckenbergiana maritima 9: (5/6) 215-259.

ENGEL, R. H., R. E. HILLMAN, M. J. NEAT and H. L. QUINBY (1971). A study of the adhesive mechanisms of various species of sea mussel. National Institute of Dental Research Report 70-2237, 15th JULY 1971. National Institute of Health, Bethseda, Maryland.

FAGER, E. W. (1964). Marine sediments: Effects of a tube-building polychaete. Science 143: 356-359.

FEATHERSTONE, R. P. and M. J. RISK (1977). Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. Journal of Sedimentary Petrology 27: 446-450.

FIELD, I. A. (1922). Biology and economic value of the sea mussel Mytilus edulis. Bulletin of the United States Burreau of Fisheries 38: 127-260.

FITTON-JACKSON, S., F. C. KELLY, A. C. T. NORTH, J. T. RANDALL, W. E. SEED, M. WATSON and G. R. WILKINSON (1953). The byssus threads of Mytilus edulis and Pinna nobilis. In: Nature and structure of collagen (Ed. J. T. Randall and S. Fitton-Jackson). Butterworths Scientific Publishers: London.

FOLK, R. L. (1966). A review of grain-size parameters. Sedimentology 6: 73-93.

FOLK, R. L. (1980). Petrology of Sedimentary Rocks. Hemphill Publishing Company: Austin Texas.

FRANKEL, L. and D. J. MEAD (1973). Mucilaginous matrix of some estuarine sands in Conneticut. Journal of Sedimentary Petrology 43: 1090-1095.

FRIEDMAN, G. M. and J. E. SAUNDERS (1978). Principles of Sedimentology. John Wiley and Sons: New York and Chichester.

FROSTIC, L. E. and I. N. McCAVE (1979). Seasonal shifts of sediments within an estuary mediated by algal growth. Estuarine and Coastal Marine Science 9: 569-577.

GABBOT, P. A. (1976). Energy metabolism. pp. 121-206. In: Marine mussels (Ed. B. L. Bayne). Cambridge University Press, Cambridge.

GAMBLE, J. C. (1971). The responses of the marine amphipods Corophium arenarium and Corophium volutator to gradients and to choices of different oxygen concentrations. Journal of Experimental Biology 54: 275-290.

GASPERO-MAGO, R. R. and F. R. TROEH (1979). Microbial affects on soil erodability. Soil Science Society of America Journal 43: 765-768.

GERZELI, G. (1961). Ricerche istomorphologiche e istochimiche sulla formazione del bisso in Mytilus galloprovincialis. Pubblicanzioni della Statione Zoologica di Napoli 32: 88-103.

GINSBURG, R. N. and H. Z. LOWENSTAM (1958). The influence of marine bottom communities on the depositional environment of sediments. Journal of Geology 66: 310-318.

GIRLING, A. E. (1984). Interactions between marine benthic macroinvertebrates and their sedimentary environment. Ph.D. Thesis, Glasgow University.

GLAUS, K. J. (1968). Factors influencing the production of byssus threads in Mytilus edulis. Biological Bulletin of Woods Hole 135: 420.

GORDON, D. C. (1966). The effects of the deposit feeding polychaete Pectinaria gouldii on the intertidal sediments of Barnstable Harbour. Limnology and Oceanography 11: 327-332.

GRANT, J. (1981). Sediment transport and disturbance on an intertidal sand flat: infaunal distribution and recolonisation. Marine Ecology Progress Series 6: 249-255.

GRANT, W. D., L. F. BOYER and L. P. SANFORD (1982). The effects of bioturbation on the initiation of motion of intertidal sands. Journal of Marine Research 40: 659-677.

GRAY, J. S. (1966a). The response of Protodrilus symbioticus (Giard) (Archinelida) to light. Journal of Animal Ecology 35: 55-64.

GRAY, J. S. (1966b). Factors controlling the localizations of populations of Protodrilus symbioticus Giard. Journal of Animal Ecology 35: 435-442.

GRAY, J. S. (1966c). The attractive factor of intertidal sands to Protodrilus symbioticus. Journal of the Marine Biological Association of the United Kingdom 46: 627-645.

GRAY, J. S. (1967). Substrate selection by the Archiannelid Protodrilus hypoleucus Armenante. Journal of Experimental Marine Biology and Ecology 1: 47-54.

GRAY, J. S. (1974). Animal-sediment relationships. Oceanography and Marine Biology Annual Review (ed. H. Barnes), 12: 223-261.

GRAY, J. S. (1981). The ecology of marine sediments. Cambridge Studies in Modern Biology 2. Cambridge University Press.

GREEN, J. (1968). The biology of Estuarine animals. Sidgewick and Jackson: London.

GROVES, D. G. and L. M. HUNT (1980). Ocean World Encyclopedia. McGraw-Hill Book Company, New York.

GRUFFYDD, L. L. D., R. HUXLEY and D. J. CRISP (1984). The reduction in growth of Mytilus edulis in fluctuating salinity regimes measured using laser diffraction patterns and the exaggeration of this effect by using tap water as the diluting medium. Journal of the Marine Biological Association of the United Kingdom 64: 401-409.

GUILCHER, A. (1967). Origin of sediments in estuaries. pp. 149-157. In: Estuaries (Ed. G. H. Lauff). American Association for the Advancement of Science, Washington.

GUINASSO, N. L. and D. R. SCHINK (1975). Quantitative estimates of biological mixing rates in abyssal sediments. Journal of Geophysical Research 80: 3032-3043.

GUST, G. and J. T. HARRISON (1981). Biological pumps at the sediment-water interface. Mechanistic evaluation of the Alphaeid shrimp Alpheus mackayi and its irrigation patterm. Marine Biology 64: 71-78.

HARDY, A. C. and R. BAINBRIDGE (1951). Effect of pressure on the behaviour of decapod larvae (Crustacea). Nature 167: 354-355.

HARGER, J. R. E. (1970). The effect of wave impact on some aspects of the biology of sea mussels. Veliger 12: 401-414.

HARGER, J. R. E., and D. E. LANDENBERGER (1970). Comparisons among growth characteristics of two species of sea mussel, Mytilus edulis and Mytilus californianus. Veliger 13: 44-56.

HAYES, W. H. B. (1980). The role of natural and synthetic polymers in stabilising soil aggregates. In: Microbial adhesion to surfaces. University of Reading Seminar, 3rd-15th Sept., Chapter 15.

HECKER, B. (1982). Possible benthic fauna and slope instability relationships. pp. 335-347. In: Marine slides and other mass movements (Ed. S. Saxon and J. K. Nienwenhuis). Plenum.

HERLIN-HOUTEVILLE, P. and P. E. LUBET (1975). The sexuality of pelecypod molluscs. In: Inter-sexuality in the Animal Kingdom (Ed. R. Reinboth), pp. 179-187. Springer-Verlag: Berlin, New York.

HINES, M. E., W. H. OREM, W. B. LYONS and G. A. JONES (1982). Microbial activity and bioturbation induced oscillations in porewater chemistry of estuarine sediments in spring. Nature, London 299: 433-435.

HJULSTROM, F. (1935). Studies in the morphological activity of rivers as illustrated by the River Fyris. Bulletin of the Geological Institution of the University of Upsala 25: 221-528.

HJULSTROM, F. (1939). Transportation of detritus by moving water. pp. 5-31. In: Recent Marine Sediments (Ed. P. D. Trask). American Association of Petrolium Geologists, Tulsa, Oklahoma. Thomas Murby: London.

HOLLAND, A. F., R. G. ZINGMARK and J. M. DEAN (1974). Quantitative evidence concerning the stabilisation of sediments by marine benthic diatoms. Marine Biology 27: 191-196.

HOWARD, and R. W. FREY (1973). Characteristic physical and biogenic sedimentary structures in Georgia Estuaries. Bulletin of the American Association of Petrolium Geologists 57: 1169-1184.

HRS-BRENKO, M. (1977). The relationship of temperature and salinity to larval development in mussels (Mytilus galloprovincialis Lamarck). pp. 259-336. In: Twelfth European Symposium on Marine Biology (Eds. D. S. Mclusky and A. J. Berry), Pergamon Press, Oxford.

HUGHES, R. N., D. L. PEER and K. H. MANN (1972). The use of multivariate analysis to identify functional components of the benthos in St. Margarets Bay, Nova Scotia. Limnology and Oceanography 17: 111-121.

HULINGS, N. C. and J. S. GRAY (1976). Physical factors controlling the distribution of meiofauna on tidal and atidal beaches. Marine Biology 34: 77-83.

INMAN, D. L. (1952). Measures for describing the size distribution of sediments. Journal of Sedimentary Petrology 22: 125-145.

JANSSON, B. O. (1967). The significance of grain size and pore water content for the interstitial fauna of sandy beaches. Oikos 18: 311-322.

KANWISHER, J. W. (1955). Freezing in intertidal animals. Biological Bulletin of the Marine Laboratory, Woods Hole 109: 56-63.

KATZ, L. C. (1980). Effects of burrowing by the fiddler crab Uca pugnax (Smith). Estuarine and Coastal Marine Science 11: 233-237.

KERMACK, D. M. (1955). The anatomy and physiology of the gut of the polychaete Arenicola marina (L.). Proceedings of the Zoological Society, London 125: 374-381.

KIKUCHI, E. and Y. KURIHARA (1977). In vitro studies on the effects of tubificids on the biological, chemical and physical characteristics of submerged rice field soil and overlying water. Oikos 29: 348-356.

KINZIE, R. A. (1973). The zonation of West Indian gorgonians. Bulletin of Marine Science 23: 93-155.

KISELEVA, G. A. (1966). Some aspects of the ecology of the larvae of Black Sea Mussels. pp. 16-20. In: The Distribution of Benthic Fauna and the Biology of Benthic Animal Life in Southern Waters. Symposium published by the Ukranian Academy of Sciences, Kiev.

KISELEVA, G. A. (1967a). Influence of substratum on settlement and metamorphosis of larvae of benthic fauna. pp. 71-84. In: Benthic Biocenosis and the Biology of Benthonic Organisms from the Black Sea. Published by Ukranian Academy of Sciences, Kiev.

KISELEVA, G. A. (1967b). Settlement of Polydora ciliata (Johnston) larvae on different substrates. pp. 85-90. In: Benthic Biocenosis and the Biology of Benthonic Organisms from the Black Sea. Published by Ukranian Academy of Sciences, Kiev.

KNIGHT-JONES, E. W. (1953). Laboratory experiments on gregariousness during settling in Balanus balanoides and other barnacles. Journal of Experimental Biology 30: 584-598.

KNIGHT-JONES, E. W. and D. J. CRISP (1953). Gregariousness in barnacles in relation to the fouling of ships and to anti-fouling research. Nature, London 171: 1109-1110.

KNIGHT-JONES E. W. and E. MORGAN (1966). Responses of marine animals to changes in hydrostatic pressure. In: Oceanography and Marine Biology Annual Review (Ed. H. Barnes) 4: 267-299.

KOMAR, P. D. and K. E. CLEMENS (1986). The relationship between a grains settling velocity and threshold of motion under unidirectional currents. Journal of Sedimentary Petrology 56: 258-266.

KRAEUTER, J. N. (1976). Biodeposition by saltmarsh invertebrates. Marine Biology 35; 215-223.

KRUMBEIN, W. C. (1934). Size-frequency distribution of sediments. Journal of Sedimentary Petrology 4: 65-77.

KRUMBEIN, W. C. and F. J. PETTIJOHN (1938). Manual of Sedimentary Petrology. Appleton-Century-Crofts: New York.

KUENEN, D. J. (1942). On the distribution of mussels on the intertidal sand flats near Den Helder. Les Archives Neerlandaises de Zoologie 6: 8-158.

LANE, D. J. W., A. R. BEAUMONT and J. R. HUNTER (1985). Byssus drifting and the drifting threads of the young post-larval mussel Mytilus edulis. Marine Biology 84: 301-308.

LANE, P. J. W. and J. A. NOTT (1975). A study of the morphology, fine structure and histochemistry of the foot of the pediveliger of Mytilus edulis L. Journal of the Marine Biological Association of the United Kingdom 55: 477-495.

LARSEN, L. H., R. W. STERNBERG, N. C. SHI, M. A. H. MARSDEN and L. THOMAS (1981). Field investigations of the threshold of grain motion by ocean waves and currents. Marine Geology 42: 105-132.

LEE, H. and R. C. SWARTZ (1980). Biological processes affecting the distribution of pollutants in marine sediments. Part II. Biodeposition and bioturbation. pp. 556-606. In: Contaminants and Sediment Analysis, Chemistry, Biology (Volume 2). (Ed. R. A. Baker). Ann Arbo Publishers, Inc.: Michigan, U.S.A.

LETZCH, W. S. and R. W. FREY (1980). Erosion and salt-marsh tidal creek banks, Sapelo Island, Georgia. Senckenbegiana maritima 12: 201-222.

LEWIS, D. B. (1968). Some aspects of the ecology of Fabricia sabella (Ehr.) (Annelida, Polychaeta). Journal of the Linnaen Society (Zoology) 47: 515-526.

LEWIS, J. R. (1964). The ecology of rocky shores. English Universities Press: London.

LONGBOTTOM, M. R. (1970). The distribution of Arenicola marina (L) with particular reference to the effects of particle-size and organic matter of the sediments. Journal of Experimental Marine Biology and Ecology 5: 138-157.

LOOSANOF, V. L. (1942). Shell movements of the edible mussel Mytilus edulis (L.) in relation to temperature. Ecology 23: 231-234.

LOW, B. V. (1949). Strength of materials. Longmans, Green and Company: London, New York, Toronto.

LOWE, D. M., M. N. MOORE and B. L. BAYNE (1982). Aspects of gametogenesis in the marine mussel Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom 62: 133-145.

LUCKENBACH, M. W. (1986). Sediment stability around animal tubes: The roles of hydrodynamic processes and bioactivity. Limnology and Oceanography 31: 779-787.

MAAS GEESTERANUS, R. A. (1942). On the formation of banks by Mytilus edulis L. Les Archives Neerlandaises de Zoologie 6: 283-326.

MAHEO, R. (1970). Etude de la pose et de l'activite de secretion du byssus de Mytilus edulis L. Cahiers de Biologie Marine 11: 475-490.

MARSHALL, K. C. (1976). Interfaces of Microbial Ecology. Harvard University Press, Cambridge, Mass.

MARTELLA, T. (1974). Some factors influencing byssus thread production in Mytilus edulis (Molluscs: Bivalvia) Linnaeus 1758. Water, Air and Soil Pollution 3: 171-177.

MARTIN, J. P. and S. A. WAKSMAN (1940). Influence of micro-organisms on soil aggregation and erosion. Soil Science 50: 29-47.

MASSEY, B. S. (1979). Mechanics of fluids (4th Edition). Van Nostrand Reinhold Company, Inc.: Princeton and New Jersey.

McCAFFREY, R. J., A. C. MYRES, E. DAVEY, G. MORRISON, M. BENDER, N. LUEDTKE, D. CULLEN. P. FROELICH and G. KLINKHAMMER (1980). The relationship between pore water chemistry and benthic fluxes of nutrients and manganese in Narrangansett Bay, Rhode Island. Limnology and Oceanography 25: 31-44.

McCALL, P. L. and M. J. S. TEVESZ (1982). Animal-sediment relations: The biogenic alteration of sediments. Plenum Press, New York.

McDOUGAL, K. O. (1943). Sessile marine invertebrates of Beaufort, North Carolina. Ecological Monographs 13: 323-374.

McLUSKY, D. S. (1968). Some effects of salinity on the distribution and abundance of Corophium volutator in the Ythan Estuary. Journal of the Marine Biological Association of the United Kingdom 48: 443-454.

McLUSKY, D. S. (1981). The Estuarine Ecosystem. Blackie, Glasgow and London.

MEADOWS, P. S. (1964a). Experiments on substrate selection by Corophium species: films and bacteria on sand particles. Journal of Experimental Biology 41: 499-511.

MEADOWS, P. S. (1964b). Experiments on substrate selection by Corophium volutator (Pallas): depth selection and population density. Journal of Experimental Biology 41: 667-687.

MEADOWS, P. S. (1964c). Substrate selection by Corophium species: the particle size of substrates. Journal of Animal Ecology 33: 387-394.

MEADOWS, P. S. and J. I. CAMPBELL (1972a). Habitat selection and animal distribution in the sea: the evolution of a concept. Proceedings of the Royal Society of Edingurgh B 73: 145-157.

MEADOWS, P. S. and J. I. CAMPBELL (1972b). Habitat selection by aquatic invertebrates. pp. 271-382. In: Advances in Marine Biology (Ed. Sir F. S. Russel and Sir C. M. Yonge), Volume 10. Academic Press.

MEADOWS, P. S. and J. I. CAMPBELL (1978). An Introduction to Marine Science. Blackie, Glasgow and London.

MEADOWS, P. S. and A. TUFAIL (1986). Bioturbation, microbial activity and sediment properties in an estuarine ecosystem. Proceedings of the Royal Society of Edinburgh 90: 129-142.

MERCER, E. H. (1952). Observations on the molecular structure of byssus fibres. Australian Journal of Marine and Freshwater Research 13: 199-204.

MILLER, M. C., I. N. McCAVE and P. D. KOMAR (1977). Theshold of sediment motion under unidirectional currents. Sedimentology 24: 507-527.

MYERS, A. C. (1972). Tube-worm-sediment relationships of Dioptera cuprea (Polychaeta: Onuphidae). Marine Biology 3: 27-78.

NEILSON, P. (1983). Entrainment and distribution of different sand sizes under water waves. Journal of Sedimentary Petrology 53: 423-428.

NELSON, C. H. and K. A. JOHNSON (1987). Whales as tillers of the sea-floor. Scientific American 256: 74-82.

NELSON, T. C. (1924). The attachment of Oyster larvae. Biological Bulletin of the Marine Biology Laboratory, Woods Hole 46: 143-151.

NEUMAN, A. C., C. P. GEBELEIN and T. P. SCOFFIN (1970). The composition, structure and erodability of subtidal mats, Abaco, Bahamas. Journal of Sedimentary Petrology 40: 274-297.

NICHOLS, F. H. (1974). Sediment turnover by a deposit-feeding polychaete. Limnology and Oceanography 19: 945-950.

NOWELL, A. R. M., P. A. JUMARS and J. E. ECKMAN (1981). Effects of biological activity on the entrainment of marine sediments. Marine Geology 42: 133-153.

ODUM, E. P. (1959). Fundamentals of Ecology. W. B. Saunders Co., Philadelphia and London.

OSMAN, R. W. (1977). The establishment and development of a marine epifaunal community. Ecological Monographs 47: 37-63.

OTT, J. A., B. FUCHS, R. FUCHS and A. MALASEK (1976). Observations on the biology of Callianasa stebbengi Borrodaille and Upogebia litoralis Risso and their effect upon the sediment. Senckenbergiana maritima 8: 61-79.

PAMATMAT, M. M. (1968). Ecology and metabolism of a benthic community on an intertidal sandflat. Internationale Revue der gesamten Hydrobiologie 53: 211-298

PARTHENAIDES, E. (1965). Erosion and deposition of cohesive soils. Proceedings of the American Society of Civil Engineers 91: 105-139.

PENAS, E. and G. GONZALEZ (1983). Relationships between benthic infauna and environmental factors in three beaches of the Rio de Arosa embayment (Spain) using Canonical Correlation analysis. Journal Experimental Marine Biology and Ecology 68: 245-256.

PIETERS, J. H., J. H. KLUYTMANS, W. ZURBURG and D. I. ZANDEE (1978). The influence of seasonal changes on energy metabolism in Mytilus edulis (L.). I. Growth rate and biochemical composition in relation to environmental parameters and spawning. pp. 285-292. In: Cyclic phenomena in marine plants and animals (ed. E. Naylor and R. G. Hartnoll), pp. 285-292. Pergamon Press, Oxford.

PIKKARAINEN, J., J. RANTANEN, M. LAMPIANO, K. KARI and E. KULONEN (1968). On collagens of invertebrates with special reference to Mytilus edulis. European Journal of Biochemistry 4: 555-560.

PIELOU, E. C. (1972). An Introduction to Mathematical Ecology. John Wiley: New York, London.

POSTMA, H. (1967). Sediment transport and sedimentation in the estuarine environment. pp. 158-179. In: Estuaries (ed. G. H. Luaff). American Association for the Advancement of Science, Washington.

POWELL, E. N. (1977). Particle size selection and sediment reworking in a funnel feeder Leptosynapta tenuis (Holothuroides, Synaptidae) Internationale Revue der gesamten Hydrobiologie 62: 385-408.

PRICE, H. A. (1980). Seasonal variation in the strength of of byssal attachment of the common mussel Mytilus edulis L. Journal of the Marine Biological Association of the United Kingdom 60: 1035-1037.

PRICE, H. A. (1981). Byssus thread strength in the mussel, Mytilus edulis. Jounal of Zoology, London 194: 245-255.

PRICE, H. A. (1982). An analysis of factors determining seasonal variation in the byssal attachment strength of Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom 62: 147-155.

PRITCHARD, D. W. (1967). Observations of circulation in coastal plain estuaries. pp. 37-44. In: Estuaries (Ed. G. H. Lauff). American Association for the Advancement of Science, Washington.

PUJOL, J. P. (1967). Formation of the byssus in the common mussel (Mytilus edulis L.). Nature, London 214: 204-205.

PUJOL, J. P., M. ROLLAND, S. LASRY and S. VINET (1970). Comparative study of the amino acid composition of the byssus in some common bivalve molluscs. Comparative Biochemistry and Physiology 34: 193-201.

PYEFINCH, K. A. (1948). Notes on the biology of Cirripedes. Journal of the Marine Biological Association of the United Kingdom 27: 464-503.

RAVINDRANATH, M. H. and K. RAMALINGAN (1972). Histochemical identification of dopa, dopamine and catechol in phenol gland and mode of tanning of byssus threads of Mytilus edulis. Acta Histochemica 42: 87-94.

RANDALL, J. T., R. D. B. FRASER, S. JACKSON, A. U. W. MARTIN and A. C. T. NORTH (1952). Aspects of collagen structure. Nature, London 169: 1029-1033.

REID, D. M. (1929). On some factors limiting the habitat of Arenicola marina. Journal of the Marine Biological Association of the United Kingdom 16: 109-116.

REDDY, N. A. and N. R. MENON (1979). Effects of ammonia and ammomium on tolerance and byssogenesis in Perna viridis. Marine Ecology Progress Series 1: 315-321.

REES, C. B. (1954). Continuous plankton records: the distribution of lamellibranch larvae in the North Sea, 1950-1951. Hull Bulletins of Marine Ecology 4: 21-46.

REINECK, H.-E. (1977). Natural indicators of energy level in Recent sediments: the application of ichnology to a coastal engineering problem. pp. 265-272. In: Trace Fossils 2 (Ed. T. P. Crimes and J. C. Harper). pp.265-272. Seel House Press, Liverpool.

REINECK, H.-E., and I. B. SINGH (1980). Depositional Sedimentary Environments. Springer-Verlag, Berlin.

REISH, D. J. and J. L. AYERS Jnr. (1968). Studies on the Mytilus edulis community in Alamitos Bay, California. III. The effects of reduced dissolved oxygen and chlorinity concentrations on survival and byssus thread formation. Veliger 10: 384-388.

RHOADS, D. C. (1963). Rates of reworking by Yoldia limulata in Buzzards Bay, Massachusetts and Long Island. Journal of Sedimentary Petrology 33: 723-727.

RHOADS, D. C. (1967). Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbour and Buzzards bay, Massachusetts. Journal of Geology 75: 461-476.

RHOADS, D. C. (1970). Mass properties, stability, and ecology of marine muds related to burrowing activity. pp. 391-406. In: Trace Fossils (Ed T. P. Crimes and J. C. Harper). Seel House Press, Liverpool.

RHOADS, D. C. (1973). The influence of deposit feeding benthos on water turbidity and nutrient recycling. American Journal of Science 273: 1-22.

RHOADS, D. C. (1974). Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology Annual Review (Ed. H. Barnes) 12: 263-300.

RHOADS, D. C. and D. J. STANLEY (1965). Biogenic graded bedding. Journal of Sedimentary Petrology 35: 956-963.

RHOADS, D. C., J. Y. YINGST and W. ULLMAN (1978). Seafloor stability in Central Long Island. Part 1. Temporal changes in erodability of fine grained sediment. In: Estuarine Interactions (Ed. M. L. Wiley).

RHOADS, D. C. and D. K. YOUNG (1970). The influence of deposit feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28: 150-178.

RHOADS, D. C. and D. K. YOUNG (1971). Animal-sediment relations in Cape Cod, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Marine Biology 11: 255-261.

RICE, A. L. (1964). Observations on the effects of changes of hydrostatic pressure on the behaviour of some marine animals. Journal of the Marine Biological Association of the United Kingdom 44: 163-175.

ROBERTS, D. (1975). The effect of pesticides on byssus formation in the common mussel Mytilus edulis. Environmental Pollution 8: 241-245.

ROWE, G. T. (1974). The effects of the benthic fauna on the physical properties of deep sea sediments. pp. 381-400. In: Deep Sea Sediments: Physical and Mechanical Properties (ed. A. L. Inderbitzen). Plenum.

RUDDAL, K. M. (1955). Distribution of collagen and chitin. Symposium for the Society of Experimental Biology 9: 49-70. Cambridge University Press.

RYLAND, J. S. (1962). The effect of temperature on the photic responces of polyzoan larvae. Sarsia 6: 41-48.

SAMEOTO, D. D. (1969). Physiological tolerances and behaviour responces of five species of Haustoriidae (Amphipoda: Crustacea) to five environmental factors. Journal of the Fisheries Research Board of Canada 26: 2283-2298.

SCHEER, B. (1945). The development of marine fouling communities. Biological Bulletin of the Marine Laboratory, Woods Hole 89: 103-121.

SCHELTEMA, R. S. (1956). The effect of substrate on the length of planktonic existence in Nassarius obsoletus. Biological Bulletin of the Marine Biology Laboratory, Woods Hole 111: 312.

SCHELTMA, R. S. (1961). Metamorphosis of the veliger larvae of Nassarius obsoletus (Gastropoda) in response to bottom sediment. Biological Bulletin of the Marine Biological Laboratory, Woods Hole 121: 354-365.

SCHWEINITZ, E. H. de and R. A. LUTZ (1976). Larval development of the northern Horse Mussel, Modiolus modiolus (L.), including a comparison with the larvae of Mytilus edulis L. as an aid in plankton identification. Biological Bulletin of the Marine Laboratory, Woods Hole 150: 348-360.

SCOFFIN, T. P. (1970). The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. Journal of Sedimentary Petrology 40: 249-273.

SEED, R. (1968). Factors influencing shell shape in Mytilus edulis L. Journal of the Marine Biological Associaton of the United Kingdom 48: 561-584.

SEED, R. (1969). The ecology of Mytilus edulis L. (Lamellibranchiata) on exposed rocky shores. I. Breeding and settlement. Oecologia 3: 277-316.

SEED, R. (1976). Ecology. pp. 13-62. In: Marine mussels: Their Ecology and Physiology (Ed. B. L. Bayne). Cambridge University Press.

SEED, R. and R. BROWN (1975). The influence of reproductive cycle, growth and mortality on population structure in Modiolus modiolus (L.), Cerastoderma edule (L.) and Mytilus edulis L. (Mollusca: Bivalvia). pp. 257-274. In: Proceedings of the Ninth European Marine Biology Symposium, Oban, Scotland, 1974 (ed. H. Barnes). Aberdeen University Press.

SEED, R. and R. BROWN (1977). A comparison of the reproductive cycles of Modiolus modiolus (L.), Cerastoderma (=Cardium) edule (L.) and Mytilus edulis L. in Strangford Lough, Northern Ireland. Oecologia 30: 173-188.

SEGERSTRALE, S. G. (1957). Baltic Sea. pp. 751-800. In: Treatise on Marine Ecology and Paleontology (Ed. J. W. Hedgepath), Volume I, Ecology. National Research Council, New York.

SHEILDS, A. (1936). Application of similarity principles and turbulence research to bed-load movement. Awendung der Ahnichkeits meschanik und der Turbulentzforschung auf die Geschiebebewegung. In: W. P. Ott and J. C. van Uchelen (Translators); Californian Institute of Technology, W. M. Keck Laboratory of Hydraulics and Water Resources, Report No. 167.

SHUMWAY, S. E. and J. DAVENPORT (1977). Some aspects of the physiology of Arenicola marina (polychaete) exposed to fluctuatong salinities. Journal of the Marine Biological Association of the United Kingdom 57: 907-924.

SIGURDSSON, J. B., W. TITMAN and P. A. DAVIS (1976). The dispersal of young post-larval bivalve molluscs by byssus threads. Nature, London 262: 386-387.

SILEN, L. (1954). Developmental Biology of Phoronida of the Gullmar Fiord area (west coast of Sweden). Acta Zoologica 35: 215-258.

SMEATHERS J. E. and J. F. V. VINCENT (1979). Mechanical properties of mussel byssus threads. Journal of Molluscan Studies 45: 219-230.

SMITH, F. G. W. (1964). Effect of water currents upon the attachment and growth of barnacles. Biological Bulletin of Woods Hole 90: 51-70.

SMYTH, J. C. (1974). Flora and fauna of the Clyde Estuary and Firth. In: Natural Environment Research Council Publications, Series C, 11: 40-42.

SMYTH, J. D. (1954). A technique for the histochemical demonstration of polyphenoloxidase and its application to egg-shell formation in helminthes and byssus formation in Mytilus. Quarterly Journal of Miroscope Science 95: 139-152.

SNEDECOR, G. W. and W. G. COCHRAN (1980). Statistical Methods (7th Edition). The Iowa State University Press, Iowa.

SOKAL, R. R. and F. J. ROHLF (1981). Biometry. W. H. Freeman and Company, San Francisco.

SOUTHWARD, J. B. (1974). Erodability of fine abyssal sediment. pp. 367-379. In: Deep-sea Sediments: Physical and Mechanical Properties (Ed. L. Inderbitzen). Plenum Press: New York.

SPRUNG, M. (1984). Physiological energetics of mussel larvae (Mytilus edulis). I. Shell growth and biomass. Marine Biology Progress Series 17: 283-293.

STERN, S. and Y. ACHITUV (1978). Effects of temperature and salinity on metabolism and byssal formation of Brachidontes variabilis. Comparative Biochemistry and Physiology 59A: 101-105

STRAATEN, L. M. J. V. van (1952). Biogenic structures and the formation of shell beds in the Dutch Wadden Sea. Proceedings K nederlandaise Akademie Wetenschappen (B) 55: 500-516.

STRAATEN, L. M. J. V. van (1954). Composition and structure of Recent marine sediments in the Netherlands. Leidsche Geologische Menedelingen 19: 1-118.

SUMMERS, R. W. (1980). The diet and feeding behaviour of the Flounder Platichthys flesus (L.) in the Ythan Estuary, Scotland. Estuarine and Coastal Marine Science 11: 217-232.

SUNDBORG, F. A. (1956). The River Klaraven, a study on fluvial processes. Geographica Annaler 38: 127-316.

SUTHERLAND, I. W. (1980). Polysaccharides in the adhesion of marine and freshwater bacteria. pp. 329-338. In: Microbial adhesion to surfaces (Ed. R. C. W. Berkeley, J. M. Lynch, J. Melling, P. Rutter and B. Vincent). Ellis Horwood, London.

SWINBANKS, D. D. (1981). Sediment reworking and biogenic formation of clay laminae by Abarenicola pacifica. Journal of Sedimentary Petrology 51: 1137-1145.

TAGHON, G., A. R. M. NOWELL and P. A. JUMARS (1984). Transport and breakdown of faecal pellets: Biological and sedimentological consequences. Limnology and Oceanography 29: 64-72.

TAMARIN, A. (1975). An ultrastructural study of the byssus stem formation in Mytilus californianus. Journal of Morphology 145: 151-178.

TAMARIN, A. and P. J. KELLER (1972). An ultrastructural study of the byssus thread forming system in Mytilus. Journal of Ultrastructure Research 40: 401-416.

TAMARIN, A., P. LEWIS and J. ASKEY (1974). Specialised cilia of the byssus attachment plaque forming region in Mytilus californianus. Journal of Morphology 142: 321-328.

TAMARIN, A., P. LEWIS and J. ASKEY (1976). The structure and formation of the byssus attachment plaque in Mytilus. Journal of Morphology 149: 199-222.

TEBBLE, N. (1976). British Bivalve Seashells. Royal Scottish Museum Publication, Her Majesty's Stationary Office, Edinburgh.

TEVEZ, M. J. S., F. M. SOSTER and P. L. McCALL (1980). The effect of size selective feeding by oligochaetes on the physical properties of river sediments. Journal of Sedimentary Petrology 50: 561-568.

THOMPSON, R. J. (1984). The reproductive cycle and physiological ecology of the mussel Mytilus edulis in a subarctic, non-estuarine environment. Marine Biology 79: 277-288.

THORSON, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25: 1-45.

THORSON, G. (1964). Light as an ecological factor in the dispersal of the larvae of marine bottom invertebrates. Ophelia 1: 167-208.

TRASK, P. D. and J. W. ROLSTON (1950). Relation of strength of sediments to water content and grain size. Science N.Y. 111: 666-667.

TSUCHIYA, M. and M. NISHIRIRA (1985). Islands of Mytilus as a habitat for small intertidal animals: effect of island size on community structure. Marine Ecology Progress Series 25: 71-81.

TWITCHELL, D. C., C. B. GRIMES, R. S. JONES and K. W. ABLE (1985). The role of erosion by fish in shaping in shaping topography around Hudson Submarine Canyon. Journal of Sedimentary Petrology 55: 712-719.

VAN WINKLE JNR., W. (1970). Effect of environmental factors on byssal thread formation. Marine Biology 7: 143-148.

VERWEY, J. (1952). On the ecology and distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply. Les Archives Neerlandaises de Zoologie 10: 171-239.

VITELLARO-ZUCCARELLO, L. (1980). The collagen gland of Mytilus galloprovincialis: An ultrastructural study and cytochemical study of secretory granules. Journal of Ultrastructure Research 73: 135-147

VOGEL, S. (1981). Life in Moving Fluids. Willard Grant Press, Boston.

WAINWRIGHT, S. A., W. D. BRIGGS, J. D. CURREY and J. M. GOSLINE (1976). Mechanical design in Organisms. Edward Arnold (Publishers) Ltd., London.

WAITE, H. G. (1983). Adhesion in byssaly attached bivalves. Biological Reviews 58: 209-231.

WAITE, H. G. and M. L. TANZER (1981). Polyphenolic substances of Mytilus edulis: Novel adhesive containing L-dopa and hydroxyproline. Science 212: 1038-1040.

WALKER, G. (1981). Adhesion of barnacles. Journal of Adhesion 12: 51-58.

WARD, L. G., W. M. KEMP and W. R. BOYNTON (1984). The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. Marine Geology 59: 85-103.

WARME, J. (1967). Graded bedding in the Recent sediments of Mugu Lagoon, California. Journal of Sedimentary Petrology 37: 540-547.

WASLENCHUK, D. G., E. A. MATSON, R. N. ZAJAK, F. C. DOBBS and J. M. TRAMONTANO (1983). Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudan sediments. Marine Biology 72: 219-225.

WEBB, J. E. (1969). Biologically significant properties of submerged marine sands. Proceedings of the Royal Society, London (B) 174: 355-402.

WEISER, W. (1959). Factors influencing the choice of substratum in Cumella vulgaris Hart (Crustacea, Cumacea). Limnology and Oceanography 1: 274-285.

WENTWORTH, C. (1922). A scale of grade and class terms for clastic sediments. Journal of Geology 30: 377-392.

WHITE, K. M. (1937). Mytilus. Liverpool Marine Biological Committee Memoirs 31.

WIDDOWS, J. and B. L. BAYNE (1971). Temperature acclimation of Mytilus edulis with reference to its energy budget. Journal of the Marine Biological Association of the United Kingdom 51: 827-843.

WILSON. D. P. (1932). On the mitraria larva of Owenia fusiformis Delle Chiaje. Philisophical Transactions of the Royal Society, London (B) 221: 231-334.

WILSON, D. P. (1948). The relation of the substratum to the metamorphosis of Ophelia larvae. Journal of the Marine Biological Association of the United Kingdom 27: 723-760.

WILSON, D. P. (1951). Larval metamorphosis and the substratum. Annee biologie 27: 491-501.

WILSON, D. P. (1952). The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of Ophelia bicornis Savingy. Annales of the Institute of Oceanography 27: 49-156.

WILSON, D. P. (1953a). The settlement of Ophelia bicornis Savingy larvae. Journal of the Marine Biological Association of the United Kingdom 31: 413-438.

WILSON, D. P. (1953b). The settlement of Ophelia bicornis (Savingy) larvae. The 1952 experiments. Journal of the Marine Biological Association of the United Kingdom 32: 209-233.

WILSON, D. P. (1954). The attractive factor in the settlement of Ophelia bicornis Savingy. Journal of the Marine Biological Association of the United Kingdom 33: 361-380.

WILSON, D. P. (1955). The role micro-organisms in the settlement of Ophelia bicornis Savingy. Journal of the Marine Biological Association of the United Kingdom 34: 531-543.

WILSON, D. P. (1968). The settlement behaviour of Sabella alveolata (L.). Journal of the Marine Biological Association of the United Kingdom 48: 387-435.

WILSON, D. P. (1977). Modiolus modiolus in small mid-tidal pools at Penrhyn Bay. Estuarine and Coastal Marine Science 5: 215-22.

WINSTON, J. E. and F. E. ANDERSON (1971). Bioturbation of sediments in a Northern temperate estuary. Marine Geology 10: 39-49.

WISELY, B. (1960). Observations of the settling behaviour of larvae of the tubeworm Spirorbis borealis Duaden (Polychaeta). Australian Journal of Marine and Freshwater Research 2: 55-72.

YALIN, M. S. (1972). Mechanics of Sediment Transport. Pergamon Press: New York.

YINGST, J. Y. and R. C. ALLER (1982). Biological activity and associated sedimentary structures in HEBBLE area deposits, western North Atlantic. Marine Geology 48: M7-M15.

YONGE, C. M. (1962). On the primitive significance of the byssus in the bivalvia and its effect in evolution. Journal of the Marine Biological Association of the United Kingdom 42: 113-125.

YONGE, C. M. (1979). Cementation in bivalves. pp. 83-106. In: Pathways in Malacology (Ed. S. van der Spoel, A. C. van Bruggen and J. Lever). W. Junk, The Hague.

YOUNG, D. A. and D. C. RHOADS (1971). Animal-sediment relations in Cape Cod Bay, Massachussetts. I. A transect study. Marine Biology 11: 242-254.

YOUNG, G. A. (1983a). The effect of sediment type upon the position and depth at which byssal attachment occurs in Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom 63: 641-651.

YOUNG, G. A. (1983b). Response to, and selection between firm substrata by Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom 63: 653-659.

YOUNG, G. A. (1985). Byssus thread formation by the mussel Mytilus edulis: effects of environmental factors. Marine Ecology Progress Series 24: 261-271.

YOUNG, G. A. and D. J. CRISP (1982). Marine animals and adhesion. pp. 19-39. In: Adhesion, volume 6. (Ed. W. K. Allen). Applied Science Publishers, Barking, Essex.

YOUNG. R. A. and J. B. SOUTHWARD (1978). Erosion of fine-grained marine sediments: Sea floor and laboratory experiments. Bulletin of the Geological Society of America 89: 663-672.

ZOBELL, C. E. and E. C. ALLEN (1935). The significance of marine bacteria in the fouling of submerged surfaces. Journal of Bacteriology 29: 239-251.

ZURBURG, W, J. H. CLUYMANS, H. PIETERS and D. I. ZANDEE (1978). The influence of seasonal changes on energy metabolism in Mytilus edulis (L.). III Organ specificity. pp. 293-300. In: Cyclic Phenomena in Marine Plants and Animals. Proceedings of the 13th European Marine Biology Symposium, Isle of Man, 1978 (Ed. E. Naylor and R. G. Hartnoll), pp. 293-300. Pergamon Press.