THE UNIVERSITY OF SOUTHAMPTON

The Ecology of Deep-Sea Holothurians

by

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

OCEANOGRAPHY

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THE ECOLOGY OF DEEP-SEA HOLOTHURIANS.

by David Stewart Martin Billett

The biology of 45 holothurian species, collected between 150 and 4830m in the Porcupine Seabight and the Porcupine Abyssal Plain in the northeast Atlantic, is described. Epibenthic sledge and otter trawl hauls have been used to calculate the abundance and biomass of each species, and spatial distributions have been examined using transect photography. The population size distributions and egg sizes of many species are related to their reproductive biology and life-history strategies.

No relationship was found between holothurian biomass and depth. Holothurians may account for up to 90% of the total invertebrate megafaunal ash-free dry weight biomass, and the greatest biomass was recorded at a depth of 2000m.

Bathymetric zonation is considered in detail using data on the abundance of each species in 100m depth bands. Some species on the upper slope occur in abundance only within a narrow depth range of 100 to 200m. Narrow zonation on the slope appears to be related to hydrographic features. Many species have an upper bathymetric limit of 1400 to 1500m which coincides with the bottom of the permanent thermocline and a change in water mass. This may act as a physiological barrier or a limit for larval dispersal. Abyssal species are more common on the abyssal plain than close to the continental slope.

Studies using chlorophyll pigments as markers of detrital food show that holothurians feed indiscriminately on freshly deposited detritus, but that selectivity occurs once the detritus is incorporated into the sediment.

One species, Kolga hyalina, forms dense aggregations that move as a herd across the seabed. The spatial pattern changes temporally and appears to be related to the seasonal deposition of detritus.

The taxonomic features of several species are discussed. Ontogenetic changes in characteristics of ypsilothuriid holothurians are examined in detail and a new species of apodid holothurian is described.

Preface

The approach of this thesis differs from that of many other dissertations since it was not initiated with a specific problem in mind. Rather, it was started when it was unclear how future investigations would progress and hence what the content of the final thesis would be. This uncertainty was unavoidable since the work was carried out as part of an on-going deep-sea benthic biology programme which changed its sampling priorities with time, and which was subject to the vagaries of the weather, cruise planning and gear reliability. It is necessary, therefore, to describe the aims of the deep-sea benthic biology programme at the Institute of Oceanographic Sciences (IOS), and to recount how that programme has progressed so that this thesis may be set in context.

The data presented have been amassed between November 1977 and December 1986 from samples taken by IOS in the Porcupine Seabight (PSB) and Porcupine Abyssal Plain (PAP) off the southwest coast of Ireland (Fig. 1). More than 200 samples have been taken over a wide bathymetric range (400 to 4800m) and from 11 months of the calendar year. This has provided a unique collection of deep-sea fauna from which seasonal and bathymetric changes in deep-sea populations can be examined.

The PSB was chosen as a study area because 1) the site was close to the British Isles, 2) the area provided soft-bottom habitats over a wide bathymetric range within a small geographic area, 3) the area had a congenial terrain with gentle slopes suitable for sampling with towed gear,

4) the area was situated in temperate latitudes where any seasonal fluctuations in surface water productivity might be manifested at abyssal depths, and 5) the soft-bottom communities could be compared with those sampled previously by IOS off northwest Africa.

A principal aim of the IOS benthic biology programme has been to quantify the abundance and biomass of benthic invertebrate megafauna using transect photography and an acoustically monitored epibenthic sledge. Good biomass data are essential if the energetics of the deep-sea ecosystem are to be understood but few relevant data are available. Little is also known about the structure of deep-sea communities or of the life-histories and behaviour of deep-sea organisms. These subjects have now been investigated by IOS using a combination of techniques including transect and time-lapse photography, mid-water trawls, benthic trawls, epibenthic sledges, box corers, multiple corers, remote traps, and, more recently, submersibles. The other aims of the benthic biology programme,therefore, have been to describe the bathymetric zonation, spatial distribution, behaviour, population structure, reproduction and feeding of many organisms ranging from meiofaunal protozoans, to macrofaunal crustaceans, to megafaunal echinoderms and fish. Ultimately an understanding of the structure of deep-sea communities, trophic relationships, carbon flux etc., will be achieved.

The many facets of the work carried out by IOS has provided a stimulating and varied approach to deep-sea biology. However, it has also had the disadvantage of providing many competing demands on sampling time, which together with poor weather and gear failures, have conspired to make some data sets less than perfect. Despite these problems the sampling intensity in the Porcupine Seabight has allowed one of the dominant deep-sea groups, the holothurians, to be studied in considerable detail. This thesis, therefore, sets out to fulfill the declared aims of the benthic biology programme for this taxon.

The first section is in part taxonomic. Work on any deep-sea group of animals necessitates the development of a taxonomic expertise since there are seldom standard taxonomic works for easy reference. Taxonomic problems that have arisen during the course of this study are identified and, where possible, dealt with. In some cases there is not enough material for a detailed study. I am particularly indebted to Dr. Bent Hansen of the Zoological Museum, Copenhagen under whose guidance my appreciation of the finer points of holothurian taxonomy has been developed. His tour de force, a monograph on the order Elasipodida (Hansen, 1975), has been a cornerstone of this thesis, and he has kindly advised me on the taxonomy of the other orders. In the instances where I have drawn upon his wealth of knowledge that is to date unpublished, I have included references to a personal communication from him.

The taxonomic expertise developed by working on the material from the Porcupine Seabight has been turned to use also in describing the holothurian fauna sampled in the Rockall Trough and adjacent areas by Dr. John Gage of the Scottish Marine Biological Association. Some of these data are included in this thesis for species not sampled by IOS in order to provide a complete picture of the holothurian fauna from around the coasts of the British Isles. I am therefore particularly indebted to Dr. Gage for the opportunity to study this material and for the encouragement he has given me during this work.

In the second part of this thesis, dealing with the ecology of deep-sea holothurians, I owe particular gratitude to a number of other researchers who have provided essential information and assistance, in particular, Dr. Paul Tyler of the Department Biological Sciences, University College, Swansea. The discussions of the population structure of many species and their relation to reproductive strategies contained in this thesis has been made in the light of his work on their gametogenic biology.

The determination of the biomass of many deep-sea organisms is a laborious and time-consuming task and could not be achieved without acting in concert with other researchers. I am grateful, therefore, to my colleagues at IOS, particularly to Dr. Richard Lampitt. Many samples were taken on cruises on which I was not present and were kindly preserved by colleagues at IOS and SMBA. In this respect I am especially indebted to Dr. Michael Thurston. Dr. John Gordon (SMBA) and Mr. Nigel Merrett (IOS) and their co-workers are especially worthy of praise for attending to the invertebrates during cruises when their time was more than taken up with processing the fish catches. My gratitude is extended also to the unsung heroes of deep-sea research who maintain the sampling gear and who iron out the ever-present problems which occur while sampling at sea, as well as to the officers and crew of "RRS Discovery" and "RRS Challenger".

Some of the work contained in this thesis has been published already in collaboration with other researchers (see Appendix 2). Where possible these papers are cited in the thesis where it is necessary to refer to the contributions by my co-workers. In this respect I would like to thank Ms. Carole Llewellyn (Institute for Marine Environmental Research) particularly for all her hard work in separating, identifying and quantifying the chlorophyll pigments in sediments and holothurian gut contents.

Thanks are also due to Mrs. Penny Jackson and Mrs. Pam Talbot for their invaluable assistance in times of great need, to Mr. Neil Kenyon and Mr. Peter Hunter for providing a new bathymetric chart of the Porcupine Seabight, and to Mr. Arnold Madgwick and Mr. Michael Conquer for their photographic expertise.

None of this would have been possible without the encouragement of Dr. Tony Rice and Dr. Martin Sheader. Their advice during the progress of this thesis has been invaluable, and I am particularly grateful for their comments on the thesis and the speed with which they reviewed the manuscript.

Finally, Sue, Jennifer and Emily deserve special praise for their support, and for bearing the fate of being a "Ph.D. widow" and "Ph.D. orphans" with such good humour during the last few months.

1. Introduction

The deep sea is often regarded as the kingdom of the holothurian. These creatures feature prominently in photographic collections of abyssal biota (Heezen and Hollister, 1971; Lemche, Hansen, Madsen, Tendal and Wolff, 1976; Rice, Aldred, Billett and Thurston, 1979; Rice, Aldred, Darlington and Wild, 1982; Ohta, 1983) and in many areas they dominate the invertebrate megafauna both numerically (Rice *et al*., 1982; Sibuet, Monniot, Desbruyeres, Dinet, Khripounoff, Rowe and Segonzac, 1984; Sibuet, 1985) and in terms of biomass (Zenkevitch and Birstein, 1960; Ohta, 1983; Sibuet *et al*., 1984; Rutgers van der Loeff and Lavaleye, 1986). Most holothurians are mobile, epibenthic animals that wander over the sea floor, seemingly aimlessly, feeding on the uppermost few millimetres of the sediment. Many photographs of the seabed show their characteristic tracks and faecal remains (Heezen and Hollister, 1971; Young, Jahn, Richardson and Lohanick, 1985; Mauviel and Sibuet, 1985) testifying to the important role that holothurians play in modifying the sediment and in structuring the communities that live within it. Few deep-sea soft-bottom habitats are free from the attentions of these rovers.

Not all holothurians live on the sediment surface. Some are infaunal and are important bioturbators of the top 10 cm or so of sediment, in some cases creating large cone-shaped mounds. A few species have developed the ability to swim and live in the water column just above the seabed.

They descend to the seabed to feed and may be important in the resuspension of sediment and in the transport of organic matter through the water column. Most deep-sea holothurians produce a pelagic lecithotrophic larval stage but in some cases development occurs directly into a juvenile in the pelagic environment without a larval stage. Pelagic development has allowed many species to have wide geographic distributions.

It is clear that holothurians are an important faunal group in the deep sea, yet little is known of their ethology and ecology. The following sections review our current knowledge of deep-sea holothurians ending with a summary that seeks to explain the success of this taxon in the deep sea. The summary also describes how information contained in the thesis fills in some of the gaps in our knowledge and highlights aspects of holothurian ecology that require further work.

1.1 Feeding.

Although the vast majority of deep-sea holothurians are deposit feeders, a few species, by virtue of their tentacle structure, are thought to feed on suspended particles. Suspension-feeding holothurians have dendritic (arborescent) or pelto-dendritic (arborescent ends on short branches arising from a short central stalk) tentacles (Hyman, 1955; Massin, 1982) with which they capture particles that are immobile or at least only partly mobile (Massin, 1982). In shallow water, benthic suspension-feeding holothurians capture phytoplankton, zooplankton (including Protozoa), and suspended organic matter (see Massin, 1982 for references), but in deep water these holothurians are likely to rely mainly on suspended detrital material. Suspension-feeding holothurians have been found in areas characterized by strong currents, such as the western flank of the Rockall Trough (Gage, Billett, Jensen and Tyler, 1985a).

Pelagic holothurians may also feed on suspended particles. The pelto-dendritic tentacles of aspidochirotid species indicate that they may be able to capture particles in midwater (Hansen and Madsen, 1956; Hansen, 1978). However, analyses of pelagic aspidochirotid and elasipodid holothurian stomach contents show that only specimens caught close to the seabed have material in their guts and that this material comes from the sediment surface (Billett, Hansen and Huggett, 1985). In addition, observations made from submersibles and with cameras indicate that these holothurians feed preferentially at the sediment surface (Pawson, 1982a; Ohta, 1985; Pawson and Foell, 1986; Billett, 1986). Massin (1982) considered that the juveniles of benthic species which occur pelagically (Grieg, 1921; Belyaev and Vinogradov, 1969; Hansen, 1975; Billett *et al*., 1985) could be suspension feeders, but there is no evidence that these juveniles feed while they are in the plankton.

Deep-sea holothurians are predominantly deposit feeders. Most are epifaunal rake-feeders which sweep the sediment surface, but some species are infaunal and feed either on superficial sediment by funnel-feeding or on deeper sediment by conveyor-belt feeding (Massin, 1982). In shallow water, molpadiids like *Molpadia oolitica* are considered to be conveyor-belt feeders (Massin, 1982) and are orientated vertically or obliquely with their mouth buried in the sediment (Rhoads and Young, 1971). *M. oolitica* forms cone-shaped mounds made from its faeces and similar mounds found in the deep sea are believed to be formed by *Molpadia blakei* (Young *et al*., 1985), a species common at abyssal depths in the North Atlantic. This suggests that shallow water and deep-sea molpadiids feed in a similar way. Khripounoff and Sibuet (1980) analysed the stomach contents of *M. blakei* and found that the granulometry of the gut samples was similar to that of the surrounding sediment indicating that deep-sea molpadiids do feed within the sediment. Moreover, the granulometry of the gut contents of *M. blakei* differed from that of epibenthic holothurians from the same area.

Like the infaunal species, epifaunal holothurians are able to swallow large amounts of sediment. Khripounoff and Sibuet (1980) showed that organo-mineral aggregates (usually 20 to 65 µm in diameter) and faecal matter are the principal nutritive particles ingested by epibenthic holothurians. Like Bordovskiy, Sokolova, Smirnov, Akhmet'yeva and Zezina (1973), they found elevated levels of organic matter in the sediment contained within the holothurian's oesophagus in comparison to the sediment on which it was feeding. This they believed demonstrated that holothurians are able to select for particles in the sediment that have a high energetic value. Unfortunately, their sediment samples were taken with a box corer, the best methodology available at that time, and the organic analyses were averaged over the top 2 cm of the sediment and therefore are not strictly comparable with material that a holothurian ingests. Photographic evidence suggests that epibenthic holothurians do not feed deeply in the sediment (Heezen and Hollister, 1971).

To overcome this problem Sibuet, Khripounoff, Deming, Colwell and Dinet (1982), in another important paper, compared the superficial sediment (top 2mm) with a mean value for the top 2cm of the sediment from the same box core samples and found the same levels of organic constituents in the two fractions, except in the case of soluble proteins (soluble in 1N NaOH). However, the organic constituents were enriched in the oesophageal contents of holothurians taken in the same area. In addition, bacterial abundance was greater in the holothurian oesophageal contents than in the surrounding sediment. Comparison of the organic constituents in the different parts of the gut showed that lipids were assimilated with the greatest efficiency, but owing to the low levels of lipid present protein was the main organic component digested. Surprisingly, bacterial protein contributed only 2% of the total protein absorbed. The significance of bacterial extracellular polymer, known to be ingested by shallow-water holothurians (Baird and Thistle, 1986), has still to be evaluated for deep-sea species.

Although the results of Khripounoff and Sibuet (1980) and Sibuet et al., (1982) indicate that deep-sea epibenthic holothurians are selective feeders there is some doubt about this conclusion. It is not known, for instance, how much of the organic matter in the oesophagus is provided by the holothurian itself, and there are doubts about the efficiency with which box corers sample the superficial sediment. Moreover, in shallow water, where SCUBA divers have been able to sample the superficial sediment in the immediate vicinity of a holothurian and have compared it with the holothurian's gut contents, some researchers have found that there is selective feeding (Massin, 1980) while others have not (Yingst, 1974).

Khripounoff and Sibuet (1980) also found a negative selection for pelagic foraminiferans and metazoan meiofauna. Analysis of the gut contents of one species indicated that it was able to avoid the ingestion of live animals with the exception of benthic foraminiferans. The importance of benthic foraminiferans, particularly those with a soft shell, in the nutrition of deep-sea holothurians has still to be assessed.

Sibuet et al., (1982) proposed that holothurians select food by a sorting mechanism which suspends smaller, less dense particles in the sediment. Briggs (1985), however, found that two epibenthic holothurians from an area below the lysocline in the Venezuela Basin ingested slightly coarser particles than those found in the sediment. This resulted from the presence of pelagic foraminiferan tests in their guts compared with the sediment where only a few were found owing to the dissolution of the calcium carbonate. Briggs (1985) proposed that foraminiferans are transported to the seabed in faecal pellets and that holothurians ingest the uppermost layer of the sediment where these freshly deposited faecal pellets collect, without necessarily modifying their feeding behaviour *per se*.

One assumption that has been made when researchers have compared gut contents with sediment samples is that organic matter in the deep sea is distributed homogeneously. This is indicated by the small variation in organic matter in the guts of different specimens from the same area. However, it is apparent from deep-sea photography that detrital material arriving at the seabed is resuspended and moved about by nearbed currents, so that it collects around sedimentary structures and within hollows (Section 5.4). The combination of nearbed currents and sediment topography, therefore, leads to a heterogeneous distribution of freshly deposited organic matter and must be taken into account when holothurian feeding selectivity is considered.

In a study of the many radionuclides that are present in northeast Atlantic oceanic plankton, nekton, benthic animals and sediments, Feldt, Kanisch, Kanisch and Vobach (1985) found that the holothurians were high in those radionuclides which had been scavenged from the water column by particulate material and then deposited on the seafloor. Some of the radionuclides had short half-lives. Likewise, Osterberg, Carey and Curl (1963) found the same short half-life radionuclides in a shallow-water and a deep-sea holothurian. These data indicate not only that particles are transported rapidly to great depths, but also that holothurians are particularly adept at feeding on these particles.

Knowledge gained from the study of shallow-water holothurians suggests that deep-sea species pick up particles from the seabed either by adherence to the tentacle surface (Massin, 1978; Hammond, 1982; Roberts and Bryce, 1982; Cameron and Fankboner, 1984) or by direct entrapment of particles between the nodules present on the surface of the tentacles (Roberts, 1979; Bouland, Massin and Jangoux, 1982). Cameron and Fankboner (1984) believed that the former method was the most important for *Parastichopus californicus* since its tentacles did not expand or relax inside the pharyngeal cavity, a necessary step if particles collected by tentacular entrapment are to be released from the internodular spaces. More recently, a detailed study on the ultrastructure of shallow-water dendrochirotid holothurian tentacles has indicated the presence of cells that may produce a proteinaceous adhesive (McKenzie, 1987). The weakness of the adhesive may select for the lighter, less dense particles, the very particles which Sibuet *et al*., (1982) suggested that deep-sea epibenthic holothurians feed on.

Digestion in deep-sea holothurians is aided by the presence of an enteric barophilic microbial population in the posterior intestine. The bacteria are directly associated with the intestinal lining in the hindgut and are thought to act as a commensal gut flora that transforms ingested detrital material (Deming and Colwell, 1982; Sibuet _et al_., 1982; Tabor, Deming, Ohwada and Colwell, 1982; Alberic, Feral and Sibuet, 1987). Microbial activity in the guts can be more rapid than in the surrounding sediment. Using the rates of microbial activity Deming and Colwell (1982) calculated that the turnover time of sediment in the gut of the abyssal holothurian _Psychropotes longicauda_ was 16 hours. However, the way in which _P. longicauda_ voids its posterior intestine episodically, forming large faecal strings (Heezen and Hollister, 1971), must bring into question the assumption that material passes through the holothurian's gut at a constant rate. Despite this reservation, the work of Deming and Colwell (1982) gives the best estimate of the rate at which sediment is processed by a deep-sea holothurian, 105g wet weight sediment per day (holothurian size unknown). A similar rate was estimated by Rowe (1974) from photographic observations for a different species.

1.2 _Locomotion and bioturbation_.

The tracks and trails made by epibenthic holothurians as they roam over the seabed are very distinctive. Some holothurians, like _Pseudostichopus_, form furrows about 1 cm deep as they plough through the superficial sediment (Heezen and Hollister, 1971; Lemche _et al_., 1976; Young _et al_., 1985). These species usually have poorly developed tubefeet and rely on the alternate extension and contraction of the whole body to move over the seafloor. This form of locomotion is also used by infaunal species which often lack tubefeet altogether. In their case purchase on the surrounding sediment is assisted by the body wall ossicles which may be shaped like anchors or wheels. Most of the deep-sea species of the order Aspidochirotida and all of the Molpadiida and Apodida are thought to move by body contractions.

Some Aspidochirotida, however, like all the benthic Elasipodida, have well developed tubefeet and use these for locomotion. Many species leave the sediment surface remarkably undisturbed, save for a series of pin-point marks made where the tubefeet have alighted on the seabed. This leads to a characteristic series of parallel lines marking the passage of the holothurian (Heezen and Hollister, 1971; Mauviel and Sibuet, 1985), although some species that are almost neutrally buoyant leave no apparent impression on the seafloor. The tubefeet of many Elasipodida are connected to intradermal ambulacral cavities which Hansen (1975) believed aided locomotion by allowing the powerful body muscles to move the tubefeet and to maintain their turgidity by forcing fluid into the tubefeet from the dermal cavities. Photographs taken of elasipodids _in situ_ on the seabed show that peristaltic waves are passed down the body wall muscles (Barham, Ayer and Boyce, 1967; Hansen, 1972; Lemche _et al_., 1976). Recent time-lapse photography has provided data on the rates of holothurian movement in the deep sea (Lampitt, 1984, 1985; Lampitt and Billett, 1985). Maximum rates of 89 cm per hour have been calculated for _Benthogone rosea_ at a depth of 2000m which is comparable with the locomotion rates of shallow-water species.

It is clear that sediment mixing by holothurians in any one area depends on the species that are present. Areas dominated by elasipodids will undergo little mixing as a result of their locomotion, but in areas where aspidochirotids like *Pseudostichopus* and *Mesothuria* are present, the top layer of sediment will be mixed. Smooth plough marks made by *Pseudostichopus atlanticus* are one of the most common Lebensspuren (features on the sediment surface) in the Venezuela Basin (Young *et al*., 1985) and similar features (simple furrows) are particularly common in an area of the Bay of Biscay, BIOGAS St. 2 (Mauviel and Sibuet, 1985), where species of *Pseudostichopus* and *Mesothuria* are found (Sibuet, 1977). Smooth plough marks are a common feature of the Madeira Abyssal Plain (Huggett, 1987).

Infaunal holothurians also play a role in sediment mixing. Apodid holothurians will move sediment as they burrow through it, but although their abundance in the deep sea is probably greater than previously thought (Gage and Billett, 1986), their effect on sediment mixing is probably insignificant in comparison to other infauna such as polychaetes which are far more abundant (e.g. Khripounoff, Desbruyeres and Chardy, 1980; Sibuet *et al*., 1984; Richardson, Briggs and Young, 1985). Molpadiid holothurians by comparison may be far more important as bioturbators in some areas. These holothurians mix the sediment through their feeding activities and locomotion over a depth of several centimetres. Cone-shaped mounds that are a common feature at abyssal depths in the Venezuela Basin (average abundance of 1 cone in every $2m^2$) are considered to be made by *Molpadia* (Young *et al*., 1985). However, it is not clear how many of these cones are active. Greater subsurface reworking rates than those measured at the sediment surface, estimated from radionuclide studies, in the Venezuela Basin were attributed to the activities of these holothurians as well as other benthic infauna (see Li, Guinasso, Cole, Richardson, Johnson and Schink, 1985).

1.3 Swimming.

Several holothurian species are known to have the ability to swim (Margolin, 1976; Pawson, 1976, 1982a). Most are benthic animals and rise up into the water either by undulating their whole body or, in those species that have a brim of fused lateral tubefeet, by passing waves along the sides of the body. The benthic holothurians are not capable of swimming for long periods and only make short excursions into the water column before gliding back to the seabed. A few species, however, spend most of their time in the water column and can be considered to be truly pelagic, although they nevertheless return to the sediment to feed. These holothurians are therefore more appropriately classed as benthopelagic organisms. They are restricted to the open ocean and are most common close to the seabed at bathyal and abyssal depths.

The first known specimens of a truly pelagic holothurian, Pelagothuria natatrix (Elasipodida), were sampled by the "Albatross" in the Gulf of Panama using a benthic trawl (Ludwig, 1894). Several specimens were observed swimming at the sea surface, but the trawl used on the expedition did not possess an opening and closing device so it was not possible to assess the depth at which the pelagic holothurians in the trawls had been taken. Further specimens were taken by The German Deep-Sea Expedition down to a depth of 1000m in the Indian Ocean using a closing pelagic net (Chun, 1900). This species is reported to have been photographed at a depth of 6776m in the Pacific (Lemche *et al*., 1976) but these records need to be substantiated. Another elasipodid, *Peniagone diaphana*, was also collected in pelagic trawls in the northeast Atlantic (Herouard, 1923). Initially only post-larval stages were described, but when the material was re-examined the presence of a larger specimen led Hansen (1975) to believe that a pelagic lifestyle was not merely confined to the post-larval stage. However, the benthopelagic lifestyle of this species was not fully appreciated until Barnes, Quetin, Childress and Pawson (1976) witnessed, from a submersible, dense aggregations of *P. diaphana* living just above the seabed. More recently another remarkable benthopelagic elpidiid, *P. leander*, has been photographed living just above the seabed in the mid-Pacific (Pawson and Foell, 1986). Photography has also been used to study the feeding and swimming of another elasipodid *Enypniastes* (Pawson, 1976,1982; Ohta, 1985) and more recently this beautiful holothurian has been observed directly from submersibles (Drs J.E. Miller and D.L. Pawson, personal communication).

Swimming holothurians are also known from the order Aspidochirotida. Hansen and Madsen (1956) described the new genus and species *Galatheathuria* from a specimen 22.5 cm long sampled at a depth of 4500m (1000m above the seabed) in the Pacific Ocean, together with some specimens captured in a benthic trawl in the Bay of Bengal. A further genus and species, *Scotothuria herringi*, was sampled by pelagic nets in the mid-Atlantic (Hansen, 1978) several thousands of metres above the seabed. Both these species have a lateral brim of fused tubefeet and swim by undulating the brim, as suggested by Hansen and Madsen (1956), in a manner similar to the swimming motion of the cuttlefish *Sepia* (Billett *et al*., 1985). The intestinal contents of both species include material derived from the seabed. Those specimens sampled close to the seabed were found to have guts full of sediment, but the intestines of those specimens captured high above the seafloor were completely empty (Billett et al., 1985). It appears, therefore, that these holothurians feed preferentially on the seabed and that they are capable of extensive migrations up the water column. The reasons for the migrations are unknown.

1.4 Reproduction.

Until recently the reproduction of deep-sea holothurians has not received much attention. Early taxonomic works concentrated on the gross morphology of the gonad (Theel, 1882) while some later publications mentioned briefly the egg size found in some species (Mortensen, 1927; Heding, 1935, 1942). More recent work has benefited from the general relationship that has been found between egg size, fecundity, and the types of development that occur (Thorson, 1950). Accordingly, for echinoderms, eggs with a diameter of about 100 µm are usually abundant and are considered to lead to planktotrophic development (the formation of a planktonic feeding larva), while eggs greater than about 1000 µm are normally scarce and lead to the direct development of a juvenile without an intermediary larval stage (Tyler, Grant, Pain and Gage, 1982). Direct development may occur by viviparity. Eggs of an intermediate size are usually moderately abundant and are considered to undergo lecithotrophic development (the formation of a pelagic non-feeding larva). Planktotrophic and lecithotrophic development may also take place on the seabed or in the bottom water layer (demersal development - Pearse, 1969; Mileikovsky, 1971).

Using maximum egg size and fecundity as indicators it has been possible to infer the type of development in many deep-sea species although some caution is necessary since the organic content of eggs is not necessarily related to their size (Strathmann and Vedder, 1977; Turner and Lawrence, 1979; Emlet, McEdward and Strathmann, 1987). Thorson (1950) suggested that most deep-living species would have direct development and hence no pelagic larval stage, but work on deep-sea bivalves has shown that lecithotrophic development with a short pelagic phase is the most common form of development in this taxon (Ockelmann, 1965; Knudsen, 1967,1970). In contrast, most of the echinoderms studied by Tyler _et al_., (1982) produced large eggs indicating direct development, but 5 species were found to produce many small eggs indicative of a pelagic feeding larva. Moreover, those species producing small eggs had an annual reproductive cycle.

Until recently, the deep-sea has been regarded by many to be a particularly stable environment free from seasonal perturbations (Menzies, George and Rowe, 1973; Rokop, 1977). The occurrence of seasonal reproduction, therefore, in any deep-sea species was not expected, even in temperate areas where surface-water production varies seasonally, since larvae would be unlikely to survive the long journey to the sea surface and back again to abyssal depths (Thorson, 1950). Schoener (1968) and Rokop (1974) were amongst the first to note the presence of periodic reproductive cycles in some continental slope species, and that development occurred with a pelagic feeding larva. However, Rokop (1974) thought that it was unlikely that any truly deep-sea species would exhibit seasonal reproduction. The time-series sampling in the Rockall Trough (Gage, Lightfoot, Pearson and Tyler, 1980) has shown this to be incorrect (Tyler _et al_., 1982).

It is improbable that the larvae of slope dwelling species migrate to surface waters since adult populations occur in restricted bathymetric ranges and therefore it is unlikely that their larvae, if dispersed by surface currents, would be able to re-locate the adult habitat. However, juveniles of species that produce small eggs indicative of planktotrophic development are known to have a wider bathymetric range than the adults (Gage, Pearson, Clark, Paterson and Tyler, 1983; Gage et al., 1985a) which indicates that larvae are dispersed widely, possibly in surface waters. Alternatively, since near-bed currents generally flow parallel to the contours of the continental slope (Section 2.1) planktotrophic larvae may undergo some form of demersal development, utilizing the annual deposition of phytodetritus as a food source (Billett, Lampitt, Rice and Mantoura, 1983; Lampitt, 1985; Rice, Billett, Fry, John, Lampitt, Mantoura and Morris, 1986). Some molluscan larvae are known to migrate to surface waters from abyssal depths (Bouchet, 1976) and it is possible that the larvae of abyssal echinoderms undergo similar intrepid migrations (Section 5.5).

Despite the presence of planktotrophic development in some deep-sea echinoderms such development is, as yet, unknown for abyssal holothurians. Hansen (1975), having examined the egg sizes produced by elasipodid species, concluded that although the egg size varied greatly within the order, even the smallest egg produced (150 µm diameter) would lead to lecithotrophic development. Of particular note in the elasipodids is the development of extremely large eggs, up to 4.4 mm diameter, in the family Psychropotidae. Hansen (1975) suggested that these eggs might help the juveniles to spend a long pelagic life without needing to feed in the plankton. Apart from providing the largest eggs known in holothurians, the elasipodids also include the only deep-sea species that is known to use brood protection during the development of its juveniles (Hansen, 1968, 1975).

More recently, the histology and gametogenic biology of elasipodids has been undertaken from time-series and depth-series samples in the northeast Atlantic (Tyler, Muirhead, Billett and Gage, 1985; Tyler, Gage and Billett, 1985; Tyler, Muirhead, Gage and Billett, 1985; Tyler and Billett, in press). The results substantiate the conclusions reached by Hansen (1975) and show no evidence of reproductive periodicity. The same set of samples have been used to study the reproductive biology of other holothurian orders in the deep sea, notably the Apodida (Gage *et al*., 1985a), the Aspidochirotida (Tyler and Muirhead, 1986), the Dactylochirotida (Tyler and Gage, 1983) and the Molpadiida (Tyler, Billett and Gage, 1987). McEuen and Chia (1985) described the lecithotrophic development of one molpadiid species, *Molpadia intermedia*, and concluded that since many molpadiids produce eggs of a similar size to *M. intermedia* they would all develop in a similar way.

1.5 Population structure.

Seasonality in the reproductive cycle of some deep-sea brittle stars and one species of sea urchin has led to population size distributions in which cohorts may be recognized (Tyler and Gage, 1980; Gage and Tyler, 1982). No such population size distributions have been reported for holothurians. Where population size distributions have been described they are usually unimodal, whether expressed in specimens' lengths (Bisol, Costa and Sibuet, 1984; Tyler *et al*., 1985b; Tyler *et al*., 1987) or weights (Smith, 1983). However, where sampling has occurred repeatedly in the same area (e.g. the Rockall Trough), and over a period of several years, the mode of the population is not consistent between samples. It is not clear whether this is the result of temporal or spatial variability (Tyler *et al*., 1987) or the result of a sampling or preservation artefact (Tyler *et al*., 1985b). Rex, Ummersen and Turner (1979) suggested that variable and infrequent larval recruitment caused similar population size distributions in the deep-sea gastropod *Benthonella tenella*.

For *Peniagone diaphana* in the Rockall Trough no relationship was evident between the mean size of each sample and bathymetry, sampling site, or the time of the year when the sample was taken (Tyler *et al*., 1985b). Three pairs of stations, each pair sampled on the same date, showed significantly different distributions. In one sample there were a number of small, immature specimens which were completely absent from another sample taken on the same day just 9 miles away.

The paucity of small holothurians in benthic trawl catches was noted by Hansen (1975) who suggested that this might result, in part, from the large mesh size of most trawls. However, most populations, including those sampled by epibenthic sledges with a fine mesh net, are dominated by large adult animals. In some particular instances, large populations of small, similarly sized specimens may occur, e.g. *Peniagone ?willemoesi* (Rowe, 1971) and *Peniagone japonica* (Ohta, 1983). In both cases these populations were found in or near to canyon systems.

1.6 Growth and longevity.

In the absence of recognizable cohorts in the population size-distributions of deep-sea holothurians it has been impossible to assess the growth rates and hence the longevity of these creatures. Observations on benthic community metabolism, microbial degradation and re-colonization (see Smith, 1978; Jannasch and Wirsen, 1977; Grassle, 1977) have indicated that life processes are much slower in the deep sea than in shallow water. In addition, slow growth rates have been measured in a deep-sea clam by radiometric chronology (Turekian, Cochran, Kharkar, Cerrato, Vaisnys, Sanders, Grassle and Allen, 1975), although the rates calculated were subject to wide confidence limits. These features and the dominance of large adults in deep-sea holothurian populations have led to the belief that abyssal species live for a long time.

More recent data have suggested that deep-sea processes are not necessarily slow (Yayanos, Dietz and Boxtel, 1979; Desbruyeres, Bervas and Khripounoff, 1980). Growth rates measured from seasonally breeding echinoderms have indicated similar growth rates to shallow-water species (Tyler and Gage, 1980; Gage and Tyler, 1982). More recently, annual growth bands in the skeletal plates of the sea urchin *Echinus affinis* have shown that this species does grow slower and live longer than its shallow-water relatives, but the growth rates measured were not exceptional (Gage and Tyler, 1985). Other studies on bivalves show similar growth rates to inshore species (Gage, 1986). Therefore, holothurians might be expected to have similar or slightly slower growth rates than shallow-water species. These appear to grow to maximum size in about 4 to 5 years (Pawson, 1966). It remains to be seen whether growth bands can be found on the plates of the calcareous ring to give a clear indication of deep-sea holothurian growth.

1.7 Metabolism.

Because of the logistic difficulties involved, the basal metabolic rate of only one holothurian species, Scotoplanes globosa, has been measured (Smith, 1983). It was found that S. globosa from a depth of 1300m in the Santa Catalina Basin, off southern California, had a similar weight-specific oxygen consumption rate to that of shallow-water holothurians. Ammonium excretion rates were also measured and although they were of a similar magnitude to one shallow-water species, Holothuria difficilis, they were an order of magnitude less than another inshore species, Eupentacta quinquesemita, of a similar size. Weight-specific oxygen consumption rates of S. globosa decreased with increasing weight. Similar studies on deep-sea ophiuroids resulted in the same general conclusions (Smith, 1983).

1.8 Chemical composition.

One of the most remarkable features of holothurians is their high water content. Most of the weight of an intact holothurian is accounted for by the perivisceral fluid (Giese, 1966), but even in the tissues themselves water accounts for 60 to 95% of the wet weight (Prim, Lawrence and Turner, 1976). Only a few data are available on the biochemical composition of shallow-water holothurians (see

Giese, 1966; Feral, 1985) and until recently little was known of the composition of deep-sea species.

Barnes *et al*. (1976) found low levels of protein, lipid, and carbohydrate in the benthopelagic species *Peniagone diaphana* with values for each component less than 0.1% of the wet weight. The total wet weight appears to include the perivisceral fluid, so the actual levels of the organic constituents in the body tissues will be higher. Sibuet and Lawrence (1981) showed that this was indeed the case for three benthic species. About half of the dry weight was ash, mainly calcium carbonate from the plates of the calcareous ring and from the dermal ossicles, while soluble protein, lipid and carbohydrate accounted for 15%, 3% and 1.5% of the dry weight respectively. The largest organic component was of a refractory nature and was considered to be principally insoluble protein, based on work on a shallow-water species (Lawrence and Kafri, 1979). Protein, therefore, is the dominant organic constituent in deep-sea species, in common with inshore holothurians (Prim *et al*., 1976; Lawrence and Kafri, 1979; Feral, 1985). Further work on a wide spectrum of deep-sea species from the orders Elasipodida and Aspidochirotida show similar results (Walker, Tyler and Billett, 1987a,b). These studies examined all the components of the body separately (body wall, testis, ovary, gut and respiratory tree (when present)) and showed an increase in lipid concentration in the ovary.

In general, the biochemical composition and the total calorific content of individual deep-sea and shallow-water holothurians are similar (Sibuet and Lawrence, 1981; Walker *et al*., 1987a,b).

1.9 Abundance and biomass.

Knowledge of the biochemical composition of holothurians allows their biomass to be expressed in a term that reflects their organic content, such as grams organic carbon or calorific value. However, since the determination of these values is time-consuming they have seldom been used. In most cases holothurian biomass has been expressed in grams wet weight (Haedrich, Rowe and Polloni, 1980; Ohta, 1983; Feldt *et al*., 1985; Rutgers van der Loeff and Lavaleye, 1986) which leads to an over-estimation of their relative importance in the benthic community owing to their high water content. The relative importance of holothurians decreases when dry weight is used in preference to wet weight (Sibuet *et al*., 1984), but in this case the proportion of holothurian biomass in the benthic community is under-estimated since their skeleton is not as well developed as in other taxa, such as the asteroids (Section 5.1).

Sibuet and Lawrence (1981), having calculated the calorific value of holothurians from their analyses of the biochemical constituents, were then able to calculate the holothurian biomass per unit area using data on the abundance of holothurians. They found that although deep-sea and shallow-water species had similar calorific values, the deep-sea holothurian biomass expressed per unit area was about 4 orders of magnitude lower than the holothurian biomass in some shallow-water habitats. This was true even for samples from 2000m in the Bay of Biscay where the holothurians were reported to account for one sixth of the total benthic biomass (Sibuet and Lawrence, 1981).

Good biomass data are dependent on reliable estimates of holothurian abundance, a task fraught with problems in the deep sea. Abundance of megafauna may be determined from trawl catches (Dahl, Laubier, Sibuet and Stromberg, 1976; Haedrich, Rowe and Polloni, 1975, 1980; Ohta, 1983; Sibuet et al., 1984; Feldt et al., 1985; Monniot and Segonzac, 1985; Sibuet and Segonzac, 1985; Sibuet, 1985; Rutgers van der Loeff and Lavaleye, 1986), epibenthic sledge samples (Dahl et al., 1976; Rice et al., 1979, 1982; Billett and Hansen, 1982; Lampitt, Billett and Rice, 1986), photography (Rowe, 1971; Rice et al., 1979, 1982; Billett and Hansen, 1982; Ohta, 1983; Sibuet, 1985), and submersible transects (Barham et al., 1967; Grassle, Sanders, Hessler, Rowe and McLellan, 1975; Pawson, 1982a; Smith and Hamilton, 1983).

Trawls are useful in that they sample a wide area and may overcome small-scale variability in the abundance of some organisms. However, they do not sample continuously while they are on the seabed and it is often difficult to assess the arrival and departure points of the trawl on the seafloor. The true abundance of megafauna is therefore under-estimated by trawls. Where comparisons have been made with abundances calculated by photography it is clear that trawls catch only about half of the organisms in their paths (Sibuet and Lawrence, 1981; Sibuet et al., 1984; Sibuet, 1985).

In contrast, the abundances of megafauna calculated from epibenthic sledge samples are similar to abundances determined from photographs (Rice et al., 1979,1982; Billett and Hansen, 1982). Epibenthic sledges have the advantage over trawls in that they take a near continuous sample while on the seabed. In addition, if they are monitored acoustically periods when the sledge lifts off the seabed can be accounted for. The area swept by a sledge is not as great as that covered by a trawl and if a net with a fine mesh is used the net may not fish efficiently for the duration of the trawl owing to clogging of the mesh.

Photography offers the best method of determining abundance for large species that are readily recognized. Photographic surveys can cover a wide area, an important factor since the abundance of many species is low. Photography also provides information on the spatial distribution of the organisms. The major drawback of photography is that very often it is not possible to identify an organism with certainty. Also, it is difficult to convert abundances calculated from photographs into an estimate of biomass since the dimensions of animals photographed _in situ_ will not be the same as those taken from trawl and sledge samples owing to the contraction of the specimens.

Submersible observations have similar advantages to photography but allow more species to be identified (Smith and Hamilton, 1983). However, this method is expensive and has been used in only a few cases (see above).

The abundance of holothurians in the deep sea is very variable. Some studies using an Agassiz trawl in the northeast Atlantic indicate that fewer than ten holothurians are found in each hectare at abyssal depths (Feldt _et al_., 1985; Rutgers van der Loeff and Lavaleye, 1986), but other studies show abundances in the range of 10 to 100 individuals per hectare at depths greater than 3000m (Sibuet, 1985; Sibuet and Segonzac, 1985). At mid-slope depths (1000 to 3000m) holothurian abundances are often somewhat higher, between 100 and 1000 individuals per hectare (Grassle _et al_., 1975; Pawson, 1982a; Ohta, 1983; Sibuet, 1985; Sibuet and Segonzac, 1985). Similar abundances may occur in some areas at abyssal depths close to the base of the continental slope (e.g. St. P2, Sibuet, 1985). At upper slope depths (200 to 1000m) in the northeast Atlantic holothurian abundance appears to be low. This is in keeping with the general dominance of crustaceans and suspension-feeders on the upper slope (Lampitt *et al*., 1986). In some areas holothurians appear to be missing over a wide bathymetric range, e.g. between 200 and 2360m off the Grand Banks of Newfoundland, northwest Atlantic (Haedrich and Maunder, 1985).

Occasionally, exceptionally large populations of holothurians may be encountered at abyssal and bathyal depths. Dahl *et al*., (1976) encountered populations of *Elpidia glacialis* at 3600m in the Norwegian Sea with an abundance up to 55,800 individuals per hectare (determined from epibenthic sledge and trawl samples). Similarly, Ohta (1983) noted populations of *Peniagone japonica* at 950m off Japan with abundances up to 79,000 individuals per hectare (determined from photographs). Abundances an order of magnitude greater than these have also been reported, notably ?*Peniagone willemoesi* at 2060m in the western Atlantic with 340,000 individuals per hectare (Rowe, 1971; determined from photographs), and *Kolga hyalina* at depths of about 4000m in the northeast Atlantic with 500,000 individuals per hectare (Billett and Hansen, 1982). In general these high holothurian abundances occur in, or near to, canyon systems. Their significance is discussed in this thesis. High abundances are also indicated to occur at hadal depths in deep-sea trenches (Hansen, 1956; 1975), although high abundance is not a general feature of hadal holothurians (Hansen, 1975).

1.10 Spatial distributions.

Estimates of abundance of some holothurian species vary widely between trawl samples taken in the same general area indicating that some species have patchy distributions (Hansen, 1956; Sibuet, 1977; Bisol *et al*., 1984). Aggregations have been noticed in photographic transects (Ross, 1970; Heezen and Hollister, 1971; Rowe, 1971, 1972; Billett and Hansen, 1982), but it is clear from the trawl samples that some species are aggregated on a larger scale that can be determined from discontinuous photographic transects. These large scale patches of holothurians and other echinoderms, have been studied most effectively by submersible transects (Grassle *et al*., 1975; Pawson, 1982a; Smith and Hamilton, 1983).

Grassle *et al*. (1975) noted aggregations of two echinoid species in the northwestern Atlantic. One, *Echinus affinis*, appeared to aggregate on food items, such as plant debris or possibly detrital patches (Grassle and Morse-Porteous, 1987), but patchiness was not a feature of the population as a whole. The echinoids dispersed once the food item had been consumed. The other, *Phormosoma placenta*, formed patches about 50m in diameter that moved as a herd across the seabed feeding, they presumed, on an evenly distributed fine-grain resource. The formation of these herds was considered to be possibly the result of an optimal feeding strategy by Jumars and Gallagher (1982), although the patches may have formed also for reproductive purposes or in response to predation pressure. Pawson (1982a) did not see any indication of these herds in a population of *P. placenta* observed from a submersible off the Bahama Islands. The population density here was an order of magnitude lower than that observed by Grassle *et al*., (1975), so it is possible that the formation of *Phormosoma* herds is density dependent. Similar herds of the holothurian Kolga hyalina were described by Billett and Hansen (1982) and are discussed in this thesis.

Pawson (1982a) compared 10 transects undertaken during a submersible dive at about 2000m depth in the northwest Atlantic and noted the abundance of many echinoderm species. Several showed patchy distributions and in the case of one holothurian, Ellipinion delagei, its abundance varied from 0 to 850 individuals per hectare on different transects. Several holothurian species reached their highest population density in the same transect, but in general their distributions did not seem to co-vary. Similarly, there was no between species correlation in the location of two mobile deposit feeders, the holothurian Scotoplanes globosa and the gastropod Bathybemix bairdii, sampled at a depth of 1300m in the Santa Catalina Basin in the northeast Pacific, even though they were aggregated in patches of a similar size, 25 to 96m in diameter (Smith and Hamilton, 1983). These authors suggested that the individuals of S. globosa may have been attracted to favourable feeding grounds, but they also considered that if the aggregations were formed for non-trophic reasons (e.g. for reproduction) then herd formation would occur as a necessity to find areas of fresh food.

1.11 Bathymetric zonation.

It has been known since the earliest days of deep-sea biological research that the deep-sea fauna changes in species composition with increasing depth and that most species have a restricted and predictable bathymetric range (Murray, 1895). Whereas the horizontal distribution of a species may extend on an oceanic scale, their vertical distribution may encompass only a few hundreds of metres. The causes for the change in species composition with depth are complex and in any one area several factors will act together to produce the observed pattern. Many of the factors have gradients, each operating on its own scale. Carney, Haedrich and Rowe (1983) considered that "if deep-sea faunal zonation is to be understood, it will be necessary to develop a theory of distribution along gradients that recognizes the possible effects of different types of gradient."

Many of these gradients are related to depth. Some are physiologically important, such as temperature and pressure (Somero, Siebenaller and Hochachka, 1983), while others are related to resources, for instance food availability and space. Superimposed on these are factors that are not necessarily depth related, such as topography and hydrography which in turn affect the sediment characteristics. A further level of complexity is provided by biological interactions, both between the biota and the environment (e.g. in regulating the structure of the sediment) and between the animals themselves (e.g. predation). All these factors must then be considered on evolutionary and ecological time-scales.

In view of the many variables it is not surprising that there is little consensus on the relative importance of the factors controlling zonation. Clues may be found by comparing the zonation of fauna from different geographic areas, by comparing the zonation of different taxa within the same area, or by a detailed analysis of the zonation of each species within a taxon, preferably over a wide geographic area. There are difficulties with the first two approaches owing to the great variety of sampling equipment used in benthic studies from different areas and for different fauna. In addition, the sampling intensity in each study has varied between depths and the statistical methods used to analyze the zonation pattern have differed. Moreover, Carney _et al_., (1983) and Ohta (1983) were perspicacious in recognizing the "sociologic" aspect of deep-sea biological studies. To quote Ohta (1983), "Just how assemblages are viewed in ordinations or in a continuum depends on the approach and attitude of the ecologist."

Several authors have noted a few broad zones in the deep sea but there is some disagreement over the terminology of the zones and the bathymetric limits to which they should be assigned. Some authors have followed the terminology of Bruun (1957) and Hedgepeth (1957) dividing the deep sea from the shelf break into bathyal, abyssal and hadal zones (Hansen, 1975; Horikoshi, 1976). Hansen (1975) from his work on elasipodid holothurians recognized a hadal zone deeper than 6000m, an abyssal zone extending from between 1800 and 2600m to 6000m, and a bathyal zone from the shelf break (200 to 400m) down to 1800/2600m. The boundary between the abyssal and bathyal zones was not distinct and appeared to act more as an upper boundary for the abyssal species rather than a lower boundary for the bathyal species.

Menzies _et al_. (1973), in contrast, recognized an abyssal zone starting between 425 and 3300m depending on geographic area. Between the abyssal zone and the shelf province there is an Archibenthal Zone of Transition which for the purposes of comparison can be considered to be equivalent to the bathyal zone (Carney _et al_., 1983). The abyssal and bathyal zones may be subdivided (e.g. Menzies _et al_., 1973; Haedrich _et al_., 1980; Rowe, Polloni and Haedrich, 1982) depending primarily on the geographic area.

One problem in defining the causes of zonation has been that depth related changes have also been correlated with distance from land and hence to sources of organic input. Carney and Carey (1976, 1982), working on the holothurian fauna off the western seaboard of North America, found that changes in faunal composition varied primarily as a function of depth and that there was little faunal change across an abyssal plain of near-constant depth despite increasing distance from land mass.

In the Rockall Trough Gage, Pearson, Billett, Clark, Paterson and Tyler (1985) and Gage (1986) found two depths where faunal change in echinoderm species was greater than at other depths. Both areas coincided with areas of increased sampling but Gage (1986) considered that sufficient samples had been taken at all depths to overcome any sampling bias. The two zones of change were correlated with features of the water mass structure, in particular with the 10°C and 4°C isotherms. The latter has been considered to mark the start of the abyssal zone (Le Danois, 1948; Bruun, 1957; Madsen, 1961; Menzies et al., 1973). Apart from the temperature effects on the physiology of deep-sea biota, pressure will also play a role by regulating cell membrane function and enzymatic activity (Somero et al., 1983). In the Antarctic animals are well adapted to their cold environment but at the expense of being sensitive to small increases in temperature (Clarke, 1983). Therefore, temperature tolerance in the deep sea may also be important in regulating the distributions of deep-sea biota.

In this study the terminology advocated by Bruun (1957) is followed. Bathyal is used to refer to species down to about 3000m and abyssal to those species that can rise to a depth of about 2500m. It will become apparent that there is some overlap between the two faunal groups.

Although there is a continuous decrease in the number of holothurian species with increasing depth, the number of species sampled at any one station at abyssal depths is generally greater than that at bathyal depths (Hansen, 1975). This apparent increase in diversity with depth does not extend into the hadal zone where only a few species are known and diversity is low (Hansen, 1975). The great abundance of holothurians at some hadal stations results from the profusion of a single species.

1.12 Geographic distributions.

Bathyal and abyssal holothurians show different characteristics in their geographic distributions. Many abyssal species are widely distributed although only a few species have truly cosmopolitan distributions. In contrast, bathyal holothurians have more restricted distributions and none are known to occur throughout the world's oceans. Hansen (1975) concluded that in general the geographic ranges of holothurians were greater with increasing depth throughout the bathyal and abyssal zones.

Several bathyal species have distributions which appear to be allied to deep oceanic current systems. In these cases Hansen (1975) believed the species would have a pelagic developmental stage and as a result their geograhic distributions would be controlled by the prevailing currents. The distributions of a few abyssal species are also possibly related to hydrographic features, but in general there appears to be little correlation with features of the physical environment (Hansen, 1975). Topographical barriers, however, do limit the distributions of some abyssal species, as demonstrated by the absence in the Arctic Ocean of most of the abyssal North Atlantic species. A similar topographical boundary may occur at the mouth of the Mediterranean Sea, but the higher temperatures at abyssal depths in the Mediterranean may also help to exclude North Atlantic species (Hansen, 1975).

Geographic distributions are not correlated with sediment type. Only three elasipodid species, known from more than one station, have been found on just one type of sediment, and in these cases the species are recorded only from a handful of stations (Hansen, 1975). In contrast, "variations in the food supply to the bottom seem to exert a great influence on the geographic distribution of deep-sea species" based on the similarity of the fauna from areas assumed to have a rich supply of organic matter (Hansen, 1975). It is possible that holothurian geographical distributions are regulated to some degree by the total organic input to an area and the temporal variability of the food supply.

Geographic variability in taxonomic characters is evident between different populations in many species. However, not enough sampling has been carried out in the deep sea to determine whether taxonomic characters change gradually over large distances or abruptly at faunal boundaries. Hansen (1975) considered that the former was more likely since the deep-sea environment changes only gradually over large horizontal distances. However, it is evident from work in deep-sea trenches that separation of populations by irregular topography can lead to marked local variation.

Complete reproductive isolation of populations, considered necessary for speciation to occur, is rare in the deep sea. Evidence for recent speciation in deep-sea holothurians is found only in the Pacific Ocean off Central America (Hansen, 1975). Despite the few opportunities for isolation and speciation in the deep sea today, Hansen (1975) still considered that deep-sea species have arisen mainly through speciation in the deep sea rather than through immigration from the sublittoral zone.

1.13 Summary.

The success of the holothurians in the deep sea has been attributed to their ability to move freely over the seabed in order to feed on large amounts of superficial sediment (Hansen, 1975; Sibuet, 1980). Moreover, the low organic content of holothurians allows them to maintain themselves in an environment where food is scarce. In the deep sea there is in general a change in feeding strategy from suspension-feeding and carnivory to deposit feeding with increasing depths (e.g. asteroids, Carey (1972)). It is not surprising, therefore, that holothurians, first and foremost deposit feeders, increase as a proportion of the total invertebrate megabenthos biomass. That is not to say that holothurians are more common in the deep sea than in shallow water, they are in fact several orders of magnitude less abundant (Sibuet and Lawrence, 1981), but that holothurians by virtue of their structure and lifestyle are able to compete more successfully with other faunal groups for the available food.

Organic carbon flux decreases exponentially with increasing depth (Suess, 1980). The organic matter that reaches great depth, however, has components that are readily assimilable, such as lipids (Tanoue and Handa, 1980; Rice et al., 1986). This material does not necessarily have to be processed by microorganisms before it is of use to higher taxa. The sediment surface holds the recently deposited material in a fine superficial layer, an ideal food source for any animal that can skim off the superficial layer over a wide area. Holothurians are well suited to this task. It has been shown by radionuclide analyses that holothurians readily feed on freshly deposited particulate material (Osterberg et al., 1963; Feldt et al., 1985), and that only a small proportion of the protein assimilated by a holothurian is of bacterial origin (Sibuet et al., 1982).

Comparisons of sediment samples with gut contents indicate that holothurians are particularly adept at selecting nutritious particles (Khripounoff and Sibuet, 1980; Sibuet et al., 1982) and generally selects the smaller, less dense particles. The glandular adhesive mechanism discussed by McKenzie (1987) for shallow water dendrochirotid holothurians may be a possible selection mechanism. Further work into the ultrastructure of deep-sea holothurian tentacles is necessary as well as further information on particles ingested.

There are few data on feeding rates in the deep sea. Data is needed on the longevity of holothurian faeces on the seafloor. Data are needed on whether holothurians feed continuously regardless of where they are, or whether they feed intensively in certain areas. Information is presented in this thesis on the spatial distribution of holothurians which indicate that they may feed more intensively in some areas. The affect of holothurian feeding and locomotion on the sediment is also addressed.

There are few reliable data on the abundance and biomass of deep-sea holothurians. Such data are essential if the impact of holothurians in the deep sea is to quantified. Data on holothurian abundance and biomass, as determined from epibenthic sledge catches, are presented here. Abundance of holothurians varies spatially, and in a few cases temporally. Data on these aspects are also included. The greatest changes in abundance are related to depth. The zonation of the holothurians in the Porcupine Seabight has been examined with reference to both the total bathymetric range of each species and their abundance within that range. The factors that are thought to regulate zonation are discussed.

The intensity of sampling in this study has allowed the population structure of many species to be examined. the population structure of each species is compared between stations and is discussed in relation to reproduction, bathymetry and temporal variability.

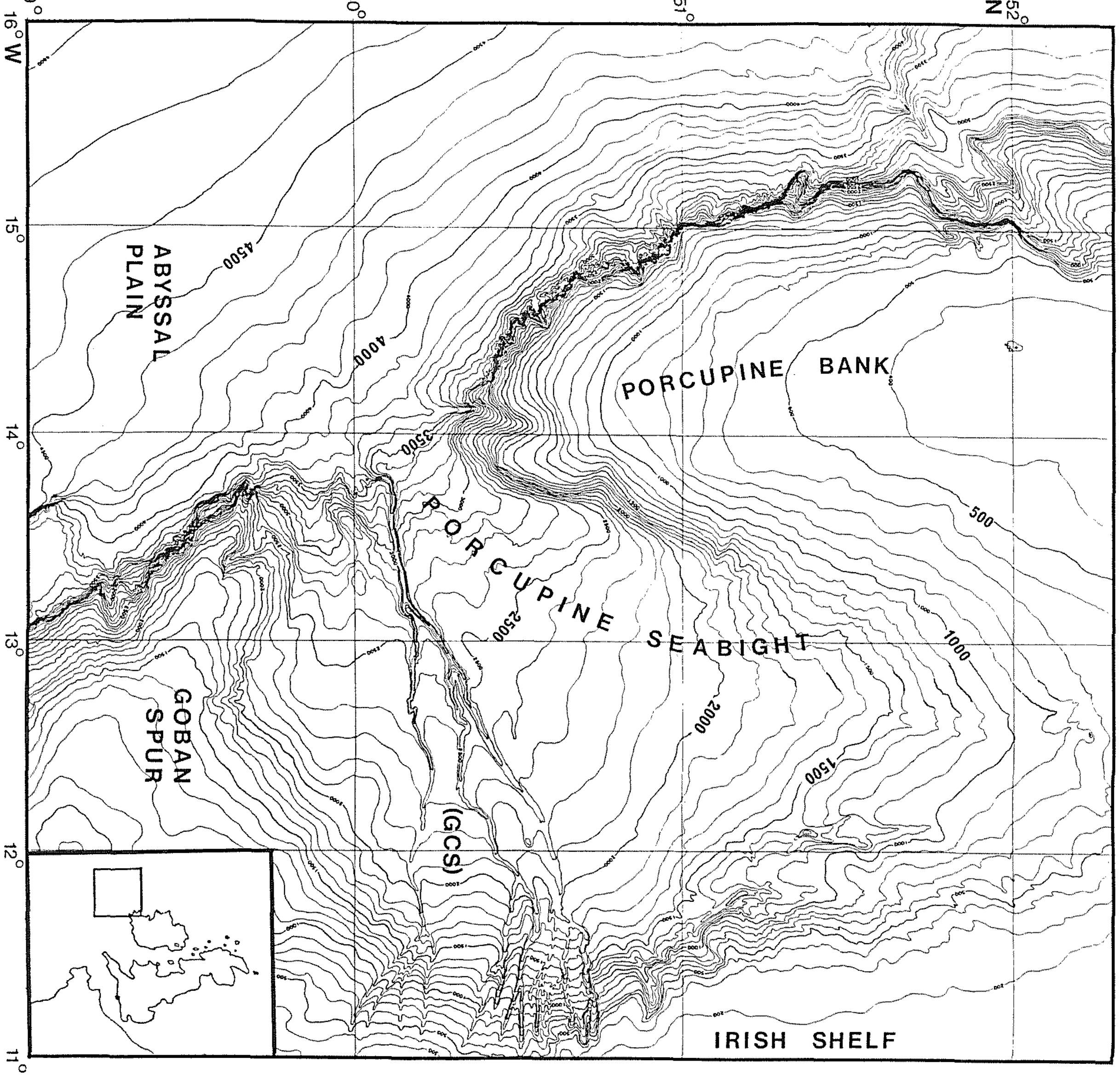
2. Materials and Methods

2.1 Study area.

The Porcupine Seabight represents the trough of an old rift system resulting from stress during a period of sea-floor spreading between Europe and Greenland (Naylor and Mounteney, 1975; Roberts, Hunter and Laughton, 1979; Naylor and Shannon, 1982). Sedimentation, principally during the Mesozoic and Tertiary, has produced gentle slopes within the trough down to a depth of 3000m, but below that depth, at the mouth of the Seabight, the seabed slopes away quite steeply before opening out onto the Porcupine Abyssal Plain. The Seabight narrows towards its northernmost end and is bounded to the west by the Porcupine Bank, to the east by the Celtic Shelf, and to the southeast by the Goban Spur (Fig. 1). The east slope, however, differs markedly from that of the west, owing to the presence of many small channels that coalesce to form a larger channel or canyon which traverses the mouth of the Seabight and opens out onto the Porcupine Abyssal Plain.

The channels, known as the Gollum Channel System (GCS), are apparently still active and differ from the submarine canyons of the continental slope further south by the absence of lateral gullies (Kenyon, Belderson and Stride, 1978). Handley (1971) using seismic reflection data concluded that sediments dipped into the GCS channels from both sides but no appreciable sedimentation was evident in

Figure 1. Bathymetric chart of the Porcupine Seabight with 100m isobaths.



49°
50°
51°
52° N
16° W
15°
14°
13°
12°
11°
ABYSSAL PLAIN
GOBAN SPUR
PORCUPINE BANK
PORCUPINE SEABIGHT
(GCS)
IRISH SHELF
4500
4000
3500
2500
2000
1500
1000
500

the centre of the channels. However, submersible observations have shown that large amounts of detrital material collect in the channels (Dr. R. S. Lampitt, personal communication), and therefore it would seem that sediments are being eroded continuously from the GCS. Curiously, for an apparently active channel system no sediment fan is evident at the point where it meets the abyssal plain (Handley, 1971). This may indicate that the material from the canyon is distributed widely over the Porcupine Abyssal Plain. The absence of canyons from the western slope of the Seabight is thought to reflect the limited sediment supply to the Porcupine Bank (Roberts _et al_., 1979). Canyons are also absent from the steep slopes to the west of the Porcupine Bank.

The main transect of stations in the Seabight (Fig. 6) extends in an arc from the top of the Porcupine Bank, down its eastern flank, through the mouth of the Seabight and out onto the Porcupine Abyssal Plain. Sediments have been analysed at 500m depth intervals along this transect. The sediments are a coccolith-foraminiferan marl with a carbonate content of 45 to 67 % sediment dry weight (Lampitt _et al_., 1986). The coarsest sediments are found at the top of the slope (median phi = 4.4 at 510m depth), but becoming finer with increasing depth (median phi = 7.4 at 960m depth). From 1500m to 4100m the median phi value is in the range of 8.0 to 8.6. The distribution of hard-shelled multilocular Foraminifera can be used as an indication of sediment transport. Negligible transport is evident down to a depth of 3000m but samples taken at the mouth of the Seabight (3600m) and on the Porcupine Abyssal Plain (4100m) have species typical of upper and middle slope depths indicating that there is downslope transport possibly via the channel system or from the steep slopes of the Goban Spur (Weston, 1985; Lampitt _et al_., 1986).

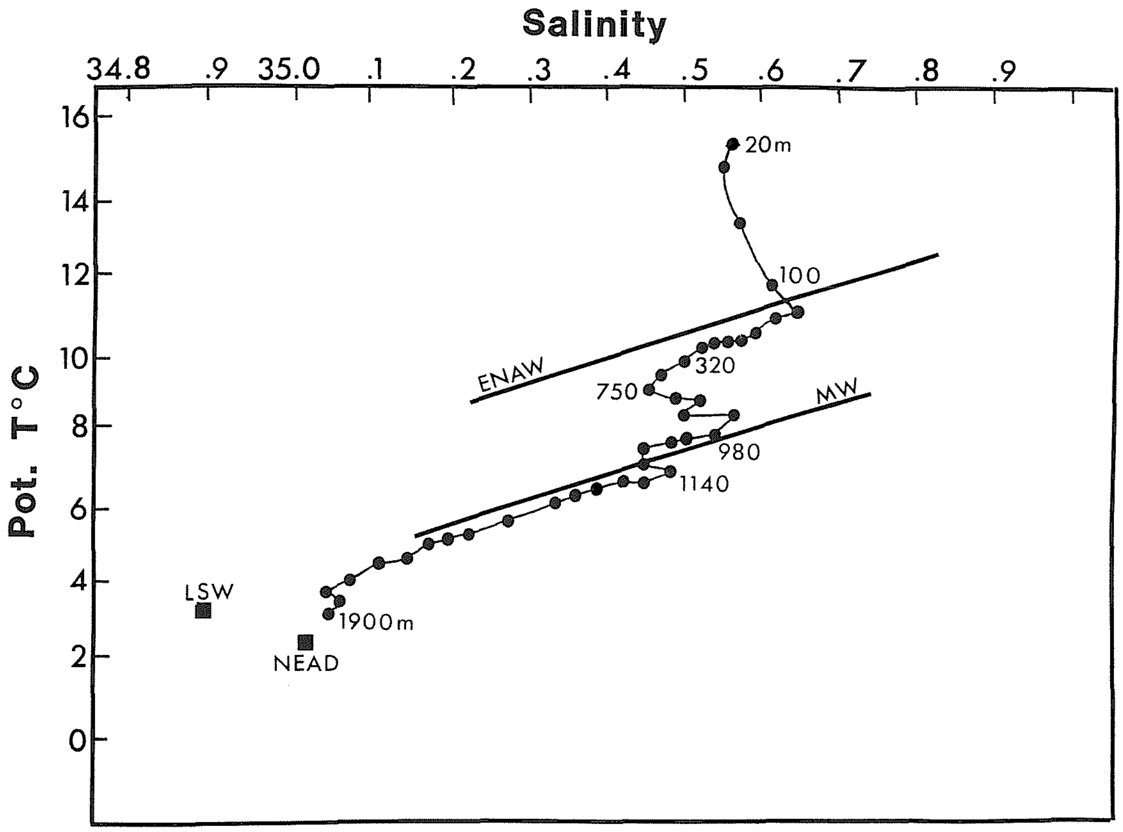
Sedimentation rates are reported to approach 10cm per 1000 years in the PSB (Kidd and Huggett, 1981). Sediments in the Seabight are oxidised over the top 9 cm or so, as indicated by the colour of the sediment. A sharp colour change from a light brown to a greenish brown occurs at a depth of 10 to 15cm at mid slope depths, but changes in colour are more gradual at the top of the Porcupine Bank and on the abyssal plain. There are difficulties in assessing the organic content of many marine sediments owing to their high carbonate content (Weliky, Suess, Ungerer, Muller and Fischer, 1983; Hedges and Stearn, 1984). However, CHN analysis of PSB sediments after acid digestion, show that organic carbon differs little from 0.5% of the sediment dry weight, and no relationship is evident between % organic carbon and bathymetric depth (Lampitt et al., 1986).

Analysis of rock debris from trawl catches in the area shows the predominance of clinker (including coal and coal shale) in samples from the PSB, particularly at the mouth of the Seabight (Kidd and Huggett, 1981). Most of the debris is of pebble and gravel size and rarely exceeds 6cm in maximum dimension although some large boulders have been taken occasionally. The igneous, metamorphic and sedimentary rocks are glacial erratics that are believed to have been dropped in the past from floating ice (Kidd and Huggett, 1981).

The temperature-salinity plot for the water column at the mouth of the Seabight (depth 4000m) has been presented by Hargreaves (1984) (Fig.2) and reflects the same general water mass structure described by previous authors (Lee and Ellett, 1965; Harvey, 1982; Vangriesham, 1985; Ellett, Edwards and Bowers, 1986). Eastern North Atlantic Water is found down to a depth of about 750m and overlies Mediterranean Water, a water mass characterized by a sal-

Figure 2. Temperature/Salinity plot for the area at the mouth of the Porcupine Seabight (St. 10115-1). (After Hargreaves, 1984).

ENAW, Eastern North Atlantic Water;
MW, Mediterranean Water;
LSW, Labrador Sea Water;
NEAD, Northeast Atlantic Deep Water


Salinity
34.8
.9
35.0
.1
.2
.3
.4
.5
.6
.7
.8
.9
Pot. T °C
16
14
12
10
8
6
4
2
0
20m
100
ENAW
320
750
MW
980
1140
1900m
LSW
NEAD

inity maximum and oxygen minimum at a depth of about 950m in the PSB. Below 1000m the Mediterranean Water becomes mixed with the underlying Labrador Sea Water which is marked by a salinity minimum and oxygen maximum at a depth of about 1700m. Below 1700m there are only small changes in temperature and salinity. A small increase in salinity at about 2000m indicates the influence of Norwegian Sea Water (Iceland-Scotland Overflow Water) (Lee and Ellett, 1965; Harvey,1982). Below 4000m the water has a southern origin, to some degree derived from Antarctic water (Vangriesham, 1985).

The features described above can be seen in temperature and salinity profiles plotted against depth (Figs 3 to 5). Three profiles are presented for the PSB, one from the mouth at a depth of 4000m taken in May 1984 (Fig. 3), one in the centre at a depth of 2000m taken in April 1983 (Fig. 4), and one on the east flank of the Porcupine Bank at a depth of 950m taken in May 1986 (Fig. 5). Attenuance has also been plotted for each depth. Light attenuance, as measured over a length of 1m by a transmissometer, gives an indication of the number of small particles in the water column. An oxygen profile is also included for the shallowest station. I am grateful to Dr. Michael Fasham (IOS) and Dr. Bill Simpson (IOS) for these profiles.

The three salinity profiles are similar for the depths and show the salinity maximum of the Mediterranean Water at depths between 800 and 1000m. The salinity minimum of the Labrador Sea Water is evident in the deeper profiles and a slight rise in salinity below 2000m can be seen in Fig.3. A seasonal thermocline forms at about 50m in summer months (Fig. 5 shows it forming in May 1986) and a permenant thermocline occurs below 600m, the depth of winter mixing (Ellett and Martin, 1973), dropping from about 10 °C to about 4 °C over a depth range of 800m (600

Figure 3. Temperature, Salinity and Attenuation profiles for the water column from the mouth of the PSB taken in May 1984 ("Discovery" St. 11106-1, 4000m).

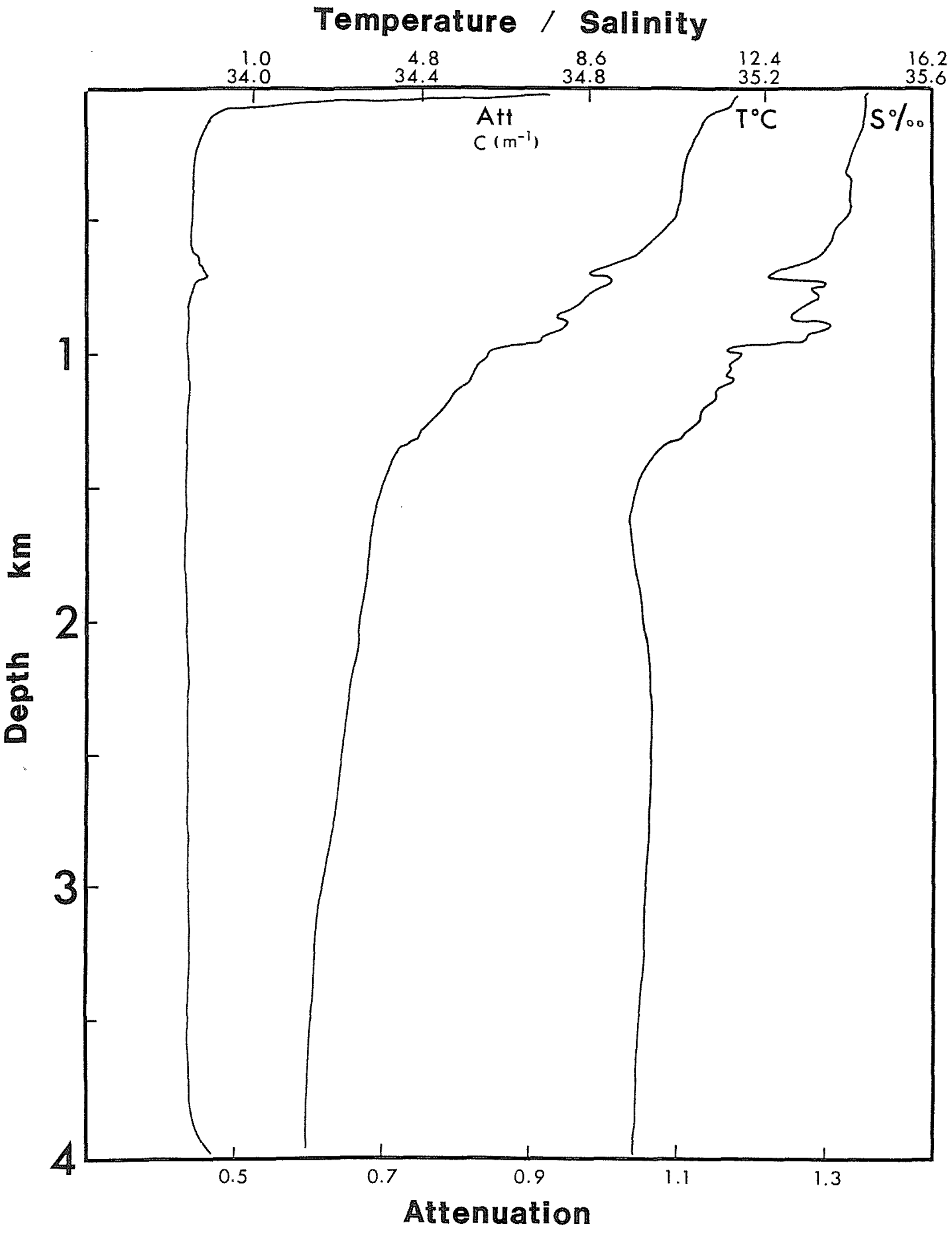

Temperature / Salinity
1.0
34.0
4.8
34.4
8.6
34.8
12.4
35.2
16.2
35.6
Att
C (m^{-1})
T°C
S‰
Depth km
1
2
3
4
0.5
0.7
0.9
1.1
1.3
Attenuation

Figure 4. Temperature, Salinity and Attenuation profiles for the water column from the centre of the PSB taken in April 1983 ("Challenger" St. 51719-4, 2000m).

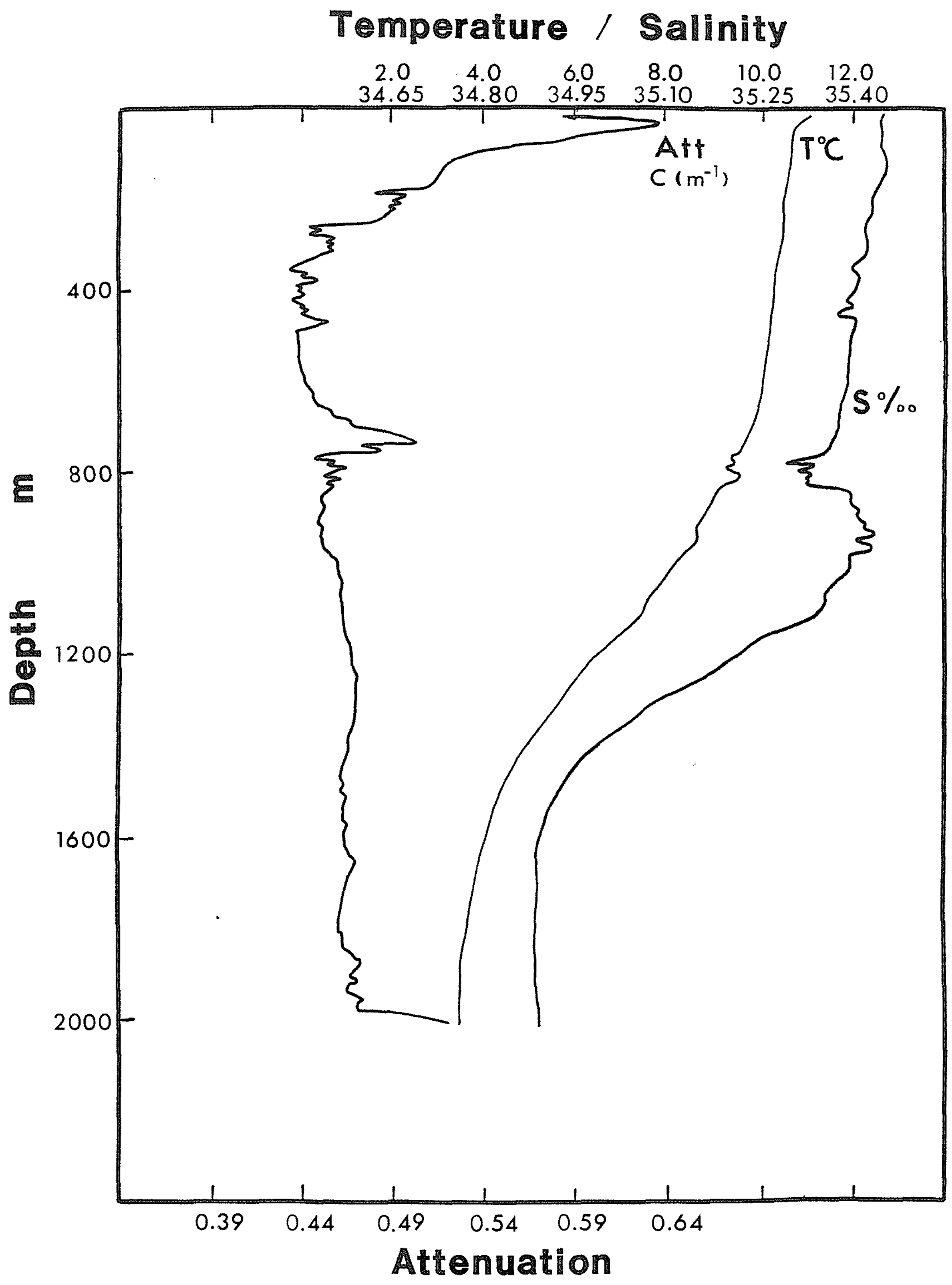
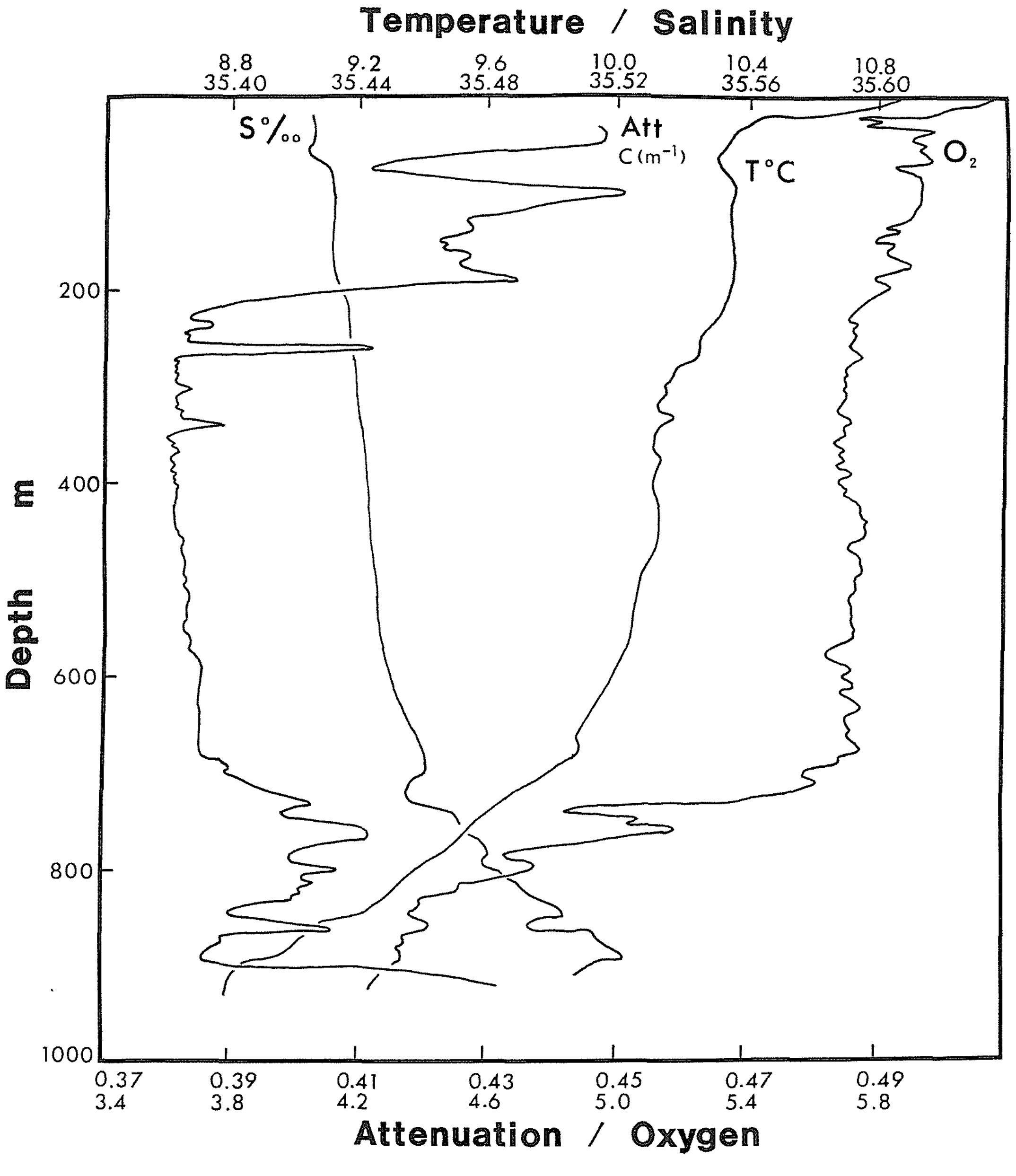

Temperature / Salinity
2.0
34.65
4.0
34.80
6.0
34.95
8.0
35.10
10.0
35.25
12.0
35.40
Att
C (m⁻¹)
T°C
S‰
Depth m
400
800
1200
1600
2000
0.39
0.44
0.49
0.54
0.59
0.64
Attenuation

Figure 5. Temperature, Salinity, Oxygen and Attenuation profiles for the water column from the eastern slope of the Porcupine Bank taken in May 1986 ("Discovery" St. 11296-1, 950m).


Temperature / Salinity
8.8
35.40
9.2
35.44
9.6
35.48
10.0
35.52
10.4
35.56
10.8
35.60
S ‰
Att
C (m⁻¹)
T °C
O₂
Depth m
200
400
600
800
1000
0.37
3.4
0.39
3.8
0.41
4.2
0.43
4.6
0.45
5.0
0.47
5.4
0.49
5.8
Attenuation / Oxygen

to 1400m). Below 1400m the temperature decreases slowly (Fig.3). The oxygen minimum of the Mediterranean Water is evident in Fig.5.

Bottom Nepheloid Layers (BNLs) and Intermediate Nepheloid Layers (INLs)are apparent in all three profiles. INLs have been found at depths of about 700m. The INLs in the centre of the PSB (Fig. 4) have been traced back to BNLs sitting on the Porcupine Bank at shallower depths (Dr. Michael Fasham, personal communication). The presence of BNLs on the Porcupine Bank were first reported by Dickson and McCave (1986) who believed the layers were formed by erosion of the seabed by internal waves and tides possibly related to upwelling events induced during periods of northerly long-slope winds. Dickson and McCave (1986) found that to the west of the Porcupine Bank the BNLs become detached from the seabed and spread off-slope along isopycnal surfaces to form INLs. It is clear that similar INLs occur to the east of the Porcupine Bank as well. The nepheloid layers are comprised mainly of small particles (8 to 40 µm), principally coccoliths derived from the Porcupine Bank sediments.

Dense coccolithophorid blooms occur along the shelf break and over the Porcupine Bank during summer months (Holligan, Viollier, Harbour, Camus and Champagne-Philippe, 1983; Holligan and Groom, 1986). These blooms are thought to be maintained by enhanced vertical nutrient fluxes caused by tidal mixing associated with internal wave activity at the shelf break (Holligan, Pingree and Mardell, 1985). Although these blooms occur primarily around the borders of the PSB, "streamers" from the blooms are carried out across the PSB probably by mesoscale activity on the continental slope (Holligan and Groom, 1986). The coccolithophorid blooms will be an important source of detrital material deposited on the seabed.

Although the deep sea has been regarded in the past as an environment free from seasonal perturbations, it is clear that in the Seabight and on the Porcupine Abyssal Plain there is a marked seasonal variation in the deposition of detritus to the seabed (Billett et al., 1983; Lampitt, 1985; Rice et al., 1986). Large amounts of detritus have been seen to accumulate on the seabed at many depths during May to July. It is evident from the phytoplankton species composition in the detritus that diatoms dominate the primary flux but that coccolithophorids and dinoflagellates are more important components of the flux in summer months (Billett et al., 1983). A similar temporal change in the total organic flux to the seabed and a change in the composition of that flux has also been noted in sediment trap studies in the Panama Basin (Honjo, 1982). Chemical analyses of the detritus from the PSB have shown that labile organic material is present in the detritus and therefore this material will be an important food source for the benthic biota. The detritus may cover the seabed completely or occur in localised patches around mounds and within hollows (Billett and Hansen, 1982). Currents in excess of 7 cm sec^{-1}, measured 1m above the seabed, readily resuspend the detritus and move it about the seabed (Lampitt, 1985).

Near-bed currents in the PSB are tidal and rarely exceed 15 cm sec^{-1} at a height of 1m above the seabed (Lampitt, 1985; Lampitt et al., 1986). The residual current runs parallel to the contours at all depths, and is part of a large, northward boundary current that runs along the european continental margin (Dickson, Gould, Griffiths, Medler and Gmitrowicz, 1986; Huthnance, 1986). The boundary current occurs throughout the year (Huthnance, 1986) but is thought to vary seasonally in mean speed, reaching maximum strength around November (Dickson et al., 1986). The current also broadens in its bathymetric range seasonally. Mean residual currents of 6, 2.2, and 9 cm sec^{-1} have been recorded on the slope in the Bay of Biscay, Goban Spur, and to the west of the Porcupine Bank respectively (Dickson, Gould, Muller and Maillard, 1985; Huthnance, 1986). The currents approaching the PSB from the south over the Goban Spur, therefore, will be a major factor in determining the deep circulation of the PSB.

In addition to the slope current, the upper slope will be affected by water cascading off the Celtic Shelf and Porcupine Bank in winter in some years (Cooper and Vaux, 1949) and by internal waves and tides inducing near-bottom motion (Huthnance, 1986). The latter will increase the sediment load of the water. Other slope processes will include turbidity currents, particularly on the lower slopes and within the channels.

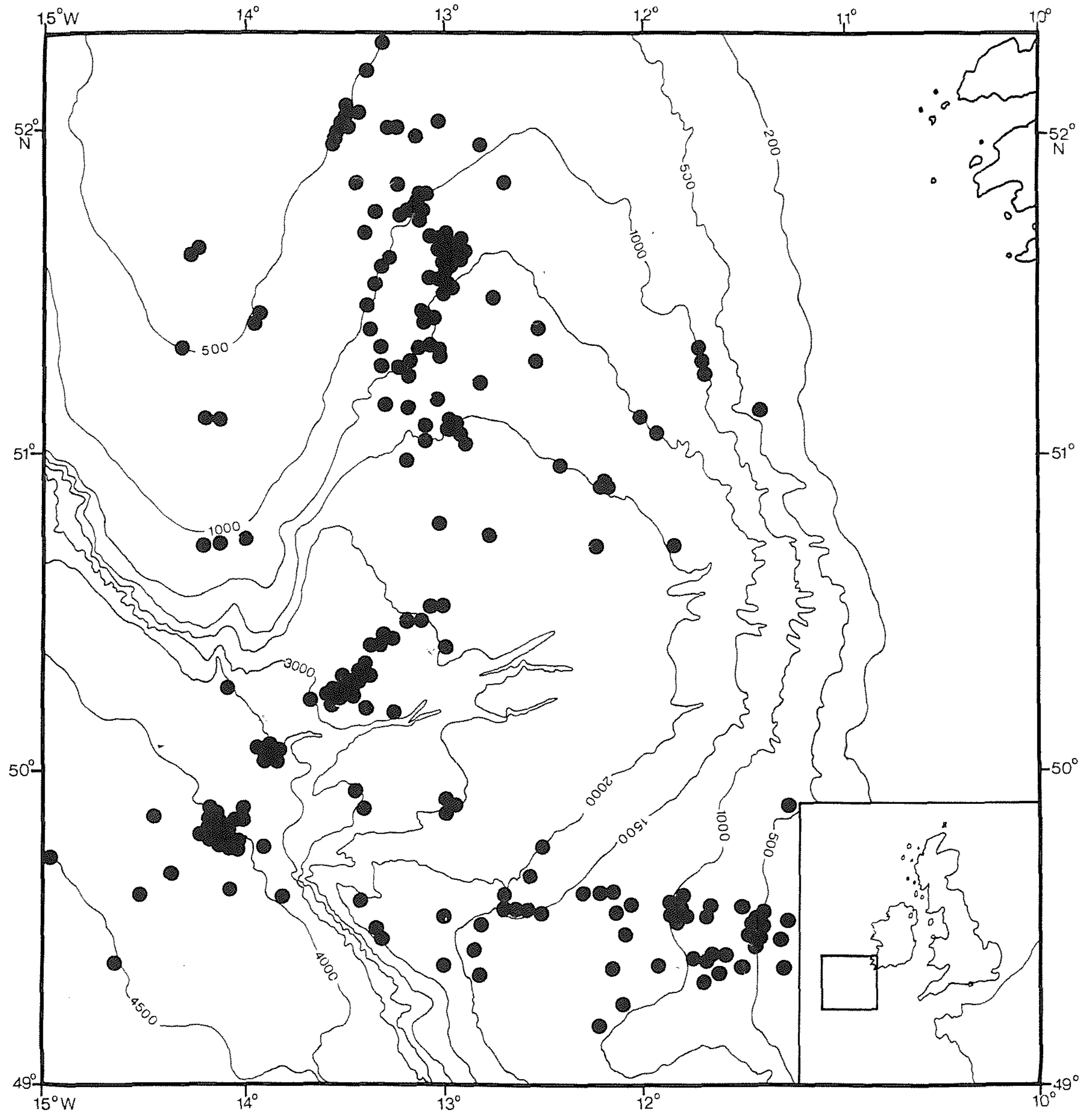
On the Porcupine Abyssal Plain currents are generally slow, flowing northward at 1 to 2 cm sec^{-1} up the central part of the abyssal plain, turning westward and southwestward as the abyssal plain shoals to the north, and thence southward and westward along the eastern side of the Mid-Atlantic Ridge (Dickson _et al_., 1985).

When the first samples from the Porcupine Seabight were taken in 1869 by "H.M.S. Porcupine" (Thomson, 1873), the bathymetry of the area had yet to be determined, although the Porcupine Bank had been discovered during an earlier "H.M.S. Porcupine" cruise. Further sampling was carried out by the "Flying Falcon" (1888), "Flying Fox" (1889), "H.M.S. Researcher" (1890), and the "Michael Sars" (1910), but it was principally the samples taken by the "Helga" and "Helga II" (1901 to 1914) for the Irish Fisheries Investigations that provided the first detailed information on the Porcupine Seabight fauna (Rice, 1986). The results from these expeditions, amongst others, were later collated and presented as part of a comprehensive account of the northeast Atlantic deep-sea fauna by Le Danois (1948). The vast majority of the samples from the Porcupine Seabight, however, were taken at depths shallower than 1500m, and the deepest station (2160m) was sampled by the "H.M.S. Porcupine" dredging expedition in 1869 (St. 43). Therefore, although the upper slope fauna has been well documented, including the fauna from the large coral areas between 700 and 1300m on the eastern slopes of the Seabight, the fauna below 1500m has yet to be fully described.

2.2 Sampling details.

During the period November 1977 to December 1986 over 250 samples of holothurians have been taken in the Porcupine Seabight and on the Porcupine Abyssal Plain between 200 and 4800m. Details of station number, type of sampling equipment, date of sampling, depth limits, location of haul, and area sampled are listed in Appendix 1. The majority of benthic samples come from a transect that extends in an arc from the middle of the Porcupine Bank to the centre of the Seabight, and thence through the mouth of the Seabight out onto the Porcupine Abyssal Plain (Fig. 6). Another transect was sampled at depths shallower than 2600m on the Goban Spur. In addition, a few samples were taken on the Porcupine Bank to the south of the main transect and in the northeast of the Seabight. One important area, the channel-ridden eastern slope of the PSB, remains unsampled for logistic reasons.

Figure 6. Stations sampled in the Porcupine Seabight with holothurians. Contours are 500m isobaths.


15°W
14°
13°
12°
11°
10°
52° N
51°
50°
49°
200
500
1000
500
1000
1000
1500
2000
3000
4000
4500
500

Benthic sampling intensity has not been constant at all depths along the transect. Taking the median depth sampled for each of the sledge (BN) and trawl (OT+GT) hauls, the frequencies of the median depths for each type of gear and for all samples combined, grouped in 200m depth bands, are plotted in Figs 7 to 9. Three sampling peaks are evident at about 1000m, 2800m, and 4000m, in Fig. 7. The upper slope peak results from the concentration of trawls at about 1000m (Fig. 9) and from a plethora of BN samples taken at about 1300m as part of a study into the sampling repeatability of the sledge within a small area (2km diameter) (Fig. 8). A similar repeat sampling area for the sledge was set up at about 4000m and led to the sampling peak at this depth (Fig. 8). Sampling at about 2800m was greater owing to the repeated BN sampling for a small enigmatic holothurian, Kolga hyalina, which was found in abundance at this depth (Fig. 8). Two troughs occur in the sampling profile (Fig. 7) and are common to both the sledge and the trawl hauls (Figs 8 and 9). The trough at about 3200m corresponds to the area of rough terrain at the mouth of the PSB (Fig. 1).

Benthic holothurians have been sampled in the Porcupine Seabight (PSB) using either an IOS epibenthic sledge (BN) (Aldred, Thurston, Rice and Morley, 1976; Rice et al., 1982) or a semi-balloon otter trawl (OT) (Merrett and Marshall, 1981). In addition, some samples have been kindly taken in the PSB by the SMBA using a single warp trawl (SWT), a Granton trawl(GT), or an Agassiz trawl (AT) (Gordon and Duncan, 1985). Samples from these three trawls were not used to quantify holothurian abundance. Apart from the IOS samples, one other holothurian was collected by Dr. J.D. Gage (SMBA) on the Porcupine Abyssal Plain (Gage et al., 1985a) and is included in this thesis. Photographic observations of benthic holothurians were made using a camera mounted on the IOS epibenthic sledge.

Figure 7. Total number of samples taken grouped in 200m depth bands. Median depth for each haul is used. Stations are banded 100 to 300m, 300 to 500m, 500 to 700m, etc.

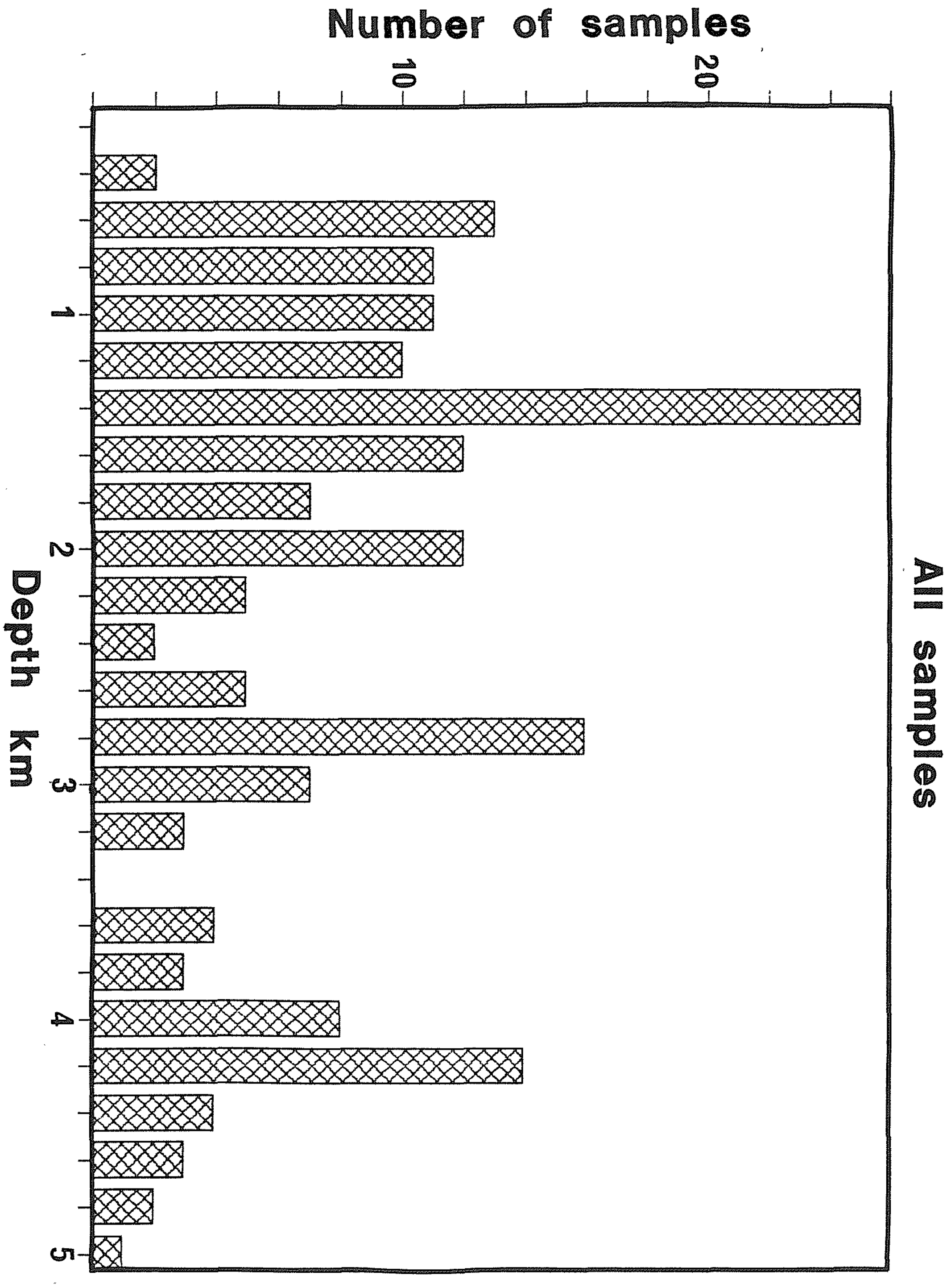

Number of samples
10
20
All samples
Depth km
1
2
3
4
5

Figure 8. Total number of Epibenthic Sledge hauls grouped in 200m depth bands.

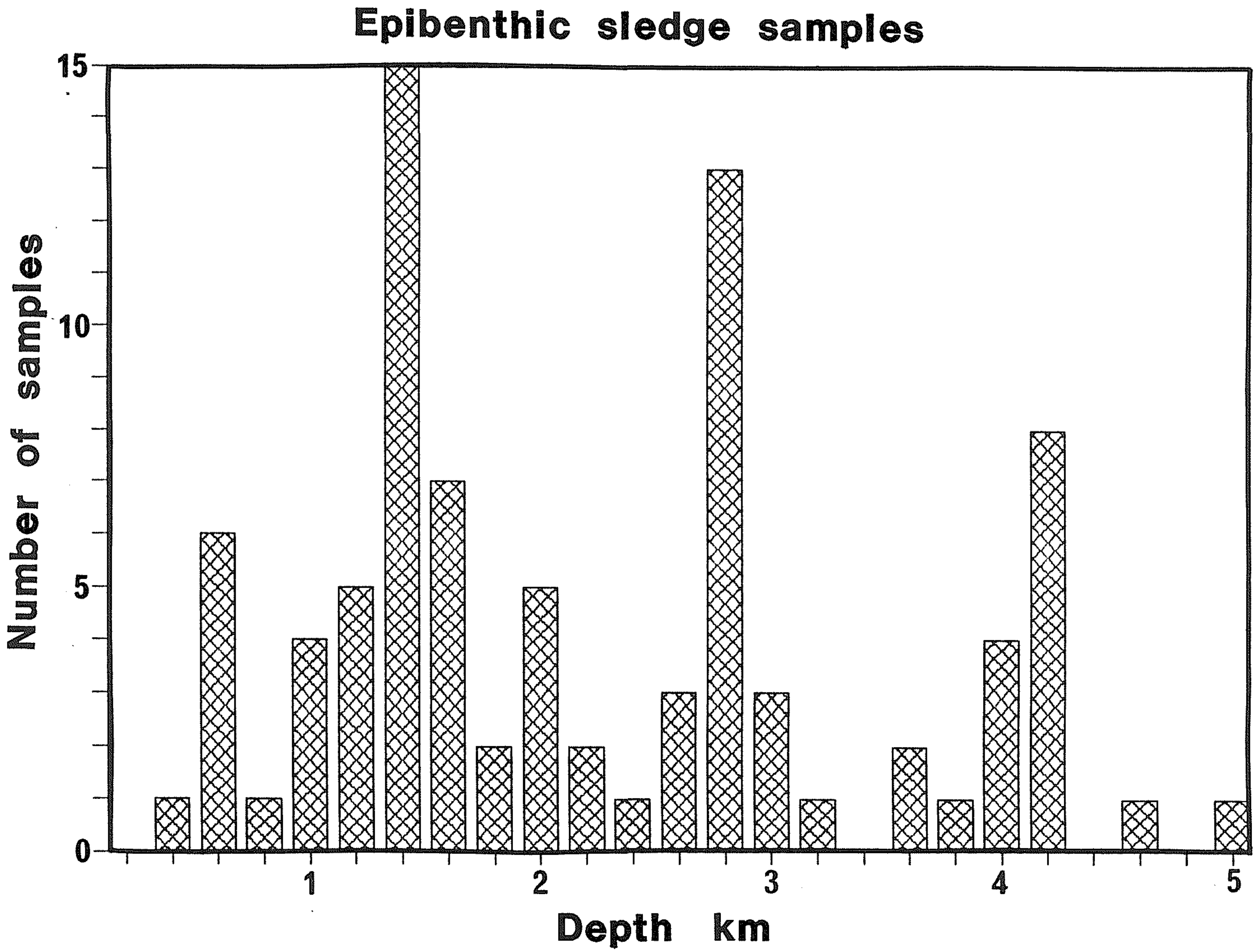
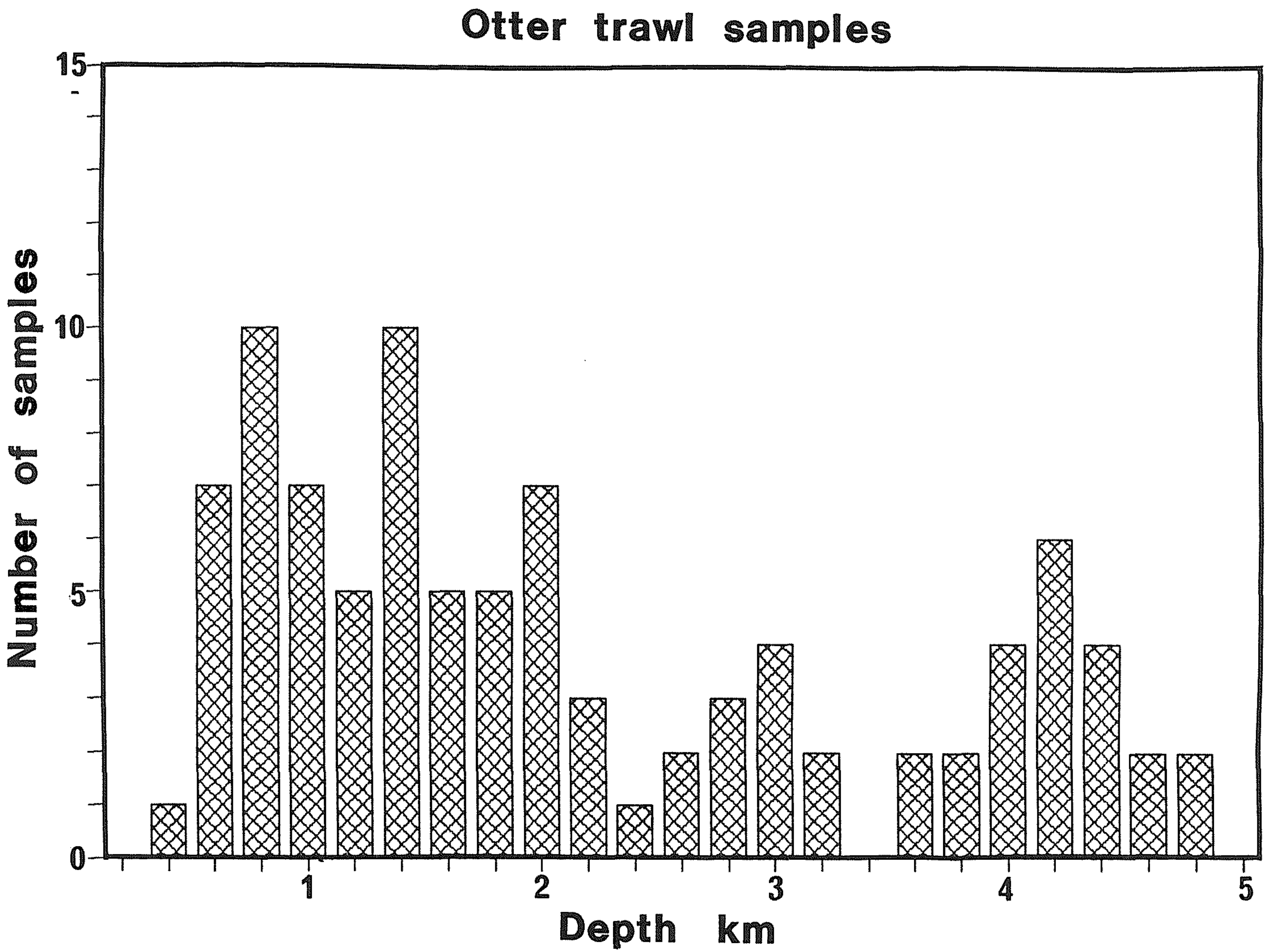

Epibenthic sledge samples

Figure 9. Total number of Otter trawl and Granton Trawl hauls grouped in 200m depth bands.


Otter trawl samples
Number of samples
0
5
10
15
Depth km
1
2
3
4
5

Apart from the benthic holothurians, benthopelagic holothurians and pelagic juveniles of benthic species were sampled in the Seabight, on the Porcupine Abyssal Plain and elsewhere in the northeast Atlantic by a rectangular midwater trawl (RMT 1+8, Baker, Clarke and Harris, 1973).

The IOS epibenthic sledge has a frame formed from scaffolding tubes connecting two lateral skids. Along the back, between the two skids, a single large net or a number of smaller nets may be fitted with a total width of 2.29m and a height of 0.61m (Aldred et al., 1976). The sledge is monitored acoustically and is fitted with an opening/closing device which occludes the mouth of the net when it is not on the seabed. Models of the sledge used since 1979 have been fitted with a suprabenthic plankton net mounted on the superstructure above the benthic net. The plankton net is also endowed with an opening/closing device and has a mesh of 0.33mm (Rice et al., 1982). The sledge is acoustically telemetered, relaying back to the ship the temperature, the depth, the angle of the sledge, the position of the opening/closing device and the distance run as recorded by an odometer mounted to one side of the sledge (Rice et al., 1982).

The single large net used on the sledge has a mouth width of 2.29m, a mouth area of 1.4m^2 and a mesh of 4.5mm. This net was replaced in many cases by a "combination" or "multi-net" consisting of three nets strapped together across the width of the sledge. One net, in the centre, has a mouth width of 0.68m, a mouth area of 0.42m^2 and a mesh of 1.0mm. This net is placed between two other nets each with a mouth width of 0.8m, a mouth area of 0.49m^2 and a mesh of 4.5mm. For the quantification of large holothurians the catch from the single large net or the combined catch from the three "multi-nets" has been used in this study, but for small holothurians that are not retained adequately by a 4.5mm mesh, only the catches from the fine mesh net of the combination system have been considered. An estimate of the area sampled by each net was obtained using the distance run. This was calculated either from the odometer records or from the positions where the sledge alighted on and left the seabed at the start and end of each haul.

For a few species abundance estimates based on these data are compared with results derived from photographic surveys undertaken simultaneously using the epibenthic sledge camera. The camera is activated when the sledge reaches the seabed and starts to sample. A photograph is taken every 15 seconds. The sledge is towed at about 1.5 knots resulting in a distance of about 12m between photographs. A change in the design of the epibenthic sledge in 1979 led to the camera being mounted at a greater height on the epibenthic sledge superstructure. This allowed the camera angle to be steepened, reducing the variability in the area covered by each photograph but also reducing the total area photographed.

Abundance data are quoted using both methods described above but the biomass data have been calculated using the odometer records only. Wet weight (WW) of the holothurians was determined after the coelomic fluid had been drained and the body had been wiped free of surface water. Dry weight (DW) was determined after drying the specimens in a freeze-dryer or under vacuum at 60° C for up to 14 hours. Subsamples were then analysed for ash-free dry weight (AFDW) by heating in a muffle furnace at 500° C for 4 hours.

The semi-balloon otter trawl has a wing-end spread of 8.6m. While it is fishing it is monitored by an acoustic beacon mounted on one of the two trawl doors. The net is constructed of 4.4cm mesh in the main part of the net, 3.7cm mesh in the middle part of the net, and 3.7cm mesh outside a 1.3cm mesh liner in the codend. The headline of the net is provided with buoyancy spheres and the height of the net from the footrope to the headline is about 1.5m (Merrett and Marshall, 1981). The area sampled by each trawl was estimated using the distance run by the trawl over the seafloor, from the point where it reached the seabed to where it lifted off the seabed at the end of the haul. In some cases only representative samples of the invertebrates were taken from the trawls. These samples have been used to determine the bathymetry of the species but have not been used for abundance estimation.

A few benthopelagic holothurians and the juveniles of benthic species have been sampled with midwater nets (see Appendix 1 for station details).The rectangular midwater trawl (RMT 1+8) uses two nets of differing mesh size (0.32mm and 4.5mm mesh) concurrently. The nets are opened and closed by a mechanical release gear which is activated acoustically, and the depth, temperature and the speed of the net through the water (from which the volume filtered, and hence the abundance of holothurians per unit volume, can be calculated) are continuously telemetered. The net was modified in order to be able to sample within 5m of the seabed at abyssal depths, at first using a system of mercury switches (Boxshall and Roe, 1980) and more recently by mounting a small echo-sounder above the nets. Some samples were obtained using a multiple midwater trawl (RMT 1+8M, Roe and Shale, 1979).

A wide-area survey camera system has been used to estimate the abundance of pelagic holothurians swimming above the seabed. The camera takes photographs covering an area of 80 square metres from a height of 10m above the seafloor (Huggett, 1987). The camera takes a photograph every

15 seconds and is towed at approximately 0.5 knots resulting in an overlap of about 40% between adjacent frames. The height of the camera above the seafloor is monitored by a near-bottom echo-sounder.

Section 5.3 describes how the apparent ability of holothurians to select for particles on the sediment surface has been investigated using chloropigments, that is the chlorophylls and their breakdown products, as markers for organic matter in both sediment and stomach content samples. The chloropigments are extracted from the samples by homogenisation with acetone and are then separated by injection onto a High Performance Liquid Chromatography System using the method of Mantoura and Llewellyn (1983) with slight modifications. The chloropigments are sequentially eluted depending on their polarity. Each chloropigment is detected by its fluorescence and a characteristic fluorescence chromatogram is produced for each sample. From the chromatogram each pigment can be recognised and its concentration calculated. The pigments were first extracted in acetone and the samples were then dried at 40 °C for 24 hours to obtain a sample dry weight. All the analyses and calculations were undertaken by Ms. Carole Llewellyn (The Institute for Marine Environmental Research) as part of a collaborative study.

The organic carbon in sediment samples was determined by the wet oxidation of sediment in potassium dichromate following the decomosition of calcium carbonate in phosphoric acid. Prior to the oxidation of the sediment large metazoan and protozoan meiofauna were removed from the samples. The salt content of each sample was determined to allow values to be expressed as a percentage of salt-free sediment dry weight.

In the species synopsis of the holothurians of the PSB (Section 4) the bathymetric range for each species is given using the shallowest and deepest records. A reduced bathymetric range is given for the depths at which each species was most abundant. However, in the text and the tables where a depth is recorded for a particular station the median depth is used which may lead to some apparent discrepancy between the data.

3. Taxonomic details

The higher classification of the holothurians used in this thesis follows Pawson (1982b). The classification adopted by the following authors for the six orders of holothurians is used : Pawson and Fell (1965) for the Dendrochirotida and Dactylochirotida, Hansen (1975) for the Elasipodida, Deichmann (1930) for the Aspidochirotida (except that *Zygothuria* is treated as a synonym of *Mesothuria*), Deichmann (1940) for the Molpadiida, and Clark (1907) for the Apodida. The classifications for the Aspidochirotida and Molpadiida proposed by Heding (1931, 1935, 1940, 1942) have been rejected in most cases and are not used here.

The Porcupine Seabight material allows a few taxonomic points to be made. Some are short and are dealt with in Section 4.2, e.g. notes on the genera *Thyone*, *Pseudostichopus*, *Benthodytes* and *Elpidia*, but three topics require greater detail and are treated separately in this section.

3.1 The family Ypsilothuriidae Heding, 1942 : taxonomy and ontogenetic changes in the body wall ossicles.

The taxonomy of the family Ypsilothuriidae Heding, 1942 has been a problem ever since the description of the type species, *Ypsilothuria talismani* E. Perrier 1886, from specimens collected in the northeast Atlantic. The diagnosis for the genus was incomplete and led to some confusion with another genus, *Sphaerothuria* Ludwig 1894, created for some specimens collected in the Pacific. A more detailed diagnosis for *Ypsilothuria* was provided by R. Perrier (1902) but confusion reigned over the precedence of *Ypsilothuria* or *Sphaerothuria* until Heding (1942), in his work on the "Ingolf" material, formed the family Ypsilothuriidae. Since then, apart from a minor diversion when Panning (1949) demoted the family to the level of a sub-family, the Ypsilothuriidae has been recognised as a distinct group incorporating the genera *Ypsilothuria*, *Echinocucumis* Sars, 1859 and *Ypsilocucumis* Panning, 1949 (Pawson, 1965). These genera possess features, notably the structure of the tentacles, which are at variance with the characters normally associated with the order Dendrochirotida, the order in which the Ypsilothuriidae were originally placed. Therefore, Pawson and Fell (1965) revised the classification of the dendrochirotid holothurians and formed a new order, the Dactylochirotida, to include the families Ypsilothuriidae, Rhopalodinidae R. Perrier, 1902 and Vaneyellidae Pawson and Fell, 1965.

Difficulties have also occurred in determining the genera and species within the Ypsilothuriidae. Ontogenetic changes in the shape of the specimens and in the form and size of the body wall ossicles have never been described adequately. Features used to characterize one species may be apparent in another species but in individuals of a different size. It is necessary, therefore, to relate the taxonomic characters of each species to the size of the individual.

Epibenthic sledge hauls in the PSB and the Rockall Trough using a 1.0mm mesh size have taken large samples of three ypsilothuriid species, Echinocucumis hispida, Ypsilothuria talismani and Y. bitentaculata attenuata. Moreover, the samples contain specimens of a variety of sizes greater than 1.0mm providing, for the first time, ideal material for examining ontogenetic changes in taxonomic characters. Using this detailed information it will be possible to investigate the relationships of the north-east Atlantic ypsilothuriids with those from the Caribbean and the Pacific. I am indebted to Dr. J.D. Gage (The Scottish Marine Biological Association) for access to material of Y. bitentaculata attenuata from the Rockall Trough.

Echinocucumis hispida (Barrett, 1857)

(i) ontogenetic changes in body shape.

Small specimens are globular and slightly U-shaped owing to the partial extension of the anterior and posterior ends which are both directed dorsally (Fig. 10A,B). This shape is similar to adult Ypsilothuria (e.g. Fig. 10R). As E. hispida increases in size, the anterior and posterior ends become drawn out relative to the rest of the body, making the body more elongate and less globular (Fig. 10C-I). The height of the body in large specimens is typically 30 to 40% of the total horizontal length. Beyond a length

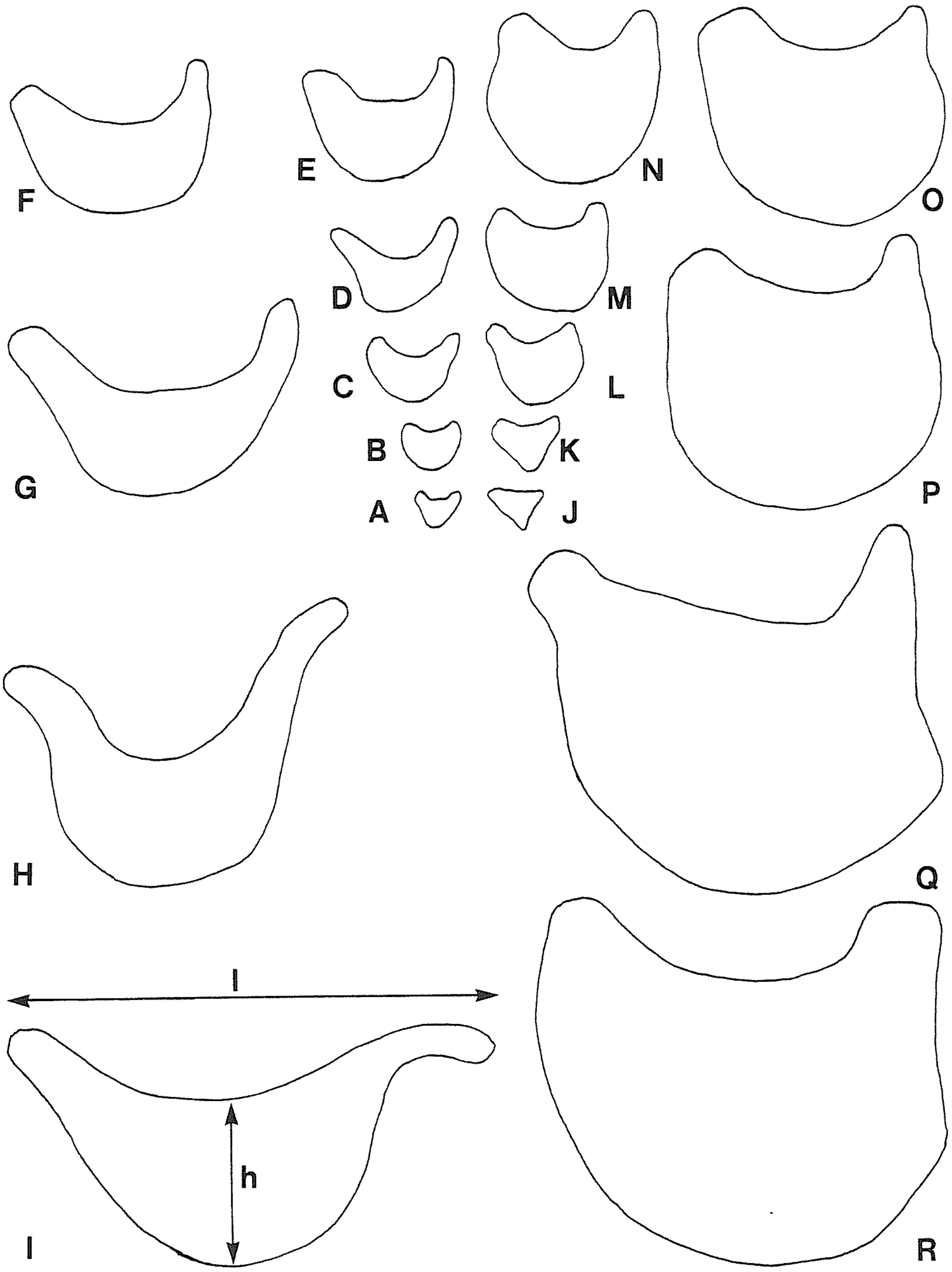
Figure 10. Ontogenetic changes in the body shape of

Echinocucumis hispida (A - I),

Ypsilothuria talismani (J - M),

Y. bitentaculata attenuata (N - R).

l = length of specimen.
h = height of specimen.


F
E
N
O
D
M
P
C
L
G
B
K
A
J
H
Q
l
h
I
R

of about 12mm (Fig. 10I) the body shape does not change appreciably although a variety of postures may be adopted owing to the contraction of the specimens during capture and preservation. Usually, the body has a shallow U-shape. In this configuration the largest specimen from the PSB measures 14mm long but the species is likely to be considerably larger in an uncontracted state.

The specimens from the PSB are similar in size to other E. hispida sampled in the northeast Atlantic (Sars, 1861; Heding, 1942). Sars (1861) examined specimens up to 20mm long but it is evident from the figures drawn that the greatest lengths may have applied to specimens with a flattened rather than a U-shaped posture. Pawson (1965) described two larger specimens, about 18 and 21mm long, from the southwest Pacific, which measured some 40 and 50mm respectively along the greatest curvature of the body (the ventral surface). In comparison, the greatest length of the PSB specimens measured in a similar fashion was 25mm. In general, the curvature length is about double the horizontal length for specimens in a U-shaped attitude.

(ii) calcareous ring plates.

There are ten plates which are unequal in size. The ventral plates may be almost twice the size of the dorsal plates. For example, in a specimen 11mm long the mid-ventral radial plate (Fig. 11A) is 400µm wide and 460µm high (including the anterior process) while the mid-dorsal interradial plate (Fig. 11F) is about 200µm wide and 280µm high. To accommodate this change in plate size the two halves of the base of some plates may be developed disproportionately (Fig. 11B,D,E,G). This feature leads to a curve in the calcareous ring so that the dorsal plates are closer to the anterior end than the ventral plates, as in Ypsilothuria. The mid-ventral and ventro-lateral radials are often slightly larger than the ventral interradial plates, as figured by Sars (1861, Fig. XI,13).

The anterior process of the plates is wide and is usually slightly bifid at its end (Fig. 11A,C,E). However, the lateral interradial plate differs from all the other plates in having a narrow tooth-like process (Fig. 11D,G). In this respect the PSB material differs from that described by both Sars (1861), who indicated that the lateral interradial plates have a bifid anterior process (op. cit. Fig. XI, 13), and Heding (1942) who noted that while most of the anterior processes were bifid, a few ended in a simple point but only in small specimens. No such relationship between specimen size and form of anterior process is evident in the PSB material. However, examination of many PSB specimens shows that the structure of the ventral interradial plates, at least, is very variable (Fig. 13A); in some cases the anterior process may be rather low and bifid (Fig. 11H) while in others it is well developed and blunt (Fig. 11B). It is not possible, therefore, to state categorically that all the anterior processes are bifid.

(iii) ontogenetic changes in body wall ossicles.

The calcareous deposits of small specimens (1 to 2mm long) comprise exclusively of primary crosses with a spire placed excentrically on the primary rod (Fig. 11I). Some of the deposits are tripartite (Fig. 11J) while others may have two columns at the base of the spire which fuse distally (Fig. 11K). The ends of the arms of the primary cross are usually perforated by one or more holes (Fig. 11I). In small specimens the primary crosses are about 150μm long, but in larger specimens they may reach a

Figure 11. *Echinocucumis hispida*.

Calcareous ring plates from 11mm long specimen :

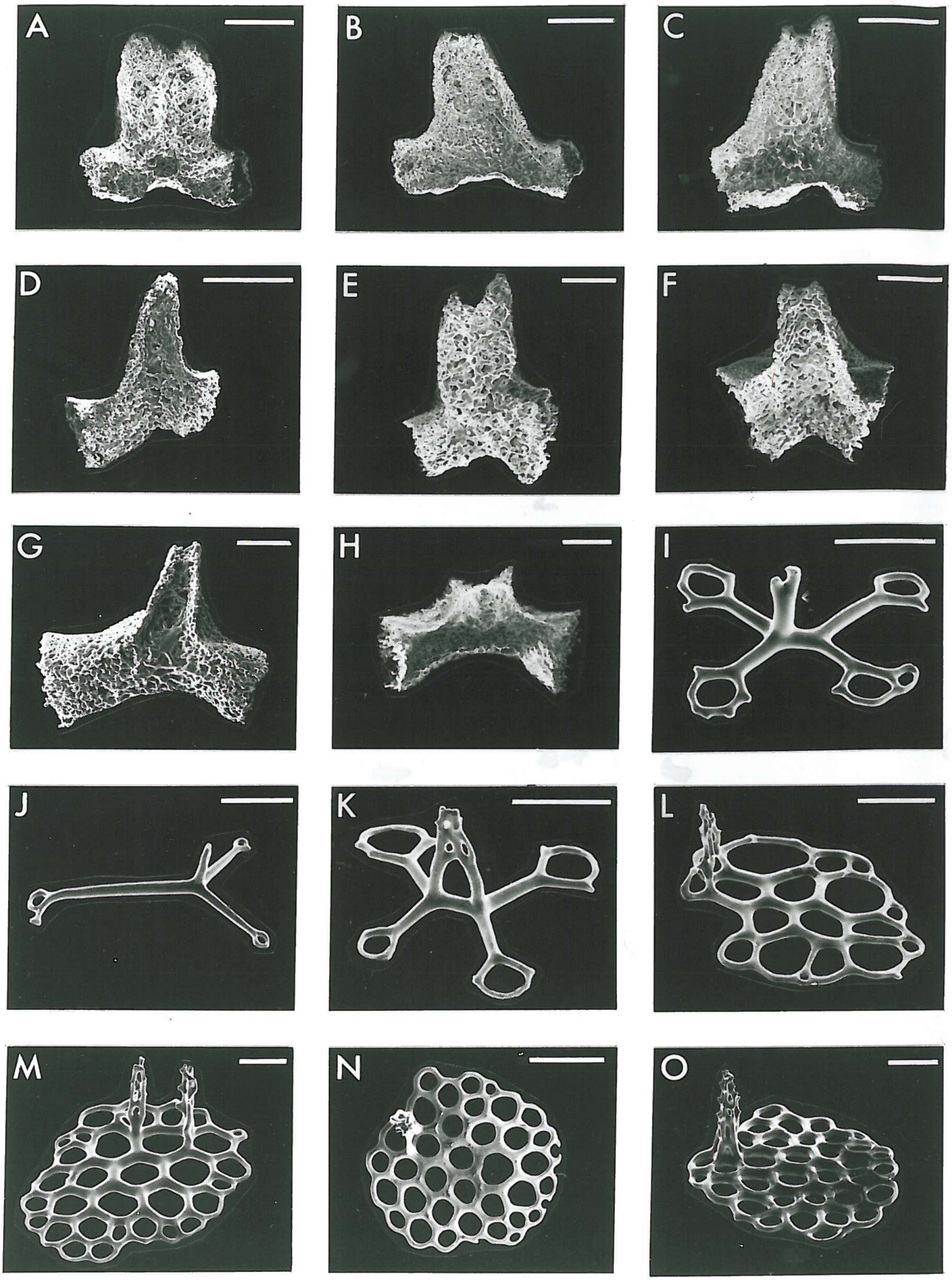
A) Mid-ventral radial ,
B) Ventro-lateral interradial,
C) Lateral radial,
D) Lateral interradial,
E) Dorso-lateral radial,
F) Mid-dorsal interradial.

Calcareous ring plates from 10mm long specimen :

G) Lateral interradial,
H) Ventro-lateral interradial.

I) Body wall ossicles from a specimen 1mm long,
J to M) Body wall ossicles from a specimen 4mm long,
N and O) Body wall ossicles from a specimen 10mm long.

Scale bars : A to D, and N) 200µm; E to M, and O) 100µm.


A
B
C
D
E
F
G
H
I
J
K
L
M
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O

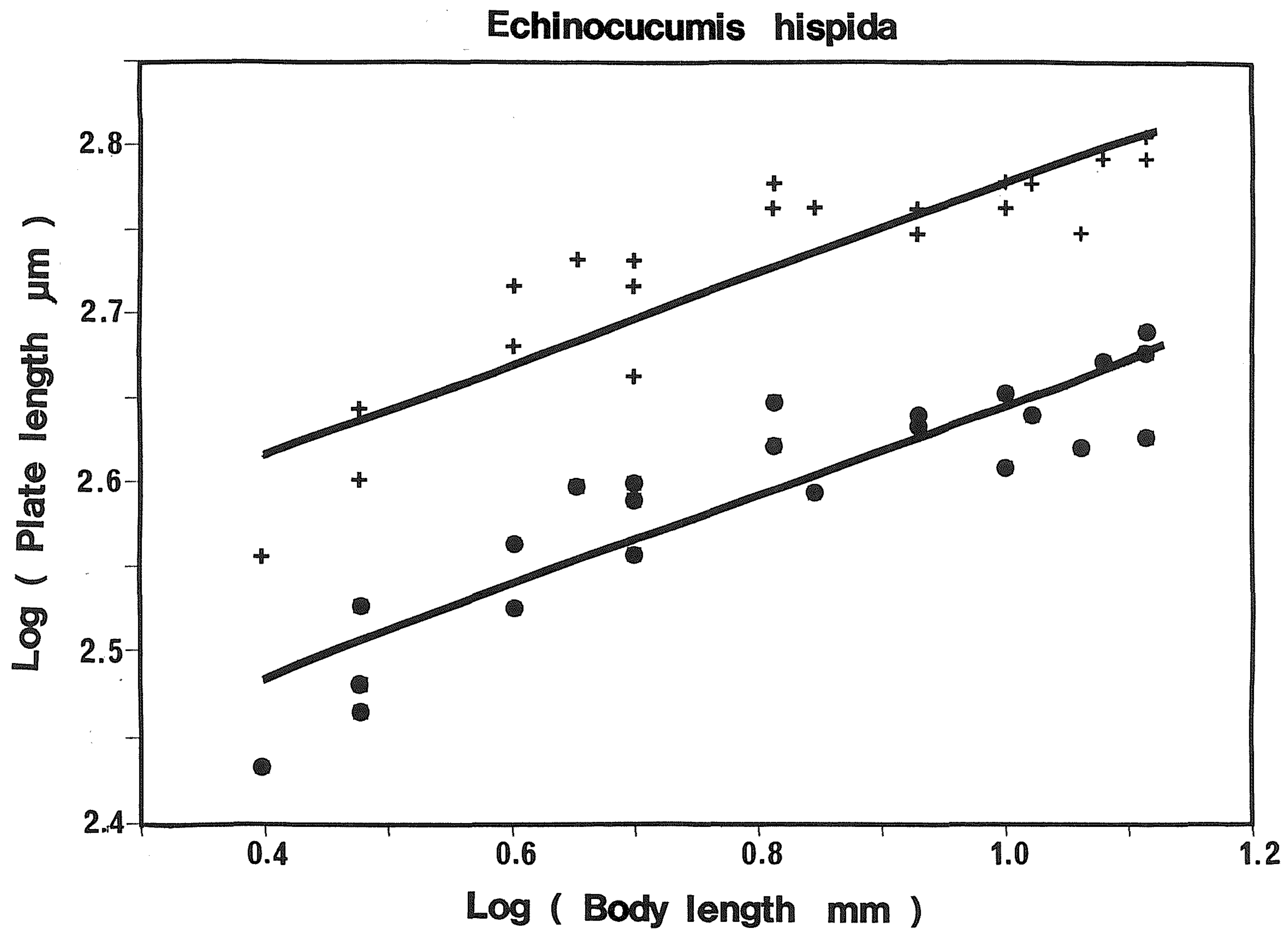
length of 300μm before developing into a reticulated plate. Adjacent arms of the primary cross are joined up during the first stages of plate formation. Development continues by the formation of spurs around the periphery of the plate which combine to make further perforations (Fig. 11L). However, the plate does not grow at the same rate around its whole perimeter since the spire is always placed close to, or on, one edge (Fig. 11N,O). The holes are generally placed in rows and are 60 to 90μm in diameter, decreasing in size towards the edge. All plates are composed of a single calcareous layer.

The spire is conical and spiny. It is formed from several columns connected together by several cross pieces (Hansen, in press) and usually has a narrow base overlying just one hole on the plate. The spire reaches a height of at least 450μm on the largest plates found in the present material (< 640μm long). In exceptional cases two separate spires may be formed (Fig. 11M).

The plates are roughly oval in shape and in a few cases one edge of the plate is indented to allow the passage of a tubefoot through the skeleton. In the mid part of the body the plates overlap only slightly but at the posterior and anterior ends they occur in several layers owing to the contraction of the holothurian. The plates at either end of the body are generally smaller than those in the middle and often lack a spire.

Plates are first developed from primary crosses in specimens some 2mm long. Plates with several holes account for about 25% and 70% of the total number of body wall ossicles in specimens 3 and 4mm long respectively, increasing to more than 95% in specimens longer than 6mm. Both the maximum plate length and the mean plate length of ossicles are correlated with the length of the specimens

Figure 12. Echinocucumis hispida. Body wall ossicles : the relationship between maximum and mean ossicle length with body length plotted on a log scale.


Echinocucumis hispida
Log (Plate length µm)
2.8
2.7
2.6
2.5
2.4
0.4
0.6
0.8
1.0
1.2
Log (Body length mm)

but the relationships are non-linear (Fig. 12). Plate growth is greatest in small specimens. The largest dimension of a plate from the largest specimens examined was 640µm. Using the regression calculated from the data (Fig. 12) specimens some 20mm long would not be expected to have plates more than about 750µm long. This is in contrast to the plates observed by Deichmann (1930) and Pawson (1965) which had an average length of 1mm.

(iv) other taxonomic features.

There are 10 digitate tentacles. The two lateral tentacles on opposite sides are very much longer than the rest. The tentacle ossicles are slender curved rods, 100 to 150µm long, perforated at either end (Fig. 13B). The centre of the rod often bears a small rounded knob pierced by a single hole. The ossicles differ from those in the introvert which are small, elongate plates (Fig. 13C), sometimes irregular in shape, each with a few holes. The tubefeet are small, indistinct, and are restricted to the radii. They appear to be missing in the mid part of the two dorsal ambulacra but are present throughout the three ventral ambulacra. They are widely spaced in a single row. In some cases an indistinct double row may occur. At the midpoint of the ventral ambulacrum a pair of tubefeet may be found. These are particularly well developed in small specimens and are 1mm long (contracted) in specimens measuring only 1.5mm in length. They are likely to act as an anchor for the holothurian during its early stages of development. The ossicles of the tubefeet are principally curved rods (Fig. 13D,E) which are particularly prevalent in small specimens. They resemble the ossicles of the tentacles in being perforated at either end and in having a central perforated, rounded knob. Some ossicles have short, irregular side branches.

Figure 13. Echinocucumis hispida.

A) Ventro-lateral interradial calcareous ring plates, all about 150μm wide, from 6 different specimens all 8 to 9mm long, showing variation in the shape of the anterior process.

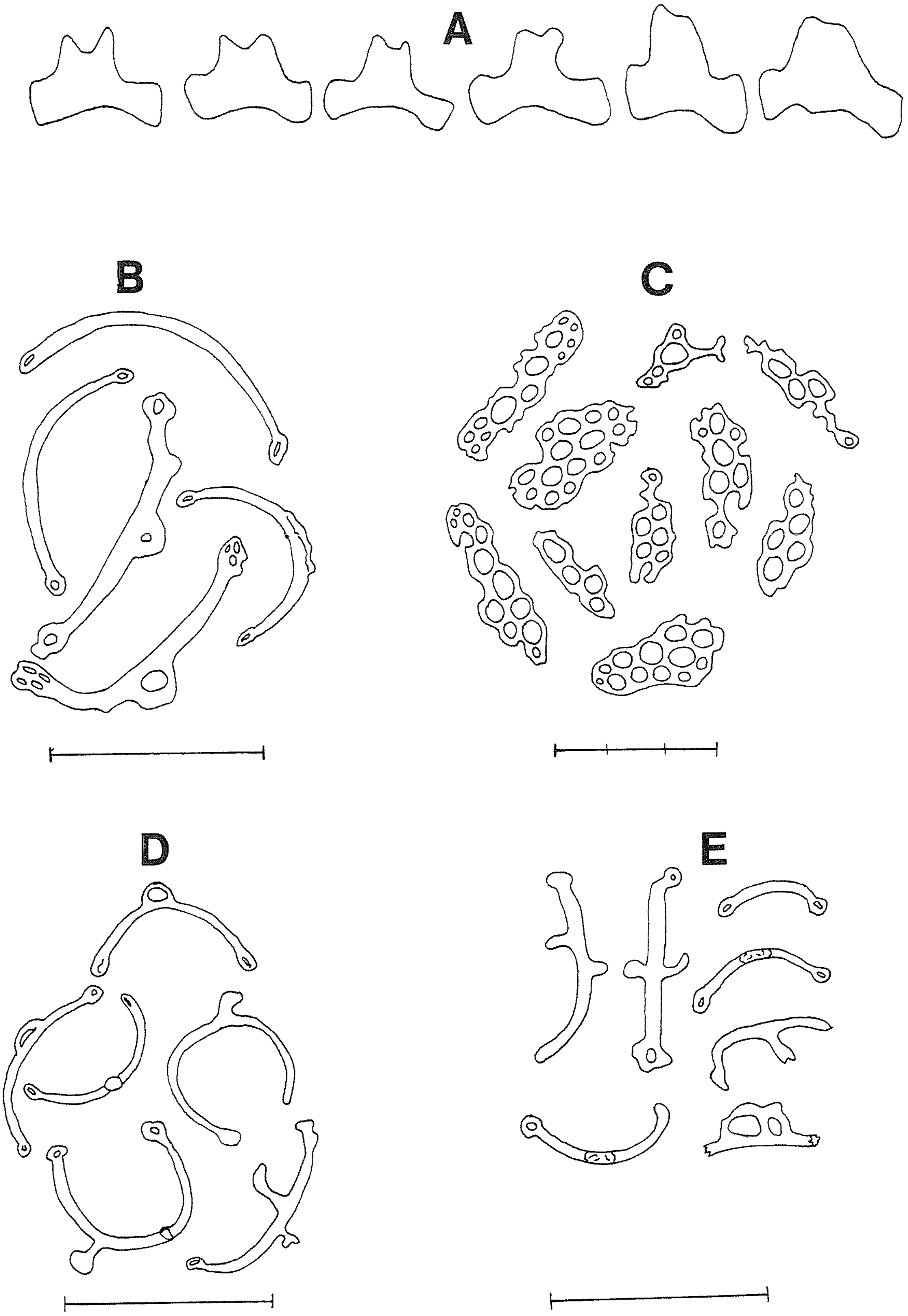
B) Tentacle ossicles from a specimen 10mm long.

C) Introvert ossicles from a specimen 10mm long.

D) Ossicles from the mid-ventral tubefeet of a specimen 1.5mm long.

E) Tubefeet ossicles from a specimen 10mm long.

Scale bars : B,D,E) 100μm, C) 300μm.


A
B
C
D
E

Ypsilothuria talismani E. Perrier, 1886.

(i) ontogenetic changes in body shape.

Small specimens (1 to 2mm long) are triangular in shape (Fig. 10J). When they are viewed dorsally they appear thin and sub-globular but as the holothurian increases in size the body becomes more globular and the anterior and posterior ends extend slightly forming two small projections (Fig. 10K-N). Beyond 4mm length the body changes only a little in shape and is identical to *Y. bitentaculata attenuata* (Fig. 10N-R). In most cases when the specimens are viewed laterally, the posterior and the anterior parts of the ventral surface are more or less parallel to each other and perpendicular to the dorsal surface forming a tight U-shape. This is the posture found in most preserved specimens although there is some variation in shape. The height of the body in large specimens is typically 70 to 80% of the horizontal length. The largest specimens measured 7mm in horizontal length and 18mm along the curvature of the ventral surface. The curvature length is usually about two and a half times greater than the horizontal length.

The PSB specimens are similar in length to other *Y. talismani* reported from the north Atlantic, including the type material (Perrier, 1886). Deichmann (1940) examined specimens up to 10mm in length while Heding (1942) referred to specimens up to 15mm long although some of these would not have been in a tight U-shaped posture.

(ii) calcareous ring plates.

There are essentially 8 calcareous ring plates (Fig. 14A-H). The two ventral interradial pieces are generally considered to be missing. However, although only 8 plates separate initially from the calcareous ring, when it is placed in an alkaline solution the two ventro-lateral radial plates separate into two halves (Fig. 14D). It would appear, therefore, that these plates are a composite of the true ventro-lateral radial and the ventral interradial pieces. The structure of this composite plate is similar in small (Fig. 14B) and large (Fig. 14D) specimens. It is wider than any of the other plates and has a short, broad anterior process. In contrast, the base of the mid-ventral radial plate is narrow and the height of the anterior process usually exceeds the width of the plate (Fig. 14F). The anterior process is often slightly bifid in large specimens, and is distinctly so in small specimens.

The mid-dorsal interradial (Fig. 14H) and the dorso-lateral radial plates (Fig. 14E) are well developed and are similar in size to the ventral plates. Each of these plates has a large bifid anterior process. Each half of the base of the lateral interradial (Fig. 14A,C,G) and the dorso-lateral radial plates (Fig. 14E) may be developed disproportionately, allowing the calcareous ring to curve so that the dorsal plates lie closer to the mouth than the ventral plates, as in *E. hispida* and *Y. bitentaculata attenuata*.

The most significant feature of the calcareous ring is that the anterior process of the lateral interradial plate ends in a simple point (Fig. 14A,C,G) which may be skewed to one side. Heding (1942) used this feature to distinguish *Y. talismani* from *Y. bitentaculata attenuata*.

Figure 14. *Ypsilothuria talismani*.

Calcareous ring plates from a specimen 2mm long :
A) Lateral interradial,
B) Ventro-lateral radial.

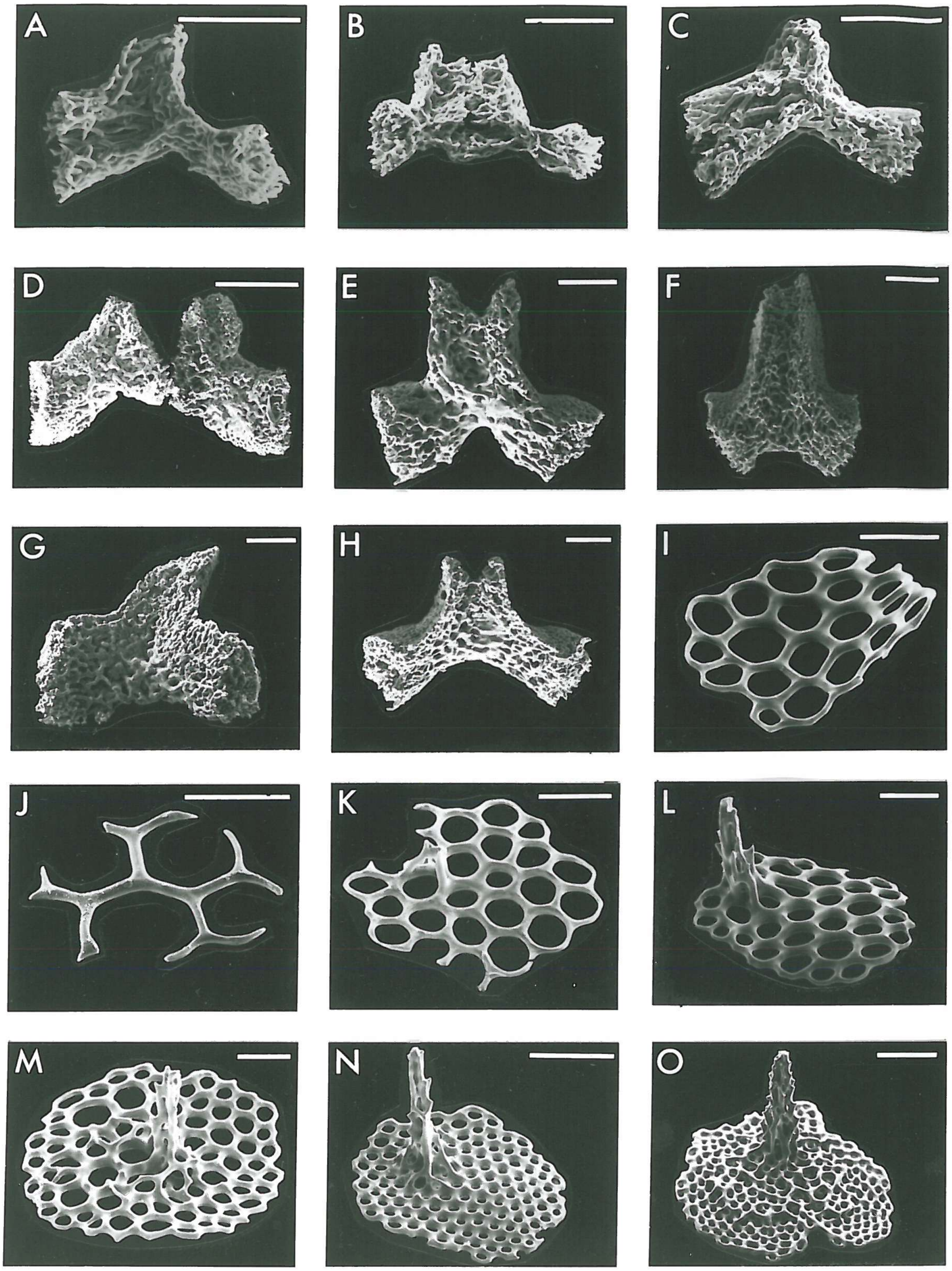
Calcareous ring plate from a specimen 3mm long :
C) Lateral interradial.

Calcareous ring plate from a specimen 6mm long :
D) Ventro-lateral radial.

Calcareous ring plates from a specimen 7mm long :
E) Dorso-lateral radial,
F) Mid-ventral radial,
G) Lateral interradial,
H) Mid-dorsal interradial.

Body wall ossicles :
I,J) 1mm long specimen,
K) 2mm long specimen,
L,M) 3mm long specimen,
N) 4mm long specimen,
O) 6mm long specimen.

Scale bars : D,N,O) 200µm; A to C, G to M) 100µm.


A
B
C
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N
O

(iii) ontogenetic changes in body wall ossicles.

The body wall ossicles of specimens about 1mm long are composed of small, circular to oval plates with an irregular outline and lacking a spire (Fig. 14I). Some of the primary plates may be misshapen and those surrounding the extremities of the body are often triangular, sometimes with one corner extended in the form of a spine, giving the body a thorny appearance. Some primary rods occur in these small specimens (Fig. 14J) but they are rare. The plates are usually 200 to 300µm long but may extend up to about 480 µm in their largest dimension.They are made of one calcareous layer only.

The spire starts to form in specimens about 2mm long (Fig. 14K). The spire is formed at its base by 4 or 5 rods which usually arise around one of the perforations (Fig. 16A) and which fuse together above the hole. The spire increases in length (Fig. 14M) as the plate increases in size. Normally it forms excentrically on the plate but in some cases it occurs close to the edge (Fig. 14L) resembling the mature plates found in specimens of E. hispida of a similar size. The spire is composed of several rods fused together by several cross pieces and carries several outwardly pointing spines (Fig. 14N). In the largest specimens examined (6 to 7mm long)it reaches a length of at least 550µm.

In small specimens (1 to 3mm long) the perforations of the plates have a diameter of 30 to 70µm (some 90µm), but as the individual increases in size and the plates become larger, smaller holes (20 to 30µm) are formed around the periphery of the plate. This process starts in specimens about 3mm long (Fig. 14L). At the same time the calcareous network of the plate starts to thicken and small projections, which will eventually form the extra calcareous layers on the plate, can be seen (Fig. 14M). The extra calcareous layers first form around the spire and these multilayered plates are present in specimens 4mm long. The perforations in the plate are now all quite small (15 to 40µm) except those underneath the spire.

In specimens 5mm long a few plates may be found which are only just starting to form extra calcareous layers but most have a well developed calcareous network, particularly around the base of the spire. The periphery of the plate, however, is always a single layer and this feature is found in plates of larger specimens (6 to 7mm long) (Fig. 14,0). The plates of large specimens are oval to circular in shape.

The dimensions of the body wall ossicles are related to the size of the specimen (Fig. 15). Both the maximum and mean plate size vary linearly with the length of the specimen. The greatest dimension of a plate from the largest specimens (7mm long) does not exceed 900µm.

(iv) other taxonomic features.

There are 8 digitate tentacles. The fusion of the ventral interradial and the ventro-lateral radial plates of the calcareous ring has led to the loss of two ventral tentacles. As with E. hispida, the two lateral tentacles are much longer than the others. The base of the tentacle is pigmented brown in many cases. The tentacle ossicles are slender, curved rods, 150 to 300µm long, perforated at each end by one or more holes (Fig. 16B). The rods are spinous and in a few cases may have one or more rounded knobs perforated by a single hole (Fig. 16B). The tentacle ossicles of the PSB specimens are usually distinctly curved, unlike those figured by Heding (1942) for the

Figure 15. *Ypsilothuria talismani*. Body wall ossicles : the relationship between maximum and mean ossicle length with body length.

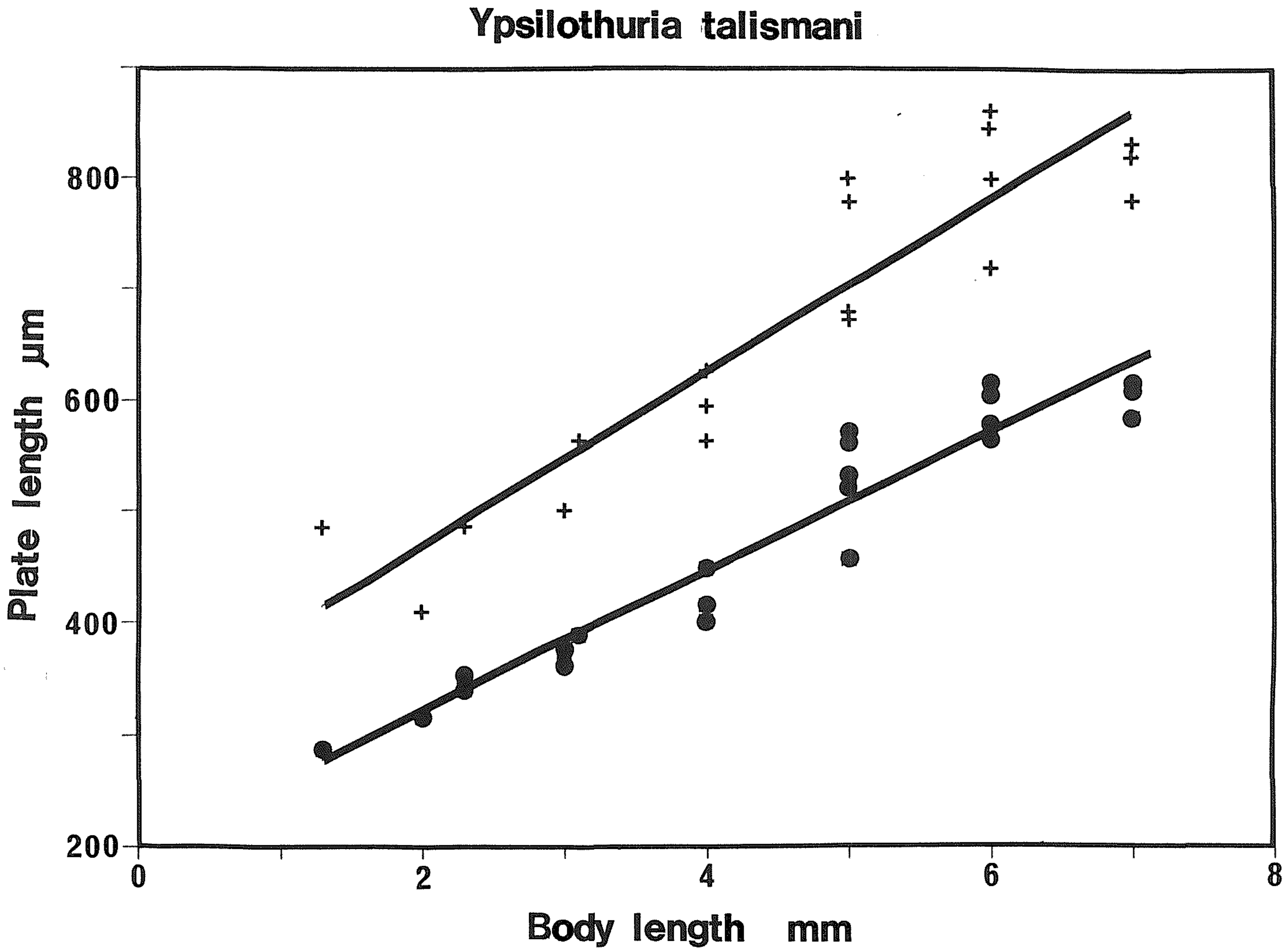

Ypsilothuria talismani
Plate length µm
800
600
400
200
0
2
4
6
8
Body length mm

Figure 16. <u>Ypsilothuria talismani</u>.

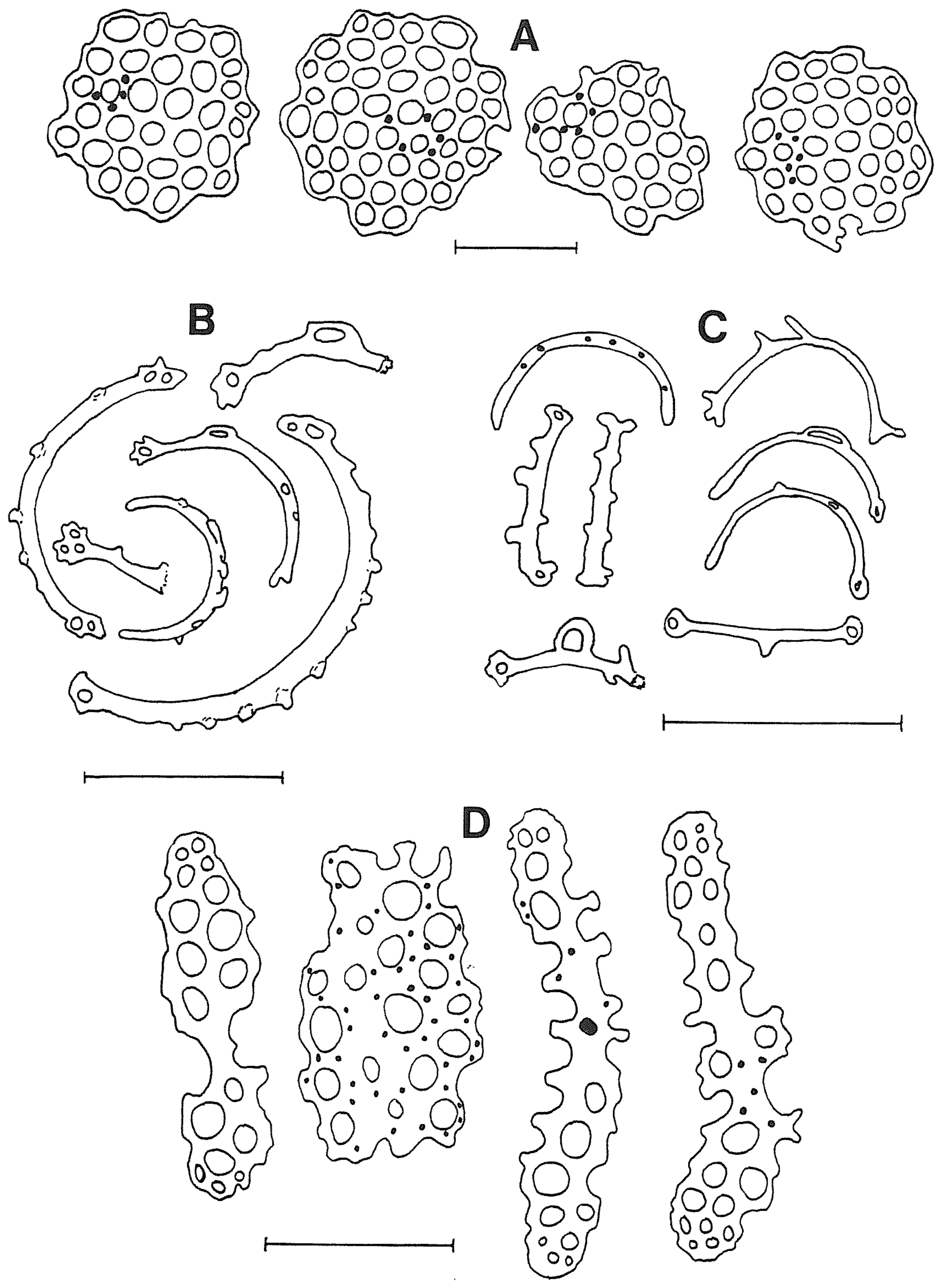
A) Body wall ossicles from a specimen 2mm long showing areas where the spire starts to form.

B) Tentacle ossicles from a specimen 7mm long.

C) Ossicles from the mid-ventral tubefeet of a specimen 2mm long (4 ossicles LHS) and from the tubefeet of a specimen 6mm long (4 ossicles RHS).

D) Introvert ossicles from a specimen 7mm long showing small knobs on the surface.

Scale bars : A) 200µm; B,C,D) 100µm.


A
B
C
D

"Ingolf" material. Heding (1942) also used the tentacle ossicles to characterize a subspecies of *Ypsilothuria talismani* found in the West Indies, *Y. talismani elegans*, but the ossicles of this subspecies fall within the range noted for the PSB material.

The ossicles of the introvert are elongate plates about 200µm long with a few holes and an irregular outline. The holes are usually smaller at the ends of the plates (Fig. 16D). The plates appear to have some fine knobs on their surface.

As in *E. hispida* the tubefeet of *Y. talismani* are small, and are restricted to the radii. They are missing from the middle of the two dorsal ambulacra but are present throughout the length of the other three ambulacra, albeit widely spaced. A single tubefoot occurs at each point except at the mid-point of the mid-ventral ambulacrum where a pair of tubefeet are found. These two tubefeet are particularly well developed in small specimens. The ossicles are curved rods (Fig. 16C), about 100µm long. The rods have a few irregular side branches and are usually perforated at each end. Some have a perforated knob at the centre of the rod.

Ypsilothuria bitentaculata attenuata (R. Perrier, 1902)

(i) ontogenetic changes in body shape.

The development of the body shape of Y. bitentaculata attenuata is identical to Y. talismani (Fig. 10J-R) changing from a triangular posture (Fig. 10J) to a U-shape (Fig. 10N-R). There is some variation in the shape of large specimens but in most cases the posterior and anterior ends of the ventral surface are perpendicular to the dorsal surface forming a tight U-shape, as in Y. talismani. As a result, the relative proportions of the body, such as the length:height ratio, are the same for the two species. However, Y. bitentaculata attenuata appears to grow to a greater size than Y. talismani. The largest specimens of Y. bitentaculata attenuata from the Rockall Trough have a horizontal length of 11mm and a curvature length of 27mm, for specimens in a tight U-shape. Larger specimens, up to 20mm long, were described by Heding (1942) from the "Ingolf" and "Godthaab" Expeditions but there was great variation in the shape of these specimens. The Rockall material is also smaller than several of the specimens of Y. bitentaculata attenuata described by Ludwig (1894) from the eastern Pacific (average length 12.6mm).

(ii) calcareous ring plates.

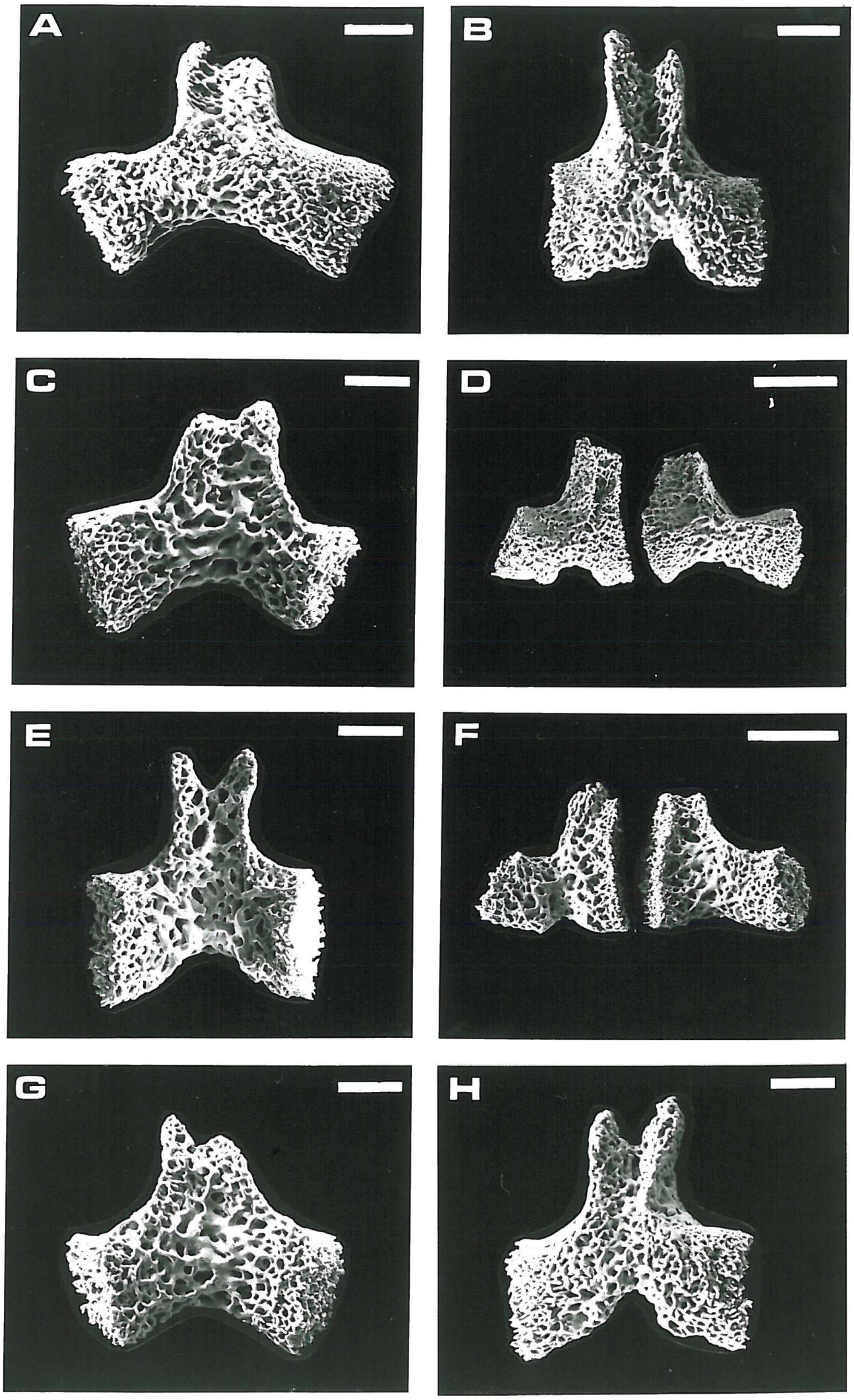
There are 8 calcareous ring plates (Fig. 17A-H). The calcareous ring lies obliquely relative to the anterior end so that the dorsal part slopes anteriorly relative to the ventral part. To accommodate this skew in the calcareous ring the two halves of the base of some plates are developed to different degrees (Figs 17A-C,H; 18A-E). Most

Figure 17. *Ypsilothuria bitentaculata attenuata*.

Calcareous ring plates from the same 6mm long specimen :

A) Mid-dorsal interradial,
B) Dorso-lateral radial,
C) Lateral interradial,
D) ventro-lateral radial,
E) Mid-ventral radial,
F) Ventro-lateral radial,
G) Lateral interradial,
H) Dorso-lateral radial.

Scale bars: A,B,C,E,G,H) 100µm; D,F) 200µm.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plates have a concave posterior edge (Figs 17A,C,E,G; 18A-E) but only a small notch may be evident on the dorso-lateral radial plates in larger specimens (Fig. 17B,H). The composite ventro-lateral radial plates, made of the true ventro-lateral radial and ventral interradial plates (Fig. 17D,F), as in Y. talismani, have two small concave areas on the posterior edge.

All the plates are identical in structure to those described in detail by Ludwig (1894) for Y. bitentaculata from the Pacific. The mid-dorsal interradial plate (Fig. 17A) has a slightly bifid anterior process but its form can vary in small specimens from a single blunt point to a bifid end with a deep cleft. The height of the anterior process is about half the width of the plate. The dorso-lateral (Fig. 17B,H) and mid-ventral radial (Fig. 17E) plates are similar in size and shape and have a distinctly bifid anterior process. The ventro-lateral radial plates usually have a broad, blunt anterior process made from the two fused plates (Fig. 17D,F) but, as Ludwig (1894) noted, a small tooth can develop on each side of the anterior process giving it a bifid appearance. In some cases a small secondary tooth may be formed in the middle. The anterior process of the lateral interradial plate is also usually bifid but the two teeth are often of different lengths (Fig. 17C,G; 18A). The bifid nature of the anterior process may not always be apparent, particularly in small specimens (Fig. 18B-E).

(iii) ontogenetic changes in body wall ossicles.

Small, circular to oval plates are the principal ossicles in the body wall of the smallest specimens from the Rockall Trough (1.5mm long). Most of the plates lack a spire (Fig. 18F). The end of some plates, generally those

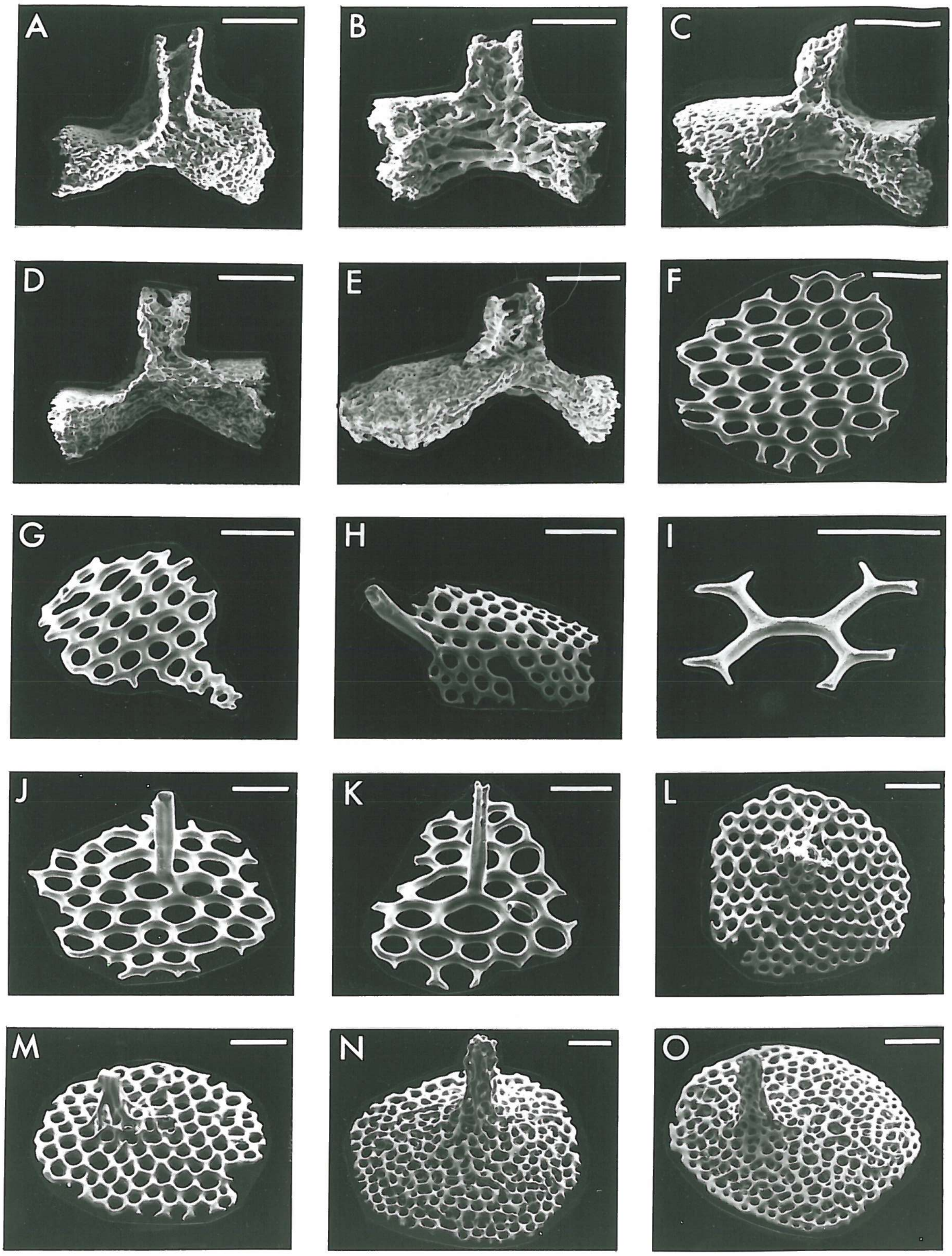
Figure 18. *Ypsilothuria bitentaculata attenuata*.

A to E) Lateral interradial plates from the calcareous rings of specimens 3mm long.

Body wall ossicles :

F,G) 1mm long specimen,
H) 3mm long specimen,
I,J,K) 2mm long specimen,
L,M) 5mm long specimen,
N) 8mm long specimen,
O) 10mm long specimen.

Scale bars : A to K) 100µm; L to O) 200µm.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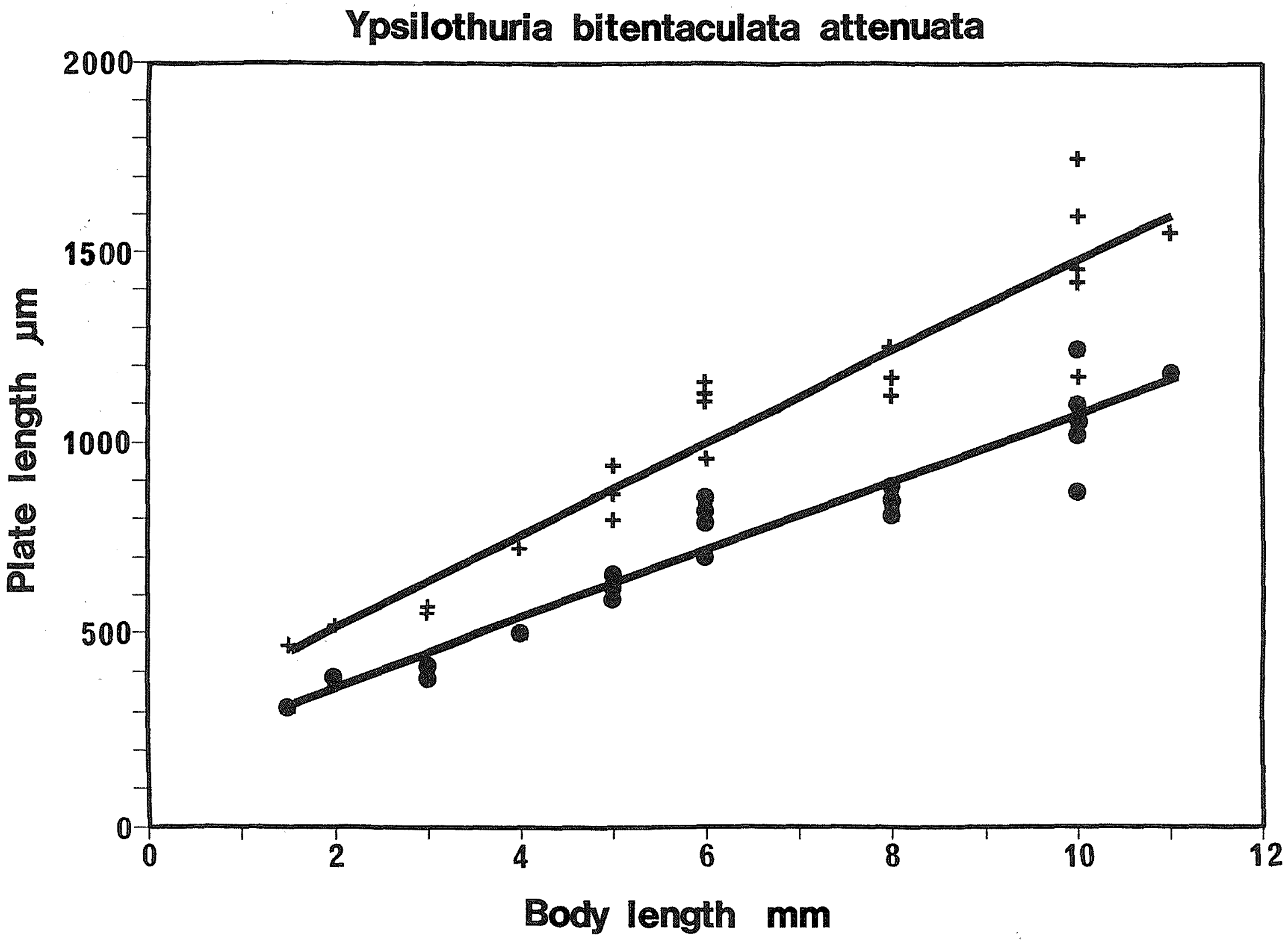
at the extremities of the body, may be drawn out (Fig. 18G) in some cases forming a spine. These are also found in larger specimens (Fig. 18H). A few primary rods occur (Fig. 18I) but they are not common. The plates in these small specimens are generally 300µm long but may extend up to 470µm. They are made of a single calcareous layer.

A few spires are present on the plates of the smallest specimens but development of a spire in most cases starts when the specimens are about 2mm long (Fig. 18J). The spire is formed initially by 1 to 3 rods which form close to each other near the centre of the plate (Fig. 20A). If more than one rod is present they fuse together making one thick spire (Fig. 18J,K). This type of development is quite distinct from Y. talismani. The spire thickens as the extra calcareous layers start to form on the plate around the base of the spire (Fig. 18L,M). None of the spires on the plates of the Rockall specimens are intact, but broken spires were found lying on the surface of some specimens and indicated that spires reach a length of at least 650µm.

In small specimens (1 to 3mm long) the perforations of the plate have a diameter between 40 and 70µm, although some are larger. As the plate grows further holes, only 30 to 40 µm wide, are formed around the periphery (Fig. 18L). Gradually a reticulated calcareous network spreads over the plate from the spire towards the edges (Fig. 18N) covering the larger holes. In specimens 5mm long only a few plates lack the reticulated calcareous layer. In larger specimens it is well developed but the periphery is always a single layer. However, in specimens some 10 to 11mm long the calcareous basal layer thickens so that the perforations are only 20 to 30µm wide (Fig. 18,O). The plates in the adults are oval to circular in outline with a smooth edge.

Figure 19. *Ypsilothuria bitentaculata attenuata*. Body wall ossicles : the relationship between maximum and mean plate length with body length.


Ypsilothuria bitentaculata attenuata
Plate length µm
2000
1500
1000
500
0
Body length mm
0
2
4
6
8
10
12

As for Y. talismani, the maximum size of a plate and the mean plate size are correlated to the size of the individual (Fig. 19) but the relationship between plate and body size is different for the two species. The largest specimens, 11mm long, have plates with a maximum length of 1.8mm.

(iv) other taxonomic features.

There are 8 tentacles. The two lateral tentacles are much larger than the others. There is no obvious pigmentation at the base of the tentacles. The tentacle ossicles are slender, curved rods (150 to 350µm) perforated at either end by one or more holes (Fig. 20B). The rods are spinous. In some cases the spines arch towards eachother and fuse forming a perforated knob (Fig. 20B).

The introvert ossicles are elongate plates, most 200 to 300µm long, with a few holes and an irregular outline (Fig. 20D). They appear to have some fine knobs on their surface. The dimensions of the plates in large specimens are not related to the size of the individual.

The tubefeet are small and are found widely spaced in the three ventral ambulacra. They appear to be missing from the mid-part of the two dorsal ambulacra. A single tubefoot occurs at each point except at the mid-point of the mid-ventral ambulacrum where a pair of tubefeet are found. These two tubefeet are particularly well developed in small specimens. In large specimens some of the tubefeet are found close to the spire in the middle of the plate and as result pass through the plate rather than around the edge. The ossicles are primarily curved rods with many irregular side branches (Fig. 20C) which are

Figure 20. *Ypsilothuria bitentaculata attenuata*.

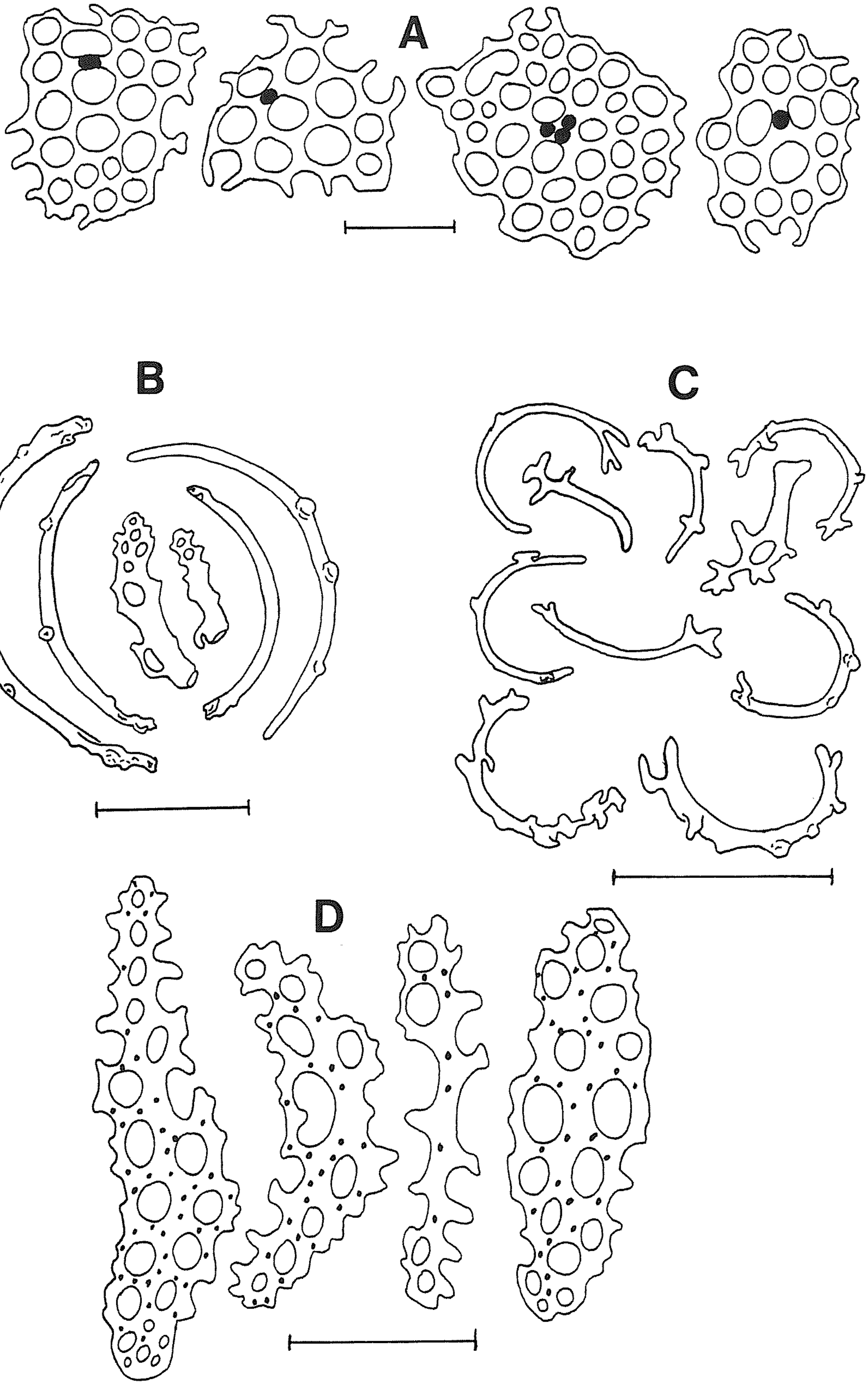
Body wall ossicles from a specimen 2mm long showing the areas where the spire starts to form.

B) Tentacle ossicles from a specimen 7mm long; the two figures in the centre are fragments from the ends of a rod.

C) Ossicles from the mid-ventral tubefeet of a specimen 2mm long.

D) Introvert ossicles from a specimen 7mm long showing small knobs on the surface.

Scale bars : A) 200µm, B,C,D) 100µm.


A
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developed to a greater degree than in Y. talismani. The ends of the rods are not obviously perforated and a central, perforated knob is not usually found. The rods are about 100µm long and are abundant in small specimens but rather scarce in large specimens.

Comparison of the species.

Of all the features that can be used to distinguish Echinocucumis and Ypsilothuria the most apparent character, and the most frequently used, is the structure of the body wall ossicles. Other features, such as the number of tentacles or the structure of the calcareous ring are difficult to use and often lead to the mutilation of the specimen.

The plate ossicles of large Echinocucumis have a single calcareous layer with large holes and a spire placed close to the edge. In large Ypsilothuria a calcareous reticulated network is built up on the plate, the holes are small and the spire is placed excentrically. These features, however, are unsuitable for distinguishing small specimens. Specimens of Ypsilothuria about 4mm long have plate ossicles (Fig. 14L) that are similar to those of Echinocucumis (Fig. 11L). Other characters must be used therefore to differentiate the two genera. First, the species examined differ in shape, although this is not always apparent, and second, the number of primary rods and simple primary plates with a few holes, is far higher in Echinocucumis hispida than either of the two Ypsilothuria species. Primary rods account for about 75 and 30% of the ossicles present in Echinocucumis specimens 3 and 4mm long respectively. In Ypsilothuria primary rods are found only rarely.

Body shape and the general plate structure are unsuitable features for separating the species of Ypsilothuria. Their shape is similar, although in many cases in the present material the posterior end of Y. talismani is longer and more pointed than in Y. bitentaculata attenuata. In addition, the latter species attains a greater size. Both species have body wall ossicles of a similar shape and the calcareous reticulated network is developed to a similar extent in specimens of the same size. However, for specimens longer than 5mm the largest plate size in the body wall is significantly greater for Y. bitentaculata attenuata than for Y. talismani (Figs 15,19) (t-test, $p>0.05$ for specimens 5mm long; $p>0.01$ for specimens 6mm long). The largest plates are found in the mid-ventral and mid-lateral parts of the body. A similar difference is found between the two species if the mean plate size of individuals is compared (Figs 15,19).

For specimens smaller than 5mm alternative features must be sought to characterize the two species. First, specimens less than 3mm long can be differentiated by the manner in which the spire is formed on the body wall plates. In Y. talismani several projections arise on the plate, usually 4 or more (Fig. 16A) which then fuse together in many cases over a perforation in the plate. In contrast, the spire of Y. bitentaculata attenuata forms from 1 to 3 rods which arise close together (Fig. 20A). Second, for specimens 4 to 5mm long the perforation size in "mature" plates may give an indication of the species; about 30μm wide in Y. talismani and about 40μm wide in Y. bitentaculata attenuata. A "mature" plate in this sense is one with a spire and a developing reticulated layer.

In specimens of intermediate size (4 to 5mm long) it is necessary to dissect the holothurian and examine the structure of the calcareous ring, in particular that of the lateral interradial plate. In *Y. talismani* the anterior process of the plate ends in a simple point (Fig. 14A,C,G) while in *Y. bitentaculata attenuata* the anterior process is bifid, often with one of the teeth longer than the other (Figs 17C,G; 18A). This feature may also be used to distinguish the two species in large specimens but the bifid nature of the anterior process in *Y. bitentaculata attenuata* is not always apparent in small specimens (Fig. 18B-E).

Finally, although the tubefoot ossicles of both species are variable in shape, the side branches on the curved rods in *Y. bitentaculata attenuata* appear to be more numerous and complex than in *Y. talismani* (Figs 16C, 20C).

Synonymy : Ludwig and Heding (1935) believed that an Indian Ocean specimen, described as *E. paratypica*, could be distinguished from *E. hispida* by having larger holes in the plate ossicles of the body wall . It is clear from the PSB material that the size of the holes in the plates of *E. hispida* vary considerably, decreasing in size towards the edge of the plate. Most holes are 60 to 90µm in diameter, a similar size to those reported for *E. paratypica*. It was suggested that a broad base to the spire in *E. hispida* might be used to distinguish the two species, but this feature may have been attributed to *E. hispida* owing to some confusion with *Ypsilothuria*. The formation of the spire is similar in *E. hispida* and *E. paratypica*. The synonymy of the two species is proposed.

The data presented here indicate that the northeast Atlantic form of *Y. bitentaculata* is identical to the type material from the Pacific. The suppression of the subspecific name should be possible after a thorough comparison with material from the Pacific.

3.2 Ossicles of juvenile *Bathyplotes natans*.

In the PSB *Bathyplotes natans* has a similar depth distribution to *Echinocucumis hispida* and *Ypsilothuria talismani*. Juvenile specimens of *B. natans* only a few mm long could be confused with juvenile *E. hispida* since both have primary cross ossicles with a spire. However, a detailed examination of the two species shows that they are distinguished easily by the following features.

First, juvenile *B. natans* have a cylinderical body shape in comparison to the U-shape of *E. hispida* (Fig. 10A). Second, juvenile *B. natans* have a number of wide, short tubefeet arranged along the ventral surface of the body. There are about 6 tubefeet in a specimen 1mm long. These tubefeet have curved rod ossicles, as in *E. hispida*, but they also have a terminal plate (Fig. 21A). In *E. hispida* a pair of long, thin tubefeet are found at the mid-point of the mid-ventral ambulacrum. Third, the spire of the primary cross ossicles in the body wall of *B. natans* is long, usually greater than 100μm (Fig. 21C), and is placed in the centre of the primary rod (Fig. 21B). In *E. hispida* the spire of the body wall ossicles is short and is placed excentrically on the primary rod (Fig. 11I). Fourth, the ends of the arms of the primary cross ossicles in *B. natans* are usually perforated by 3 to 4 holes (Fig. 21B,C) whereas in *E. hispida* there are only one or two holes (Fig. 11I,K).

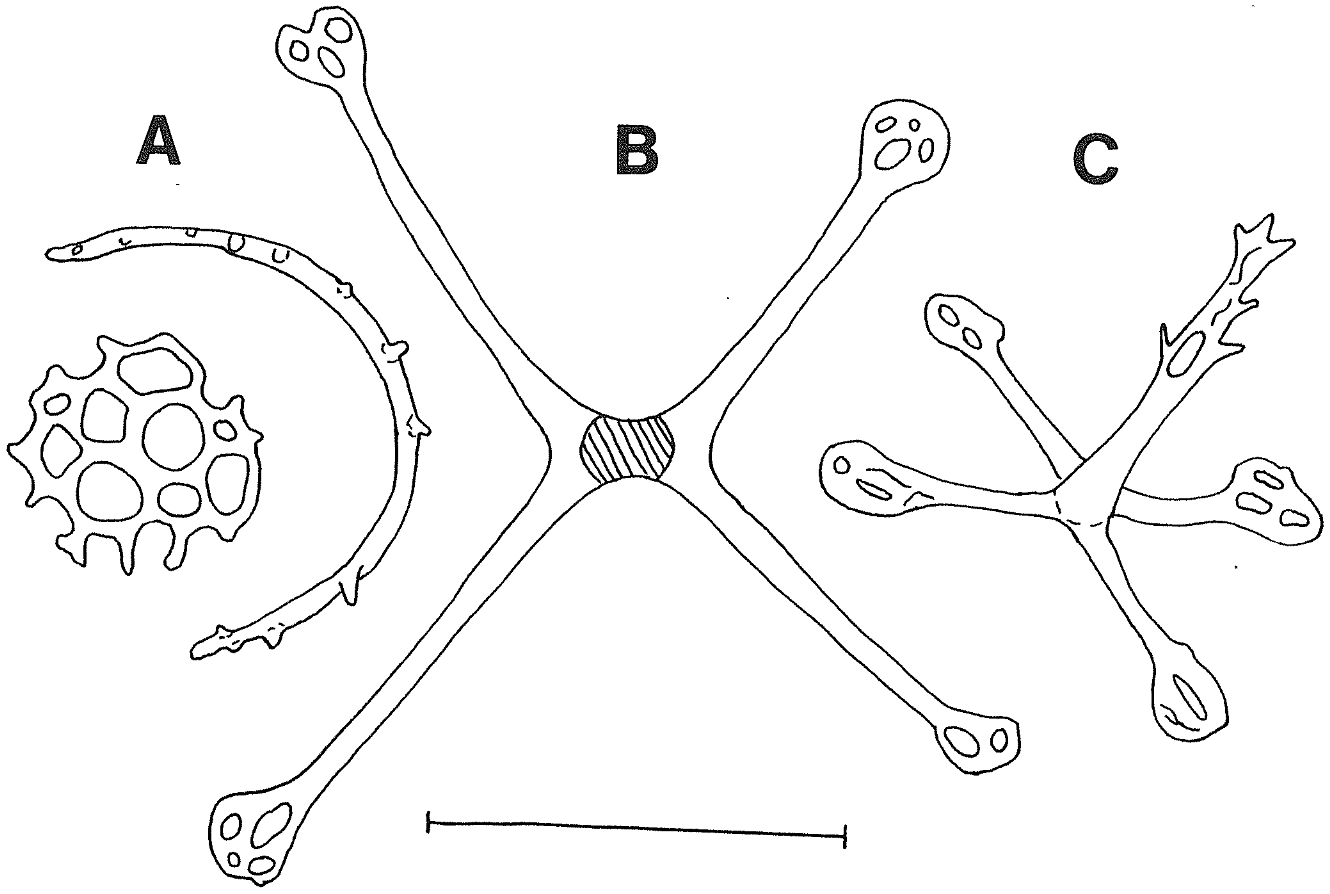
Figure 21. Bathyplotes natans.

Ossicles from a specimen 1.7mm long :

A) curved rod and terminal plate from a tubefoot,

B,C) Body wall ossicles viewed dorsally and obliquely.

Scale bar, 100µm.


A
B
C

3.3 A new species of apodid holothurian.

In a few epibenthic sledge hauls from abyssal depths in the PSB a new species of the apodid genus *Siniotrochus* was taken. A description of this species published in Gage and Billett (1986), along with descriptions of other new apodid species from the Rockall Trough, is reproduced here.

The features used to characterise the species are the same as those used for the ypsilothuriids, namely the structure of the calcareous plates of the circum-oesophageal ring (the calcareous ring plates) and the ossicles of the body wall. The wheel-shaped ossicles, commonly known as wheels, are the most important feature in determining the myriotrochid genera and species. The parameters of the wheels that can be counted and measured to characterize the wheels have been summarized by Belyaev (1970) and Gage and Billett (1986). Wheels are described in terms of the wheel diameter, the width of the hub, the number of holes in the hub, the number of spokes, the number of primary and secondary outward-pointing teeth on the rim of the wheel, and the number of inward-pointing teeth on the rim. In addition, the numerical proportion of the spokes and teeth, expressed as a percentage, may be used. Although considerable variation is known to occur in these parameters, Belyaev (1970) considered that average values based on a large number of measurements would be sufficiently stable to characterize a species. The calcareous ring plates are described using the orientation and terminology of the features first proposed by Belyaev and Mironov (1982).

Siniotrochus myriodontus Gage and Billett, 1986

Material examined : Holotype from St. 50604-1 (1 anterior end), Paratypes from Stas 9756-14 (3 posterior ends, 1 anterior end), 50603-1 (1 posterior end, 1 anterior end), 50604-1 (1 posterior end), 51415-1 (1 anterior end). Depth range, 3470 to 4000m.

Description : The holotype anterior end is 11mm long with a width of 4.8mm at the calcareous ring, widening to 5.5mm. The posterior end from the same sample (St. 50604-1) is 21mm long and 6mm wide. Both pieces are contracted and it is possible that they are fragments of the same specimen. Similarly, the anterior end from St. 50603-1 is 4mm long and has a uniform width of 5mm, while the posterior end from the same sample is 12mm long and 6mm wide. The three posterior ends from St. 9756-14 range between 11 and 15mm long and between 4.5 and 5.5mm wide.

The body wall has a single layer of exclusively wheel-shaped ossicles which are more numerous anteriorly and posteriorly on both the dorsal and ventral surfaces. They are more dispersed towards the middle of the body on the dorsal surface and are practically absent from the mid-part of the ventral surface.

There are 12 tentacles, each with a large central part which is bilobed at its end. Laterally there are 4 pairs of digits (Fig. 22A). The tentacle ossicles are exclusively simple rods, 70 to 230µm long. They resemble those figured by Pawson (1971) for Siniotrochus phoxus and by Belyaev and Mirinov (1981) for S. spiculifer.

The 12 tentacles are accommodated in the calcareous ring, which consists of 10 calcareous plates, by the development of two anterior processes on each of the two dorso-lateral radial plates (Fig. 22B), as in the genus *Myriotrochus*. The calcareous plates are of unequal size increasing in width passing from the mid-ventral radial to the dorso-lateral radials. The mid-dorsal interradial is similar in size to the ventral interradials. These three plates, together with the mid-ventral radial, all have a concave posterior edge on their outer face, but the other plates often bear a posterior projection. The anterior process of the plates is usually as high as, or greater than, the height of the plate at its articulating face (Fig. 22B), and the process is of a similar size on both radial and interradial plates (Fig. 22B). The anterior process overhangs the radial canal pore on the outer face of the radial plates (Fig. 22B,C) and also forms a spur over the radial canal pore on the inner face. When viewed anteriorly the central crest of the anterior process can be seen to form ridges in between the tentacles (Fig. 22D). The lateral (articulating) face is rectangular in shape on the outer edge but widens towards the inner edge (Fig. 22C).

The stone canal is well developed and with the gonoduct passes along the longitudinal axis of the mid-dorsal interradial plate. It appears to connect to the outside with the gonoduct at a pore situated immediately behind the tentacles.

The ossicles of the body wall are exclusively wheels of one form, although simple rods, like those present in the tentacles, can be found around the anus, within the buccal membrane, and around the gonopore. The wheels are concave and have a wide hub, which has a variable number of angular perforations in its centre (Fig. 22E). The rim has

Figure 22. _Siniotrochus myriodontus_.

A) anterior view of retracted tentacle showing the bi-lobed end.

B) Outer surface of double-toothed dosrso-lateral radial and adjacent interradial plates of the calcareous ring.

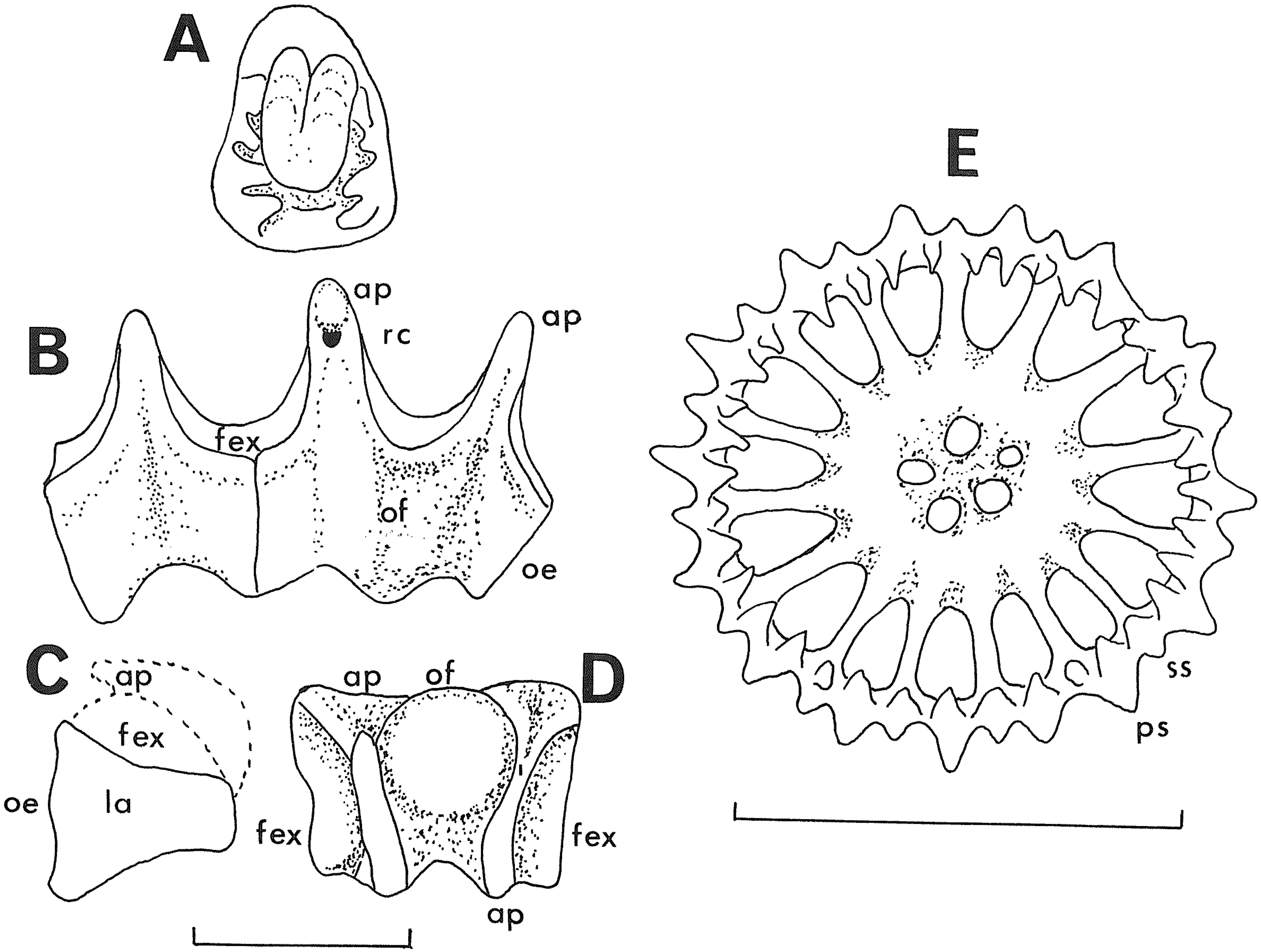
C) view of lateral (articulating) surface of a dorso-lateral radial plate (interrupted line shows the shape of the anterior process).

D) anterior view of the same radial plate.

E) outer view of a wheel ossicle from the body wall showing outward-pointing teeth of the primary (ps) and secondary (ss) series.

ap, anterior process;
rc, radial canal apperture;
f ex, frontal excavation for the tentacle;
of, outer face;
oe, outer edge;
la, lateral (articulating) face.

Scale bars : A to D) 1mm, E) 300µm.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E
ss
ps

a series of outward-pointing, and a more numerous series of inward-pointing, blunt teeth. The outward-pointing teeth consist of one series of primary teeth corresponding to the spaces in between the spokes of the wheel, and a secondary series of smaller teeth, corresponding to the positions of the spokes themselves. The former are often equal in number to the spokes but the teeth of the latter series are generally less common and more variable in number than the primary teeth. The secondary teeth also occur at a slightly different elevation on the rim.

Table 1. The parameters of the wheel ossicles from three posterior end fragments of Siniotrochus myriodontus, each from a different station in the PSB. Mean values are given with the range in parentheses.

D µm	diameter of wheel in microns
dh%	the diameter of the hub expressed as a percentage of the total wheel diameter
ns	the number of spokes
n-it	the number of inward-pointing teeth
s/t%	the ratio of spokes to inward-pointing teeth expressed as a percentage;
n-opt	the number of primary outward-pointing teeth;
n-ost	the number of secondary outward-pointing teeth
n-ot	the total number of outward-pointing teeth
np	the number of holes in the hub.

Parameter	St. 9756-14 n = 56	St. 50603-1 n = 76	St. 50604-1 n = 92
D, µm	378 (310-475)	470 (410-560)	373 (285-475)
dh%	49.4 (44 - 58)	51.6 (43 - 58)	50.0 (45 - 57)
ns	17.2 (14 - 25)	20.7 (16 - 25)	15.7 (12 - 20)
n-it	37.1 (30 - 47)	51.6 (41 - 59)	31.9 (22 - 43)
s/t%	46.3 (36 - 60)	40.3 (30 - 48)	49.7 (41 - 68)
n-opt	17.8 (14 - 28)	20.6 (16 - 24)	12.8 (7 - 20)
n-ost	8.5 (0 - 17)	14.0 (3 - 27)	7.2 (0 - 15)
n-ot	26.2 (15 - 38)	34.6 (26 - 48)	20.0 (10 - 32)
np	3 to 17	9 to 26	3 to 14

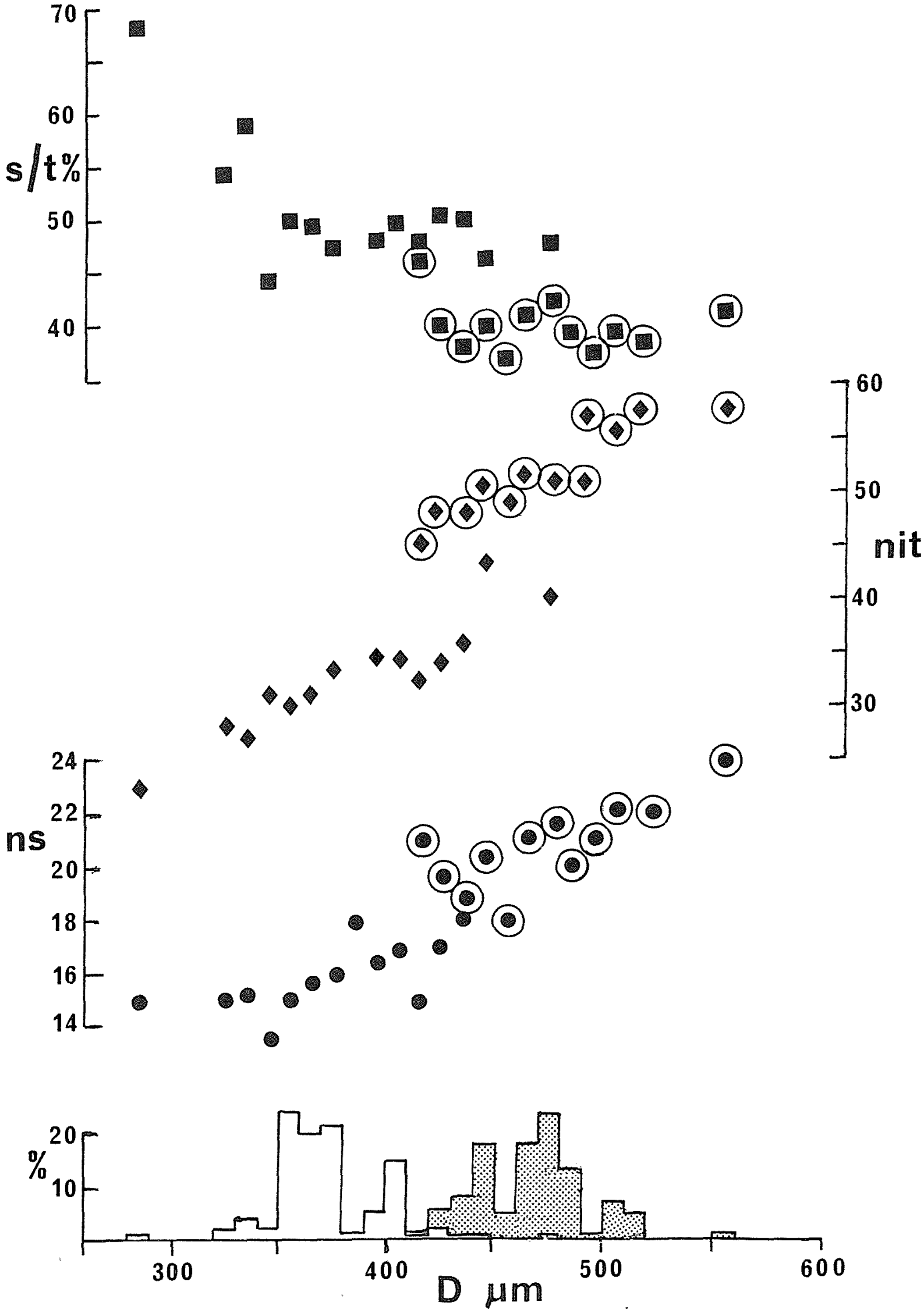
The measurements of wheel parameters are summarised in Table 1. Data are given for three specimens from different stations. Analysis of variance shows highly significant variation in the wheel diameter and the ratio of spokes to teeth between individuals (Dr. J.D. Gage personal communication). The specimen from St. 50603-1 possessed markedly larger wheels than the other specimens. It was not possible to ascertain whether this was related to the size of the specimens. The number of spokes and inward-pointing teeth both increase with an increase in the size of the wheel (Fig. 23). Although a similar relationship is found between the number of spokes and the wheel diameter in the specimens from Stas 50603-1 and 50604-1, the specimen from the former station had considerably more teeth resulting in a lower ratio of spokes to teeth (s/t %) (Fig. 23).

Remarks : Pawson (1971) erected the genus Siniotrochus on three incomplete specimens taken in the northwest Atlantic, referring all the specimens to the single species S. phoxus. Belyaev and Mironov (1981) described another species, S. spiculifer, from the northwest Pacific which differed from S. phoxus in two major details : the presence of rod ossicles in addition to wheel ossicles in the body wall, and the absence of outward-pointing teeth around the rim of the wheel ossicles. S. spiculifer differs from S. myriodontus in these same details.

Siniotrochus myriodontus is similar to S. phoxus in several respects : body size, the presence of small rod ossicles in the tentacles, and in the distribution of the wheel ossicles in the body wall. Previous authors have been unable to describe the structure of the calcareous ring plates for Siniotrochus and therefore a comparison of this feature is not possible. S. myriodontus is also

Figure 23. *Siniotrochus myriodontus*. Size-frequency distribution of wheel diameters (bottom) and relationship of wheel parameters to wheel diameter. Filled-in frequency and circled symbols refer to measurements made from the specimen from St. 50603-1, other symbols from the specimen from St. 50604-1.

D µm,	diameter of wheel,
ns,	number of spokes,
nit,	number of inward-pointing teeth,
s/t%,	the ratio of spokes to teeth expressed as a percentage.


70
60
s/t%
50
40
60
50
nit
40
30
24
22
ns
20
18
16
14
20
%
10
300
400
500
600
D µm

similar to S. phoxus in several features of the wheel ossicles, but differs in having a greater number of outward-pointing teeth. This results from a secondary series of outward-pointing teeth occupying a position corresponding to the spokes of the ossicles. These occur in addition to a primary series placed at positions corresponding to the spaces between spokes (Fig. 22E). The latter series occur on ossicles from S. phoxus but a distinct secondary series was not noted by Pawson (1971).

The average number of outward-pointing teeth exceeds slightly the mean number of spokes on S. phoxus. This may indicate that extra secondary teeth are indeed present. However, this seems unlikely since data for S. myriodontus (Table 1) show that in some specimens the number of primary teeth may exceed the number of spokes (St. 9756-14). In addition, in S. myriodontus the mean total number of outward-pointing teeth is always very much greater than the average number of spokes (Table 1).

The number of secondary teeth on the wheel ossicles is variable but the majority of the wheels have a significant number. Only 6 of the 170 wheels examined were completely devoid of secondary teeth and the number of wheels at Stas 9756-14, 50603-1 and 50604-1 with 6 or more secondary teeth was 80%, 95% and 65% respectively. This feature, therefore, although variable, is typical of many wheel ossicles and may be used to distinguish S. myriodontus from S. phoxus.

4.Species synopsis

4.1 Species list.

Class HOLOTHURIOIDEA

Order Dendrochirotida

Family Psolidae
Psolus squamatus (Koren, 1844)

Family Cucumariidae
Staurocucumis abyssorum (Theel, 1886)
Thyone gadeana R. Perrier, 1902

Order Dactylochirotida

Family Ypsilothuriidae
Echinocucumis hispida (Barrett, 1857)
Ypsilothuria talismani E. Perrier, 1886

Order Aspidochirotida

Family Stichopodidae
Stichopus tremulus (Gunnerus, 1767)

Family Synallactidae
Bathyplotes natans (M. Sars, 1868)
Benthothuria funebris R. Perrier, 1902
Paelopatides grisea R. Perrier, 1902
Mesothuria candelabri Herouard, 1923
Mesothuria lactea (Theel, 1886)
Mesothuria bifurcata Herouard, 1906
Mesothuria cathedralis Heding, 1940
Mesothuria maroccana Perrier, 1902
Mesothuria intestinalis (Ascanius and Rathke, 1767)
Mesothuria verrilli (Theel, 1886)
Paroriza pallens (Koehler, 1896)
Paroriza prouhoi Herouard, 1902
Pseudostichopus villosus Theel, 1886
Pseudostichopus sp.

Order Elasipodida

Family Deimatidae

Deima validum validum Theel, 1879
Oneirophanta mutabilis mutabilis Theel, 1879

Family Laetmogonidae

Laetmogone violacea Theel, 1879
Benthogone rosea Koehler, 1896

Family Psychropotidae

Benthodytes typica Theel, 1882
Benthodytes sordida Theel, 1882
Psychropotes depressa (Theel, 1882)
Psychropotes longicauda Theel, 1882
Psychropotes semperiana Theel, 1882

Family Pelagothuriidae

Enypniastes diaphana (Gilchrist, 1920)

Family Elpidiidae

Peniagone diaphana (Theel, 1882)
Peniagone azorica von Marenzeller, 1893
Amperima rosea (R. Perrier, 1896)
Kolga hyalina Danielssen and Koren, 1879
Elpidia sp.

Order Molpadiida

Family Molpadiidae

Molpadia blakei (Theel, 1886)
Cherbonniera utriculus Sibuet, 1974

Family Caudinidae

Hedingia albicans (Theel, 1886)

Order Apodida

Family Synaptidae

Labidoplax southwardorum Gage, 1984
Protankyra brychia (Verrill, 1885)

Family Myriotrochidae

Myriotrochus bathybius H.L. Clark, 1920
Myriotrochus giganteus H.L. Clark, 1920
Siniotrochus myriodontus Gage and Billett, 1986
Prototrochus zenkevitchi rockallensis Gage and Billett, 1986
Parvotrochus belyaevi Gage and Billett, 1986

4.2 Description of species

Order DENDROCHIROTIDA

Family Psolidae

Psolus squamatus (Koren, 1844)

OT 9752-1 (2), OT 50524-1 (192), OT 50601-1 (132),
OT 50702-1 (89), OT 50707-1 (3), OT 51811-1 (7).

Bathymetric range in PSB : 685 to 1042m. 98% of the specimens were collected between 736 and 927m.

Distribution : *P. squamatus* is known from 4 widely separated localities; the northeast Atlantic, around the southern part of South America, off Japan and along the eastern border of the Pacific (Gage *et al*., 1985). It appears to be more common at higher latitudes. The total bathymetric range of *P. squamatus* is 7 to 1087m (Pawson, 1969). The apparent narrow depth range of the PSB specimens (685 to 1042m) may result, in part, from a sampling artefact since few samples have been taken at depths shallower than 700m on the eastern flank of the PSB. Specimens collected in the Rockall Trough come from a similar depth (Gage *et al*., 1985).

Six samples of *P. squamatus* were taken from two localities in the PSB; one in the northeast PSB and the other on the northern side of the Goban Spur. *P. squamatus* is likely to occur extensively along the eastern slopes of the PSB, an area that harbours a large suspension feeding assemblage dominated by the cold-water corals *Madrepora* oculata and *Lophelia pertusa* (Le Danois, 1948). *P. squamatus* has been sampled also on the steep slopes of the Hebridean Terrace (Gage *et al*., 1985). The steep slopes on the eastern side of the PSB are notable for the abundance of rocks and boulders, the preferred habitat for psolid holothurians and some specimens were recovered from the trawls still attached to rock fragments. *P. squamatus* was absent from soft-bottom areas of the PSB at comparable depths.

Ecological remarks : The morphology of *P. squamatus* is ideally suited to life on hard substrates. Its body shape in many respects resembles a limpet in having an arched, armoured dorsal surface and a flat ventral surface. The calcareous plates of the dorsal surface are penetrated by the mouth which bears ten arborescent tentacles. The tentacles are similar to those of the closely related species, *P. chitinoides* Clark, a suspension-feeder that captures particles either by direct tentacular entrapment or by using adhesive papillae on the tentacle buds (Fankboner, 1978).

Analysis of the stomach contents of the PSB specimens shows that *P. squamatus* too feeds on suspended material. The guts of specimens sampled in June 1979 are packed with diatoms mixed with amorphous organic material, a similar diet to that found in *P. tuberculosus* Theel 1886 (Miller and Pawson, 1984) and *P. pawsoni* Miller and Turner 1986 (op. cit.). The gut contents of *P. squamatus* are identical to the phytodetrital material deposited in the PSB during the summer months (Billett *et al*., 1983; Rice *et al*., 1986). This material is readily resuspended by nearbed currents (Lampitt, 1985) and hence would be utilised by *P. squamatus*. Similar material is present in the intestines of specimens sampled in July 1979, although in reduced quantities. In contrast, the intestines of specimens sampled in September 1983, October 1979 and April 1978 are almost empty. The material present is largely unidentifiable but includes a few diatoms, coccoliths, foraminiferans, tintinnids, crustacean fragments and sand grains. The interpretation of differences between the gut contents of specimens from different samples is difficult without data on current velocities prior to sampling since both high and low current velocities may inhibit feeding. However, current knowledge of the periodicity in detritus deposition would suggest that the food supply for P. squamatus varies seasonally.

Despite seasonal variability in its food supply, P. squamatus reproduces continuously. Eggs of all sizes are present in the ovaries of specimens collected in both October and June. The maximum egg size found was 450µm and fecundity is low indicating some form of abbreviated lecithotrophic development, as suggested by Tyler and Gage (1983) for Ypsilothuria talismani, a species which has a similar maximum egg size and fecundity. It is surprising that with this type of development P. squamatus should have such a wide and apparently discontinuous geographic distribution.

Family Cucumariidae

Staurocucumis abyssorum (Theel, 1886)

SWT 15 (1).

Bathymetric range on PAP : 4810m

Distribution : Cosmopolitan; total bathymetric range, 1121 to 4810m; adult bathymetric range, 1655 to 4810m, the PAP specimen being the deepest record for this species. Ekman (1927) referred to a juvenile specimen (4mm long) from 385m in the Antarctic, but Hansen (1975) believed that it may have been misidentified. Two small specimens (11mm long) from off Japan described by Ohshima (1915) as *Cucumaria sluiteri* were considered to be *S. abyssorum* by Heding (1942) (as *Abyssocucumis abyssorum*) despite the shallow depths at which the specimens were found (869 and 1121m). The identity of the specimen at the shallower depth is uncertain so the upper bathymetric limit of *S. abyssorum* (*C. sluiteri*) should be regarded to be 1121m.

It is curious that only a few specimens of *S. abyssorum* have been found over a wide geographic area. Most of the specimens have been taken in close proximity to mid-oceanic ridges, fracture zones and steep terrain. The specimen from the PAP is an exception in occurring in the centre of an abyssal plain. *S. abyssorum* possesses 10 dendritic tentacles of the typical dendrochirotid form (Hymen, 1955; Massin, 1982), indicating a preference, at least, for feeding on suspended particles. Hydrographic conditions suitable for suspension feeders are generally found around areas of steep topography. It is possible, therefore, that *S. abyssorum* is more common in areas of rough terrain, areas that have been sampled inadequately by conventional trawls and sledges.

Taxonomic remarks : The PAP specimen (10cm long) is the largest specimen recorded in the North Atlantic although several other individuals of a similar size were taken by the "Challenger" Expedition in the South Pacific (Theel, 1886a). The posterior end is caudiform but, unlike Theel's description, the skin is fairly thick and possesses many ossicles. The specimen is yellowish-white in colour with numerous small light brown pigment spots distributed all over the surface, as originally described by Marenzeller (1893). The tubefeet are more abundant than figured for the type specimen. The PAP specimen has about 36 tubefeet in each ambulacrum arranged in an irregular double row. Comparison with the specimens taken by the "Challenger" Expedition held at the British Museum (Natural History) indicates that such a high number is not unusual. The body wall ossicles of large specimens are mainly four-armed crosses lacking a spire but with one arm disproportionately developed (Heding, 1942; Hansen, in press). This arm, which protrudes obliquely from under the skin, is very spinous at its end and has several small tooth-like spines on the stem.

Cherbonnier (1941) considered that specimens of *Staurocucumis* from the Panama Basin (as *Abyssocucumis albatrossi*) were distinct from typical *S. abyssorum*. However, Hansen (in press) indicates the synonymy of the two species. This synonymy is based on an examination of material from the eastern Pacific, Kermadec Trench, Antarctic Ocean and the North Atlantic (Hansen, personal communication). *S. abyssorum* until recently has been referred to the genus *Abyssocucumis*. However, Hansen (in press) has shown that there are similarities in the development of the ossicles in *Abyssocucumis* and *Staurocucumis*, indicating the synonymy of these genera.

Thyone gadeana R. Perrier, 1902
(syn. T. wahrbergi Madsen, 1941)

BN 50607-2 (4), BN 50609-1 (1).

Bathymetric range in the PSB : 400 to 700m.

Distribution : Northeast Atlantic from the coasts of Norway, from the Trondheim Fjord to the Oslo Fjord (20 to 200m) (Madsen, 1941; B. Hansen, personal communication), Bay of Biscay (335 to 1045m) (Cherbonnier, 1969, 1970), to southern Spain (Perrier, 1902) and the Mediterranean (80 to 285m) (B. Hansen, personal communication). Total bathymetric range, 20 to 1045m. In the PSB T. gadeana is known only from the mid-part of the Porcupine Bank.

Taxonomic remarks : The specimen from St. 50609-1 (30mm long) is considerably larger than the four specimens from St. 50607-2 (10 to 15mm long). The body wall ossicles of all the specimens are similar. They have generally 8 or more holes, seldom as few as 4. The spire on the plate ossicles is short, about 30µm high. The terminal plates of the tubefeet are small, only about 90µm in diameter. Rod deposits are common in the tentacles. The largest rods, 340µm long, occur at the base of the tentacle, but rods that are present further down the tentacle are not greater than 240µm in length. Small curved plates are found distally in the tentacles.

The largest specimen is greatly contracted and as a result the introvert has parted from the body although the two pieces are still held together by the gut. The relative dimensions of the calcareous ring plates of this specimen are indentical to those figured for T. wahrbergi by Madsen (1941; Fig. 9). The present material exhibits characteristics of both T. gadeana and T. wahrbergi, supporting the proposed synonymy of the two species (Reys, 1959).

Ecological remarks : *T. gadeana* has dendritic tentacles in common with other dendrochirotid holothurians, indicating that it is a suspension feeder. Observations on the closely related species, *T. fusus*, have shown that particles are trapped by eight, large, finely branched tentacles which are then wiped clean in the mouth with the aid of two smaller ventral tentacles (Hunter-Rowe, Jeal and West, 1976). The tentacles are arranged in a similar fashion in *T. gadeana*. The intestinal contents of *T. fusus* consist mainly of detritus and feeding activity appears to be related to the strength of the prevailing current (Hunter-Rowe *et al.*, 1976). *T. gadeana* is found on the Porcupine Bank in communities dominated by the suspension-feeding sea-pen *Kophobelemnon stelliferum*.

The maximum egg size found in the present material is 400µm, the same size as reported by Madsen (1941) for *T. wahrbergi*. This may lead to direct development (Madsen, 1941) or, as suggested for *Ypsilothuria talismani* (Tyler and Gage, 1983) and *Psolus squamatus* (above), to some form of abbreviated lecithotrophic development.

Order DACTYLOCHIROTIDA

Family Ypsilothuriidae

Echinocucumis hispida (Barrett, 1857)

BN 9776-2 (9), BN 9779-1 (3), BN 10108-1 (12),
BN 10109-8 (1), OT 50503-1 (1), BN 50606-1 (6),
BN 50606-5 (88), BN 50607-2 (34), BN 51403-1 (835),
BN 51403-2 (668), BN 51403-3 (372), BN 51403-4 (891),
BN 51403-5 (492), BN 51403-6 (269), BN 51406-1 (10),
BN 51420-1 (932), BN 51420-2 (100), BN 51420-3 (534),
BN 51420-4 (223), BN 51707-1 (1).

Bathymetric range in PSB : 992 to 1333m on the transect through the centre of the PSB. 99% of the specimens were collected in a narrow depth range between 1278 and 1333m. This coincides with a set of epibenthic sledge samples taken to study sampling repeatability within a restricted area (see Section 2.2, page 55; Fig. 8). The samples were sorted to a fine scale (> 1mm) and contained many small *E. hispida*, leading to a sampling bias in the data since few other samples from the Porcupine Bank have been sorted to such a fine degree. However, data on the abundance of large specimens (> 4mm long, see below) which to some degree overcome this sampling bias, indicate that *E. hispida* does indeed have a restricted bathymetric range in the PSB.

E. hispida occurs at shallower depths on the southern slopes of the Porcupine Bank (700 to 1140m) but the lower bathymetric limit is a sampling artefact since no samples have been taken deeper than 1140m in this area. A few specimens have been collected on the Goban Spur (770 to 1404m).

Distribution : Northeast Atlantic (about 50 to 1430m) from the Norwegian coast to the Bay of Biscay (Mortensen, 1927) and perhaps as far south as northwest Africa (Herouard, 1923). Also known from the West Indies (Deichmann, 1930) and east of New Zealand (Pawson, 1965, 1970). The proposed synonymy of E. hispida and E. paratypica Ludwig and Heding, 1935 (see section 3.1, page 107) indicates that this species occurs in the Indian Ocean and has a wide, if discontinuous, geographic distribution. Some records of E. hispida are of dubious validity since in some cases it has been confused with Ypsilothuria (Mortensen, 1927). The present data show that E. hispida and Y. talismani do occur sympatrically, even at bathyal depths, and indeed the two species have been sampled in the same box core sample at a depth of about 1000m in the Rockall Trough (Gage et al., 1985).

Taxonomic remarks : see section 3.1, page 69.

Ecological remarks : The body shape of the ypsilothuriids (Fig. 10) and the poor development of the tubefeet suggests that these holothurians are essentially sedentary, infaunal animals, as originally proposed by Mortensen, 1927. This lifestyle is substantiated by the absence of any ypsilothuriids in the many photographs of the seabed taken from a camera mounted on the epibenthic sledge.

The absence of visible signs of the ypsilothuriids is not surprising since the size distributions of both E. hispida (Fig. 24A) and Y. talismani (Fig. 24B) are skewed to the smaller size classes and most of the preserved specimens are smaller than 4mm long. Several samples, all from a small area of PSB (Stas 51403-1 to 6, 51420-1 to 4), were separated into 3 broad size fractions

Figure 24. The population size distributions of *Echinocucumis hispida* (A) and *Ypsilothuria talismani* (B) from BN 51403-4. Length in 1mm size classes.

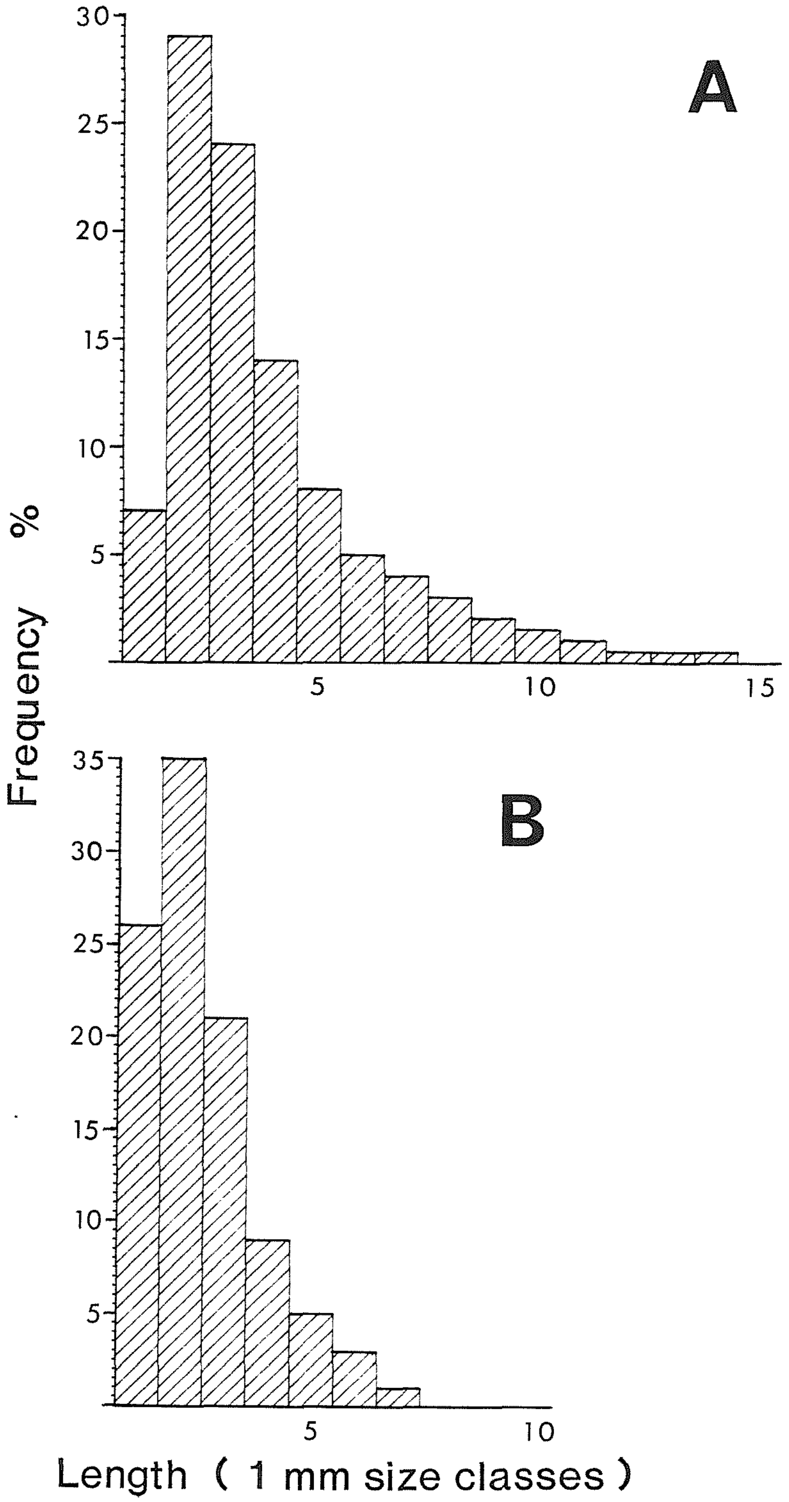

A
B
Frequency %
30
25
20
15
10
5
35
30
25
20
15
10
5
5
10
15
5
10
Length (1 mm size classes)

Table 2. The number of *E. hispida* and *Y. talismani* in the centre fine-mesh nets (1mm mesh) of the IOS epibenthic sledge from Stas 51403-1 to 5 and 51420-1,3,4, and their relative proportion in each of three size fractions sorted from the sample expressed as a percentage in parentheses The mean percentage for all stations and the standard deviation of the mean are also given.

Station			51403		
Species	-1	-2	-3	-4	-5
E. hispida					
>4mm	153 (19)	52 (8)	25 (7)	123 (14)	77 (22)
2 to 4mm	141 (17)	95 (15)	94 (27)	234 (27)	103 (29)
1 to 2mm	529 (64)	473 (77)	227 (66)	496 (59)	176 (49)
Total	823	620	346	853	356
Y. talismani					
>4mm	276 (10)	88 (6)	49 (5)	255 (9)	92 (11)
2 to 4mm	737 (26)	273 (18)	325 (30)	938 (34)	313 (36)
1 to 2mm	1851 (64)	1184 (76)	693 (65)	1538 (57)	453 (53)
Total	2864	1545	1067	2731	858

Station		51420		All stations	
Species	-1	-3	-4	Mean%	S.D.
E. hispida					
>4mm	157 (19)	95 (21)	56 (33)	18	8.4
2 to 4mm	233 (28)	89 (20)	55 (33)	25	6.4
1 to 2mm	442 (53)	260 (59)	56 (33)	57	12.8
Total	832	444	167		
Y. talismani					
>4mm	182 (9)	147 (8)	112 (24)	10	5.9
2 to 4mm	596 (30)	429 (25)	149 (31)	29	5.7
1 to 2mm	1232 (61)	1167 (67)	213 (45)	61	9.4
Total	2010	1743	474		

(> 4mm, 2 to 4mm, and 1 to 2mm). The relative proportion of the number of specimens in each size fraction (Table 2) is similar for all the samples indicating that the population size structure is stable over the region sampled (a circular area with 2km diameter). The dominance of small specimens may indicate that predation of the ypsilothuriids is high in comparison to most other holothurians in the PSB which have population size distributions dominated by large adults.

The abundance of E. hispida has been calculated from the epibenthic sledge samples by the methods described in Section 2.2, page 63. Data are presented for specimens greater than 1mm long, based solely on the catches from the centre fine-mesh net, to give an overall abundance for the species (Table 3). However, in order to be able to compare the abundance of E. hispida from a number of depths it is necessary to consider only specimens greater than 4mm long since many samples were taken without the facility of the fine-mesh net. The abundance of the large ypsilothuriids has been calculated from 1) all three nets of the multiple net system, or 2) a single large coarse-mesh net (see Section 2.2, page 62). The abundance of these large specimens is likely to be underestimated since some specimens, by virtue of their shape, will slip through the coarse mesh net. In the multiple net system this is borne out by the greater abundance of large specimens in the centre fine-mesh net than in the coarse mesh nets to either side (Table 3). Despite this limitation the comparison of the relative abundance of large ypsilothuriids is still possible.

Abundances up to 3 individuals per square metre were recorded in the PSB for E. hispida (Table 3). However, this species is only common in a restricted area on the upper slope to the northwest of the PSB; an area

Table 3. Abundance (A) of *Echinocucumis hispida* and *Ypsilothuria talismani* in epibenthic sledge samples, expressed as number per hectare. For details see text. Samples on main transect unless otherwise stated.

	Station	Mean Depth m	Specimens >4mm All nets A/Posn	Specimens >4mm All nets A/Odo	Specimens >4m Centre net A/Posn	Specimens >4m Centre net A/Odo	All specimens Centre net A/Posn	All specimens Centre net A/Odo
	Echinocucumis hispida.							
	BN 50607-2		73	232				
a	BN 9776-2		2	5	6	8	17	164 +
	OT 50503-1		>1					
	BN 51406-1		40	68				
	BN 50606-1		14	44				
a	BN 10109-1		1					
	BN 50606-5		211					
	BN 51707-1		1					
	BN 51420-4		658	1892	1152	2059	3537	6325
	BN 51403-6			2853		5993		5988
	BN 51403-5		870	2007	1266	2917	6444	14864
	BN 51420-3		1495	1934	2714	3506	12970	16779
	BN 51403-1		341	874	1141	2925	6226	15955
	BN 51420-2		880	1610				
	BN 51403-2		424	1086	738	1891	8796	22515
	BN 51403-3		327	486	535	796	7406	11029
	BN 51403-4		485	1682	1237	4301	8582	29791
	BN 51420-1		1498	2758	3060	5629	16216	29843
a	BN 10108-1		23		36		43	
a	BN 9779-1		3	10	10	35	14	52
	Ypsilothuria talismani.							
	BN 51406-1	1082	152	257				
	BN 50606-1	1115	9	29				
	BN 50606-5	1130	45					
	BN 51208-3	1178	327	989				
	BN 51208-1	1185	2	8				
	BN 51420-4	1283	1119	2002	2305	4118	9849	17614
	BN 51403-6	1287		4006		7199		
	BN 51403-5	1293	1269	2926	1513	3485	15306	35302
	BN 51420-3	1296	2111	2731	4200	5424	50766	65675
	BN 51403-1	1303	633	1623	2058	5277	21581	55299
	BN 51420-2	1307	1012	1852				
	BN 51403-2	1321	586	1499	1248	3200	21919	56106
	BN 51403-3	1322	506	753	1049	1561	22839	34010
	BN 51403-4	1326	888	3082	2565	8916	27477	95379
	BN 51420-1	1327	1796	3305	3548	6523	39216	72168
	BN 51104-1	1380	118	324				
	BN 51708-2	1450	12	28				
b	BN 9754-3	1484	217		180			
	BN 51407-1	1500	54	195				
	BN 51113-2	1535	5	13				

a Goban Spur   b northeast PSB   + weak link parted on bottom net bar inhabited, for the mostpart, by a unique suspension-feeding community with a similarly restricted bathymetric range. This community is dominated by the sponge *Pheronema grayi* (Dr. A.L. Rice, personal communication) which has a very restricted distribution (see Section 5.2). The hydrographic features that influence the distribution of *Pheronema* are poorly understood but they appear to play a role also in limiting the distribution of *E. hispida*, although probably not for the same reasons. The distribution of *E. hispida* crosses the lower boundary of the *Pheronema* assemblage and the greatest abundance of *E. hispida* lies below this boundary.

The tentacle structure of *E. hispida* indicates that it is not a suspension feeder but a surface deposit feeder, probably feeding in a similar way to bivalves but using its tentacles rather than a siphon. Two of the ten tentacles of *E. hispida* can be extended greatly and have a long stalk with numerous buds along the side (Dr. D. Roberts, personal communication). The tentacles probably sweep the sediment surface picking up particles which are then deposited in the mouth with the aid of the other, smaller tentacles.

Analysis of stomach contents from specimens collected in March shows that the gut is full of sediment containing sand grains, amorphous organic material, foraminiferans and a few diatom tests. Little of the material is readily recognisable.

The essentially sedentary lifestyle of the ypsilothuriids means that they rely on the deposition of particles on the seabed for their nutrition. The abundance of suspension feeders indicates that the currents at about 1300m to the northwest of the PSB carry a high concentration of suspended material. *E. hispida* is likely to occur in localized areas where a decrease in the currents leads to deposition of the suspended particles.

A maximum egg size of 320µm was found in the present material from specimens sampled in March. There is a range of egg sizes present and therefore no reproductive periodicity is indicated. Each specimen has a fecundity of about 150 eggs but no more than half of these are close to full development. The morphology of the ovary and the testis is similar to that described for *Y. bitentaculata attenuata* under the name of *Y. talismani* by Tyler and Gage (1983). The maximum egg size is also similar and suggests some form of abbreviated larval development (Tyler and Gage, 1983).

Ypsilothuria talismani E. Perrier, 1886

BN 9754-3 (719), BN 50606-1 (4), BN 50606-5 (19),
BN 51104-1 (46), BN 51113-2 (3), BN 51208-1 (1),
BN 51208-3 (79), BN 51403-1 (2902), BN 51403-2 (1595),
BN 51403-3 (1097), BN 51403-4 (2771), BN 51403-5 (1097),
BN 51403-6 (378), BN 51406-1 (38), BN 51407-1 (28),
BN 51420-1 (2138), BN 51420-2 (115), BN 51420-3 (1877),
BN 51420-4 (549), BN 51708-2 (6).

Bathymetric range in PSB : 1072 to 1540m on the transect through the middle of the PSB. 98% of the specimens were collected between 1278 and 1333m, the same restricted 50m depth range as *E. hispida*. As described for the latter species, the narrow depth distribution of *Y. talismani* is related to a unique suspension feeding community with a similarly restricted bathymetric range (Section 5.2).

Y. talismani is also found between 1120 and 1140m on the southern slopes of the Porcupine Bank, its narrow depth distribution recorded here probably resulting from the low sampling effort conducted in the area.

Distribution : North Atlantic, about 550 to 2018m. The present records and those from the Rockall Trough (Gage *et al*., 1985; Harvey, Gage, Billett, Clark and Paterson, in press) support Heding's (1942) proposal that *Y. talismani* is an upper slope species rarely occurring deeper than 1500m. Heding (1942) recognised a separate sub-species, *Y. talismani* elegans for a specimen from the West Indies.

Taxonomic remarks : See Section 3.1, page 82.

Ecological remarks : Many of the points concerning the ecology of *Y. talismani* have been made in a general sense with regard to *E. hispida* since both species have a similar structure, lifestyle and distribution. Like *E. hispida*, specimens smaller than 4mm long dominate the population size structure (Fig. 24B), and there is little variation in the population size structure between samples (Table 2).

The abundance of *Y. talismani* was calculated in the same way as detailed for *E. hispida*. A maximum abundance of 10 individuals per square meter was found for *Y. talismani* in the PSB (Table 3), and the samples in which *Y. talismani* was abundant all came from the same confined area as *E. hispida*. The distribution of the two species in the PSB, therefore, appears to be limited by the same factors.

The gut contents are similar to those found in *E. hispida*, and include sand grains, foraminiferans, diatoms, intact coccolitho-phorids and single coccoliths, and amorphous organic material.

The maximum egg size in the present material is 340μm diameter, almost identical to that described for *Y. bitentaculata attenuata* (Tyler and Gage, 1983; as *Y. talismani*). This indicates some form of abbreviated lecithotrophic larval development. Each individual has some 150 to 200 eggs of which about half are close to full development. The morphology of the ovary and testis is as that described for *Y. bitentaculata attenuata* by Tyler and Gage (1983).

The average wet weight of an ypsilothuriid specimen collected by a coarse-mesh net (> 4mm) was 80mg (including the coelomic fluid). Water, skeletal and organic tissue account for 82, 14 and 4% respectively of the body weight.

Order ASPIDOCHIROTIDA

Family Stichopodidae

Stichopus tremulus (Gunnerus, 1767)

OT 9776-1 (2), BN 9776-2 (1), OT 9777-2 (4),
OT 9778-1 (1), BN 10109-8 (10), BN 10110-1 (1),
BN 10120-1 (1), OT 50503-1 (6), GT 50506-1 (5),
GT 50507-1 (3), OT 50523-1 (15), OT 50524-1 (4),
OT 50601-1 (147), OT 50607-1 (61), BN 50607-2 (27),
BN 50608-2 (42), BN 50609-1 (3), OT 50609-3 (47),
OT 50702-1 (148), OT 50705-1 (1), GT 50707-1 (19),
GT 50714-1 (2), GT 50716-1 (4), GT 50717-1 (26),
OT 50806-1 (8), OT 50807-1 (6), OT 50808-1 (2),
GT 50817-1 (17), OT 50819-1 (20), OT 50820-1 (11),
OT 50821-1 (3), OT 50904-1 (2), OT 50905-1 (2),
OT 51002-1 (1), OT 51025-1 (15), OT 51026-1 (4),
BN 51102-1 (18), BN 51112-1 (12), BN 51112-4 (18),
OT 51302-1 (4), OT 51303-1 (14), OT 51304-1 (3),
GT 51312-1 (4), GT 51315-1 (1), OT 51318-1 (1),
OT 51319-1 (5), OT 51401-1 (7), OT 51404-1 (11),
BN 51405-1 (5), BN 51622-1 (1), OT 51810-1 (1),
OT 51811-1 (3), OT 51812-1 (5).

Bathymetric range in the PSB : Total range 158 to 1130m; 158m on the Celtic Shelf (the shallowest depth sampled in this study); 205 to 1130m on the Goban Spur; 297 to 785m to the northeast of the PSB; and 310 to 1035m on the slopes of the Porcupine Bank. *S. tremulus* occurred in nearly all the samples taken shallower than 800m but in only a third of the samples taken between 800 and 1200m.

Distribution : Northeast Atlantic - Norway to the Canary Islands, generally between 60 and 1918m. It can be found as shallow as 20m in Scandanavian waters (Jespersen and Lutzen, 1971). The deepest records come from a few specimens sampled off Portugal and northwest Africa (Perrier, 1902; Herouard, 1923). The distribution of *S. tremulus* in the Rockall Trough is similar to that in the PSB (168 to 1020m, Gage *et al.*, 1985; Harvey *et al.*, in press).

Ecological remarks : The abundance of *Stichopus* in the PSB is highly variable. Data from the epibenthic sledge show that it is most abundant at depths shallower than 700m, particularly on the Porcupine Bank (Table 4). However, it is evident from St. 10109-8 that *S. tremulus* may be fairly common in localised areas even at the bottom of its bathymetric range. The abundance of *S. tremulus* calculated from the epibenthic sledge samples is at least 5 times greater than that estimated from the otter trawls, demonstrating that trawls cannot sample epibenthic invertebrates quantitatively. Despite this limitation the abundance of *S. tremulus* decreases in otter trawl samples deeper than 700m.

S. tremulus is particularly abundant in two otter trawl samples from an area in the northeast of the PSB (Table 4) where suspension-feeders, such as the corals *Lophelia pertusa* and *Madrepora oculata* and the holothurian

Table 4. The abundance (A) of *Stichopus tremulus* in the epibenthic sledge and otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise stated. n = number of specimens taken.

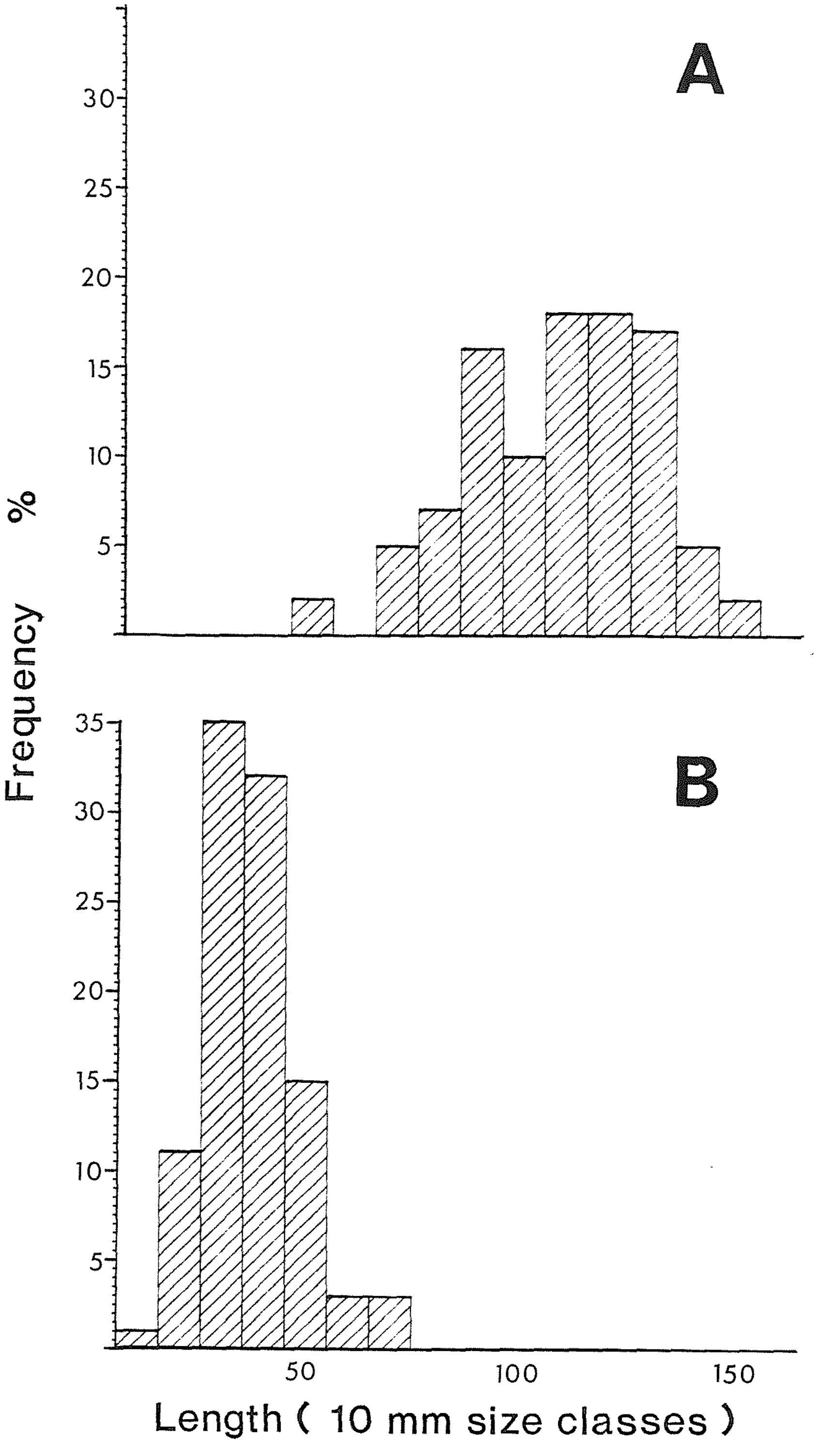
Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
a BN 51622-1	158	1	3.8	5.9
BN 50609-1	400	3	35.4	43.7
b BN 10120-1	400	1	3.7	9.9
BN 51405-1	498	5	16.6	39.4
BN 50608-2	510	42	49.5	197.0
BN 51112-1	523	12	31.6	60.1 *
BN 51102-1	525	18	58.3	129.0 +
BN 51112-4	555	18	35.1	127.0 *
BN 50607-2	700	27	57.9	184.0
b BN 9776-2	778	1	1.9	5.4 +
b BN 10110-1	925	1	1.8	-
b BN 10109-8	1125	10	12.3	-
Otter trawl samples.				
b OT 9777-2	243	4	0.6	
c OT 51401-1	297	7	1.9	
OT 50609-3	408	47	12.3	
b OT 50523-1	473	15	4.5	
OT 50819-1	506	20	6.3	
b OT 50806-1	513	8	1.8	
OT 50607-1	706	61	13.7	
OT 50820-1	720	11	2.0	
b OT 50705-1	743	1	0.3	
OT 51404-1	750	11	2.7	
b OT 50524-1	763	4	0.7	
c OT 50702-1	785	148	58.0	
OT 50905-1	788	2	0.4	
b OT 50807-1	793	6	1.5	
b OT 9776-1	804	2	0.5	
c OT 50601-1	849	147	28.8	
OT 50821-1	986	3	0.6	
OT 50503-1	1017	6	1.6	
OT 50904-1	1028	2	0.4	
b OT 9778-1	1036	1	0.3	

a Celtic Shelf
b Goban Spur
c northeast PSB

*no tickler chain
+weak link parted on bottom net bar

Figure 25. The population size distributions of Stichopus tremulus. Length in 10mm size classes.

A) OT 50607-1, 7: 7:79, 706m, n = 60.
B) OT 50601-1, 1: 7:79, 847m, n = 147.


A
B
Frequency %
30
25
20
15
10
5
35
30
25
20
15
10
5
50
100
150
Length (10 mm size classes)

Psolus squamatus are common. However, whereas most S. tremulus in the PSB are greater than 100mm long (after preservation) (Fig. 25A) even at the bottom of the bathymetric range, the specimens from the coral area are only 15 to 70mm long (after preservation) (Fig. 25B). The reasons for the prevalence of many small S. tremulus in coral areas is unknown but it is not confined to slope depths. In shallow Scandanavian waters (80 to 160m deep) Jespersen and Lutzen (1971) noted that S. tremulus was more abundant and substantially smaller in areas with gravel, boulders and dead coral (Lophelia) than in areas with a mud substrate.

The correlation between specimen length and dry weight is poor ($r^2 = 0.49$) owing to the variable state of contraction of the specimens. The biomass of S. tremulus was measured directly at Stas 51102-1 and 51112-4. A wet weight, dry weight and ash-free dry weight biomass of 9376g, 816g and 423g per hectare respectively was calculated for St. 51102-1. Similarly for St. 51112-4 the values are 8371g, 867g and 522g per hectare respectively. Walker et al. (1987) report a calorific content of 25.6 J/mg AFDW for the body wall of S. tremulus producing a calorific biomass of 4890 KJ and 3686 KJ per hectare for the two stations.

Water, skeletal and organic tissue comprise about 90%, 4% and 6% respectively of the body weight. In terms of biomass S. tremulus is an important component of the epibenthic invertebrate community. At Stas 51102-1 and 51112-4 S. tremulus contributes 27% and 39% respectively to the total wet weight biomass. However, the high water content of S. tremulus tends to exaggerate its importance in the community, for in terms of AFDW biomass it contributes only 9% and 19% of the total biomass at the two stations.

Although S. tremulus was regarded to be a non-selective deposit feeder by Jespersen and Lutzen (1971), Hauksson (1979) concluded that this species did select for particles, such as sediment aggregates and faecal pellets, with a higher organic content than the general surface sediment. Microscopical analysis of the gut contents of S. tremulus from the PSB could not resolve this difference. Small specimens collected from the coral areas had intestines packed with coarse material, principally sand grains and foraminiferans with a few organic aggregates including faecal pellets. Specimens from the Porcupine Bank, however, had much finer particles in their intestines although sand grains and foraminiferans still accounted for much of the material. In the latter case there seemed to be little selectivity for faecal pellets and other aggregates. A comparison of the grain size of the surficial sediment and the gut contents is necessary.

Assuming that specimens from the Porcupine Bank are as active as specimens collected in shallow Scandanavian waters, the feeding rate of S. tremulus in the PSB can be estimated. When the gut is full, the dry weight of the sediment in the guts of shallow water S. tremulus is about 130% of the dry weight of the specimen (Hauksson, 1979). About half of the gut contents are voided when the holothurian defaecates, an event that occurs about every 20 hrs (Hauksson, 1979). Using these data together with abundance estimates for S. tremulus from the epibenthic sledge (Table 4) the rate of sediment turnover by this species can be estimated for Stas 51102-1 and 51112-4. The total dry weight of S. tremulus from these stations is 113g and 123g respectively (18 specimens in each sample), producing a defaecation rate of 73.5g and 80.0g sediment DW per 20hr for the two populations.

In shallow water about 2% of the sediment dry weight is assimilated by the holothurian during its passage through the gut (Hauksson, 1979). In deeper water, however, where the organic content of the sediment is low (less than 1% sediment DW as opposed to 5% in shallow water), the proportion of the sediment dry weight assimilated will be smaller. Hence, the amount of sediment defaecated will be almost equivalent to the amount ingested and no correction factor is necessary for the proportion assimilated.

Each individual will process on average 4.9g and 5.3g sediment DW per day, or 1789g and 1935g annually, at Stas 51102-1 and 51112-4 respectively. Using the abundance data calculated from the odometer records (Table 4), some 23.1g $/m^2$ or 24.6g$/m^2$ of sediment DW will be consumed annually by the two populations. This is a similar rate to that calculated for the shallow water Scandanavian populations of S. tremulus (20g sediment DW$/m^2$ - Hauksson, 1979).

The sexes are separate in S. tremulus. In Scandanavian waters pelagic eggs are spawned seasonally in July/August (Jespersen and Lutzen, 1971). For the PSB specimens a maximum egg size of 120µm, the uniformity of egg size in individual specimens, and their high fecundity, all indicate that deep water populations also reproduce seasonally using planktotrophic development, although spawning occurs in April/May. Despite the evidence for seasonal breeding, seasonal recruitment has not been found in deep or shallow water populations. Specimens smaller than 30mm are seldom found (Rustad, 1938; Jespersen and Lutzen, 1971) and the populations in the PSB, except those from the coral areas, follow this pattern.

S. tremulus is reported to be predated by some seastars and fish (Ostergren, 1938; Jespersen and Lutzen, 1971) but the number of predators is small. The holothurian produces copious amounts of slime that contains a toxic substance (Jespersen and Lutzen, 1971).

The bizarre endoparasitic gastropod *Enteroxenos*, reported in shallow water *S. tremulus* (Jespersen and Lutzen, 1971; Lutzen, 1979) also occurs in deep-water specimens in the PSB.

Family Synallactidae

Bathyplotes natans (M. Sars, 1868)

BN 9754-3 (1), OT 9774-1 (1), BN 9779-1 (21),
BN 10108-1 (4), BN 10109-8 (80), OT 50503-1 (1),
GT 50505-1 (3), OT 50519-1 (193), GT 50520-1 (1),
OT 50522-1 (1), OT 50601-1 (1), BN 50606-1 (2),
OT 50606-2 (23), BN 50606-5 (3), OT 50611-1 (63),
OT 50704-1 (11), GT 50709-1 (11), GT 50713-1 (1),
OT 50801-1 (56), OT 50808-1 (1), GT 50809-1 (8),
OT 50903-1 (30), OT 50904-1 (14), OT 51008-1 (5),
OT 51023-1 (18), OT 51027-1 (1), OT 51306-1 (8),
OT 51314-1 (4), BN 51403-1 (24), BN 51403-2 (18),
BN 51403-3 (15), BN 51403-4 (22), BN 51403-5 (15),
BN 51403-6 (6), OT 51403-7 (78), BN 51406-1 (3),
BN 51407-1 (6), BN 51420-1 (18), BN 51420-2 (7),
BN 51420-3 (7), BN 51420-4 (11), BN 51707-1 (8),
BN 52009-1 (1), BN 52204-1 (10), BN 52218-1 (12).
(Number of specimens includes juveniles.)

Bathymetric range in PSB : 770 to 1572m, but only common between 1100 and 1465m (96% of the specimens collected). On the main transect *B. natans* was most common in the proximity of the area dominated by the sponge *Pheronema*.

Distribution : Cosmopolitan. In the northeast Atlantic *B. natans* usually occurs between 600 and 1600m, rising to about 200m off Norway. *B. natans* occurs at similar depths in the Rockall Trough (1000 to 1265m) (Gage *et al*., 1985; Harvey *et al*., in press).

Taxonomic remarks : Details of the ossicles found in juvenile *B. natans* are given in Section 3.2, page 108. Many of the specimens were orange in colour.

Ecological remarks : The greatest abundance of *B. natans* was recorded in an area lying across the lower boundary of the *Pheronema* community (see Section 5.2). A maximum abundance of 178 individuals per hectare was found at St. 51403-4 (230 individuals per hectare including small juveniles) (Table 5). The abundance of *B. natans* estimated from the sledge hauls is about 5 times greater than that estimated from the trawls (using ship's position to calculate the distance trawled). For the epibenthic sledge, the abundance of *B. natans* is some 2 to 3 times greater when the area sampled is calculated from the odometer record rather than the ship's position.

The dry weight biomass of *B. natans* was determined directly at a number of stations (Table 5). Water accounts for about 91% of the fresh body weight, varying between 86 and 94%. Large specimens tend to have a higher water content than small specimens. The ash-free dry weight biomass of *B. natans* could not be determined directly, but assuming that the AFDW of *B. natans* is one third of its dry weight, as determined for a similar synallactid (*Mesothuria lactea*),then a maximum AFDW biomass of 196g per hectare can be calculated (St. 51420-1). Walker *et al.*, (1987a) report a calorific content of 25.5 J/mg AFDW for the body wall of *B. natans*, producing a calorific biomass of 5000 KJ per hectare for the same station.

The greatest biomass of *B. natans* on the main transect occurred in the areas of its greatest abundance, between 1278 and 1333m. The biomass of *B. natans* was determined at 9 stations sampled between these depths, 5 within the *Pheronema* community (1278 to 1314m) and 4 just below the

Table 5. The abundance (A) and biomass (B) of Bathyplotes natans in epibenthic sledge and otter trawl samples, expressed as number or g DW per hectare. Samples from the main transect unless otherwise stated. Abundance values are given for 1) all specimens, 2) excluding juveniles. n = number of specimens including juveniles.

	Station	Mean Depth (m)	n	All specimens A/Posn	All specimens A/Odo	Adult specimens A/Posn	Adult specimens A/Odo	g DW B/Odo	
	Epibenthic sledge samples.								
	BN 51406-1	1082	3	12.0	20.3	12.0	20.3	46	
	BN 50606-1	1115	2	4.5	14.6	4.5	14.6		
a	BN 10109-8	1125	80	98.0		98.0			
	BN 50606-5	1130	3	7.2		7.2			
	BN 51707-1	1218	8	8.4		8.4			
	BN 52009-1	1221	1	3.2	6.4	3.2	6.4		
	BN 51420-4	1283	11	67.7	121.0	12.3	22.0	122	
	BN 51403-6	1287	6		63.6		63.6	167	
	BN 51403-5	1293	15	73.8	170.1	73.8	170.1	243	
	BN 51420-3	1296	7	59.8	77.4	8.6	11.1	43	
	BN 52204-1	1303	10	108.6	140.9	108.6	140.9		
	BN 51403-1	1303	24	53.5	137.2	42.4	108.6	164	
	BN 51420-2	1307	7	43.1	78.8	43.1	78.8		+
	BN 51403-2	1321	18	76.4	195.5	67.9	173.7	395	
	BN 51403-3	1322	15	96.0	143.0	70.4	104.9	229	
	BN 51403-4	1326	22	66.2	229.9	51.2	177.6	460	
	BN 51420-1	1327	18	104.9	193.1	75.8	139.5	588	
a	BN 10108-1	1388	4	8.4		8.4			
a	BN 9779-1	1401	21	30.0	109.6	30.0	109.6		
a	BN 52218-1	1440	12	27.9	51.7	27.9	51.7		
b	BN 9754-3	1484	1	2.1		2.1			
	BN 51407-1	1500	6	11.5	41.7	11.5	41.7	22	
	Otter trawl samples.								
	OT 50601-1	849	1	0.2					
a	OT 50522-1	983	1	0.3					
	OT 50503-1	1017	1	0.3					
	OT 50904-1	1028	14	2.8					
	OT 50606-2	1100	23	5.6					
	OT 51306-1	1218	8	2.6					
	OT 50903-1	1258	30	6.5					
a	OT 50801-1	1265	56	11.7					
	OT 51403-7	1293	78	18.8					
	OT 50611-1	1388	63	10.1					
a	OT 50519-1	1448	193	39.1					
b	OT 9774-1	1533	1	0.2					

a Goban Spur
b northeast PSB

+ Abundance estimated from outer nets only. Centre net catch discarded.

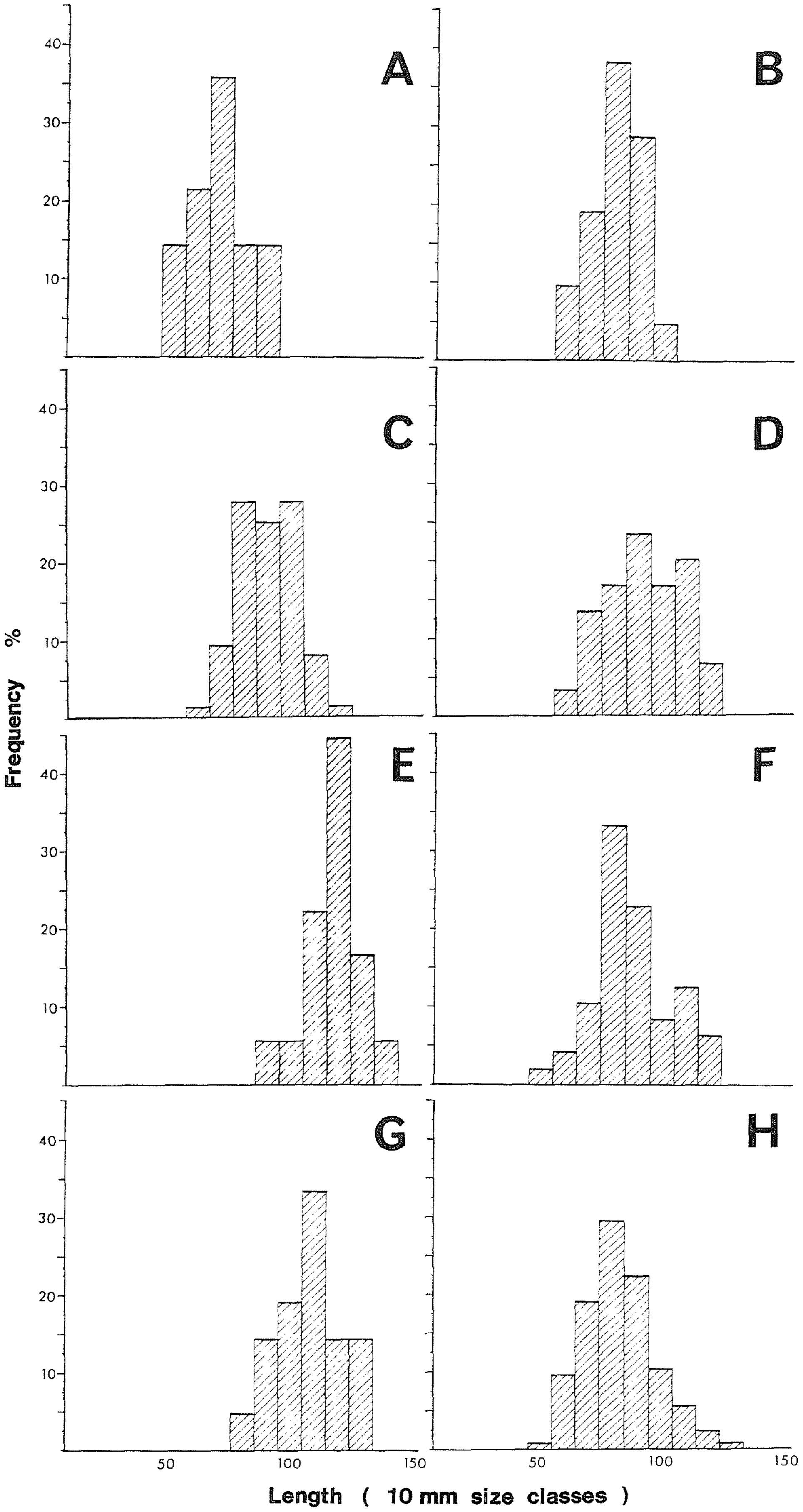
lower boundary of the sponges (1317 to 1333m). The biomass of the latter stations is significantly greater than the former stations (t-test, $p>0.05$). The contribution of *B. natans* to the total AFDW biomass within the *Pheronema* community is less than 3% (in 3 samples less than 1%), but in the area immediately below the sponges *B. natans* accounts for 8 to 11% of the biomass. The proportion of *B. natans* AFDW biomass at Stas 51406-1 (1082m) and 51407-1 (1500m) is negligible (much less than 1%).

The soft body of *B. natans* can lead to considerable mutilation of the specimens during capture. Coupled with the variable state of contraction of the specimens this results in a poor correlation of specimen length with dry weight ($r^2 = 0.50$). The comparison of the population size distributions of preserved samples, however, shows some differences between *B. natans* from different depths (Fig. 26). The largest specimens occur in the middle of the bathymetric range (e.g. Stas 51403 and 51420 combined) while small specimens dominate the populations sampled at the shallowest and deepest part of the range (e.g. Stas 50904- 1 and 50519-1) (Fig. 26).

The population size distributions of *B. natans* do not show any evidence of seasonal recruitment even though Tyler and Muirhead (1986) indicate that there may be periodic, possibly seasonal, production of oocytes. Only a few fully developed oocytes are evident in specimens collected in late April to May, but later in the year (September/ October) mature eggs are more common and in many specimens a bimodal distribution of oocyte size is found (Tyler and Muirhead, 1986). These features show some similarity to the oocyte production found in other deep-sea echinoderms that reproduce seasonally (Tyler *et al*., 1982). A few, small juveniles, only 1 to 2mm long, were present in samples taken in late March (Stas 51403,

Figure 26. The population size distributions of *Bathyplotes natans*. Length in 10mm size classes.

A) OT 50904-1, 8:11:80, 1027m, n = 14.
B) OT 50606-2, 6: 7:79, 1100m, n = 21.
C) BN 10109-8, 7: 9:79, 1125m, n = 76.
D) OT 50903-1, 7:11:80, 1257m, n = 30.
E) BN 51403/51420, 25: 3:82, 1300m, n = 18.
F) OT 50611-1, 8: 7:79, 1388m, n = 48.
G) BN 9779-1, 24: 4:78, 1401m, n = 21.
H) OT 50519-1, 8: 6:79, 1448m, n = 126.


A
B
C
D
E
F
G
H
40
30
20
10
Frequency %
50
100
150
50
100
150
Length (10 mm size classes)

51420). Their abundance, as determined using the odometer records, ranged between 0 and 100 individuals per hectare (8 samples). Data are not available from other times of the year for comparison.

B. natans produces an egg with a maximum diameter of 280µm (Tyler and Muirhead, 1986). Eggs of this intermediate size (see Section 5.5) are likely to undergo some form of lecithotrophic larval development.

B. natans is an epibenthic deposit-feeding holothurian that glides over the seabed on its numerous, small latero-ventral tubefeet. No perceptible mark is left on the seabed. When disturbed *B. natans* is able to swim for short periods by undulating its body (Sars, 1868).

The commensal polychaete, *Harmothoe bathydomus* Ditlevsen 1917, described by Wesenberg-Lund (1941) in association with *B. natans* in the PSB, was not found on any of the specimens examined.

Benthothuria funebris R. Perrier, 1902

OT 9638-2 (4), OT 9640-1 (46), BN 9756-14 (1),
BN 10115-1 (2), OT 50512-1 (1), OT 50514- 1 (3),
BN 50603-1 (1), BN 50605-1 (3), OT 50811- 1 (2),
OT 50812-2 (9), OT 50813-1 (2), OT 50906- 1 (1),
OT 50907-1 (2), OT 50910-1 (1), BN 50913- 1 (1),
OT 51012-1 (1), BN 51109-1 (2), BN 51109- 2 (1),
OT 51214-1 (20), BN 51216-1 (3), OT 51216- 4 (20),
OT 51309-1 (1), OT 51411-1 (2), BN 51412- 1 (1),
OT 51413-1 (130), OT 51414-1 (4), BN 51414- 2 (1),
BN 51415-1 (16), BN 51604-1 (2), OT 51610- 1 (139),
OT 51611-1 (1), OT 51803-1 (2), OT 51804- 1 (3),
BN 52214-1 (1).
In the Rockall Trough : OT 50701-1 (67).

Bathymetric range in PSB : 2470 to 4400m, but only common between 2770 and 3820m (83% of the specimens collected) in an area bordering the steep and rugged terrain at the mouth of the PSB (Fig. 1, page 37). *B. funebris* occurred in 11 of the 12 samples taken between 3400 and 4000m. The sample from the Rockall Trough cited above came from an area close to the base of the continental slope to the north of the Porcupine Bank (2870 to 2890m).

Distribution : Northeast Atlantic from northwest Africa to off southwest Greenland; 782 to 4400m including the present records. The PSB specimens and those reported recently from the Rockall Trough (Gage *et al*., 1985; Harvey *et al*., in press), provide a geographic link between the previous widely separated records of this species. If *B. funebris* is synonymous with *B. valdiviae* Heding, 1940 (see Taxonomic remarks) then the lower bathymetric limit is 4636m and the species also occurs in the Antarctic Ocean. The bathymetric distribution of *B. funebris* is rather curious since it appears to occur at greater depths in northerly latitudes (2700 to 4400m) than off northwest Africa (782 to 1430m, depth limits including the records cited below).

Taxonomic remarks : Although *B. funebris* may be sampled in good condition, the watery dorsal surface (see below) is notoriously difficult to preserve, leading to difficulties in identification. Heding (1940) proposed five species for the genus *Benthothuria*, although he questioned the validity of *B. cristatus* and considered *B. funebris* to be synonymous with *B. valdiviae*. The latter two nominal species differ in two respects; the number of polian vesicles and the presence or absence of large dorsal papillae. Like the "Ingolf" specimen (Heding, 1942) the PSB specimens, and those sampled in the Rockall Trough (Gage *et al*., 1985), possess two polian vesicles, which is at variance with the single polian vesicle reported from the type specimen of B. funebris. However, two specimens of B. funebris sampled off northwest Africa ("Discovery" St. 10874-1, 14° 50.8'N, 17° 50.6'W, 1430m), in an area not far from the type locality, both had two polian vesicles. It was not possible to ascertain the presence of large dorsal papillae on these specimens owing to their poor state of preservation. However, like B. valdiviae, the PSB specimens do possess a few larger papillae along the dorsal ambulacra (Fig. 27B). Both species have in addition small papillae that are scattered over the dorsal surface, particularly in the lateral interambulacra. These observations support Heding's proposed synonymy of the two species.

Ecological remarks : The abundance of B. funebris is variable with the greatest abundance of B. funebris occurring close to the base of the continental slope (St. 51415-1, 55 individuals per hectare). The reasons for the prevalence of B. funebris at the mouth of the PSB may lie in the holothurian's rather bizarre form. B. funebris has a flat ventral surface and a high arched dorsal surface (Fig. 27B). The coelomic cavity, however, occupies at most only about one third of the body volume. Most of the dorsal region is composed of a mass presumed to be connective tissue, since although the body is quite firm when the holothurian is first sampled it rapidly turns gelatinous when preserved. Collagenous connective tissues in the body wall of holothurians are known to be able to control the stiffness of the body by changing their mechanical properties (Motokawa, 1984).

It is clear from observations made at sea that B. funebris is almost neutrally buoyant despite its large size, possibly aided by its watery (96.5%) dorsal region. It is not known whether B. funebris can float above the

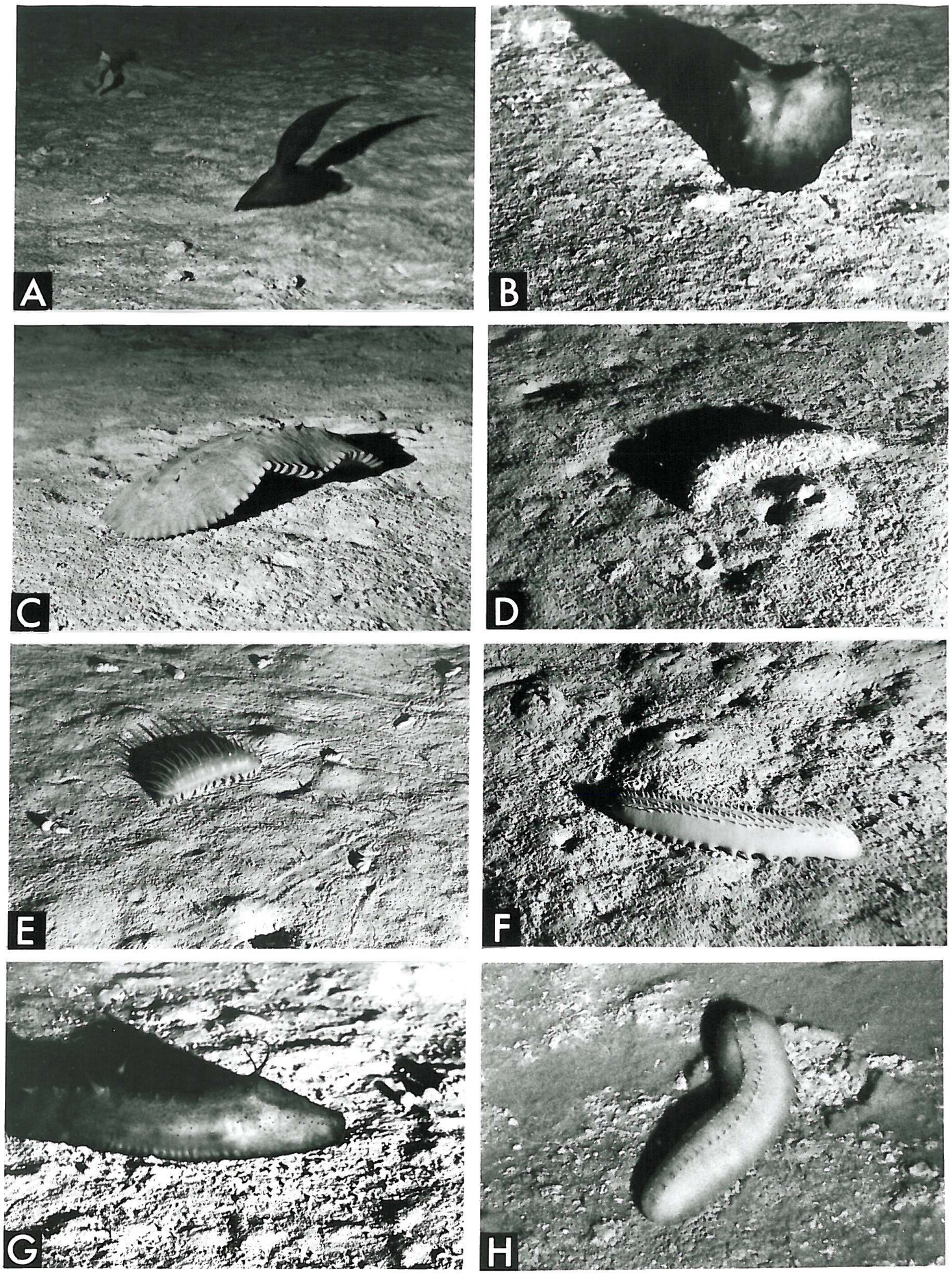
Table 6. The abundance (A) of *Benthothuria funebris* in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 51412-1	2775	1	1.3	2.9
BN 50605-1	2875	3	3.2	
BN 51604-1	2905	2	6.9	14.2
BN 50913-1	3020	1	1.6	
BN 51415-1	3490	16	39.3	55.1
BN 9756-14	3689	1	1.0	6.9
BN 10115-1	3925	2	5.1	14.7
BN 51109-1	3950	2	4.4	9.1
BN 51109-2	3985	1	1.5	4.5
BN 50603-1	4000	1	1.3	
BN 52214-1	4063	1	0.7	2.2 +
BN 51216-1	4070	3	6.4	10.4
BN 51414-2	4080	1	1.7	3.4
Otter trawl samples.				
OT 51411-1	2485	2	0.3	
OT 50906-1	2645	1	0.1	
OT 51611-1	2670	1	0.1	
OT 51413-1	2855	130	16.6	
OT 50907-1	2975	2	0.2	
OT 50512-1	3066	1	0.2	
OT 51610-1	3485	139	14.0	
OT 50813-1	3678	2	0.2	
OT 9640-1	3753	46	4.8	
OT 51214-1	3810	20	3.9	
OT 51216-4	3985	20	3.2 *	
OT 50514-1	4056	3	0.4	
OT 9638-2	4074	4	0.8 o	
OT 50812-2	4088	9	0.9	
OT 51414-1	4155	4	0.4	
OT 51309-1	4223	1	0.1	
OT 50910-1	4312	1	0.1	
OT 50811-1	4375	2	0.3	

+ small catch owing to recovery of sledge during a gale.
* trawl doors found tangled on recovery. Abundance could be higher.
o acoustic monitor lost from trawl. Precise distance travelled by trawl unknown.

Figure 27.

A) *Psychropotes semperiana*.
B) *Benthothuria funebris*.
C) *Paelopatides grisea* showing undulations of the lateral brim used in swimming.
D) *Mesothuria intestinalis* with rough surface caused by the accretion of foreign particles.
E) *Laetmogone viloacea* showing dorsal papillae, tubefeet, tramline track and faecal strings.
F) *Benthogone rosea* showing papillae, tubefeet and faint track.
G) *Benthodytes sordida* showing the variable size of the dorsal papillae.
H) *Benthogone rosea* feeeding on the detrital layer.


A
B
C
D
E
F
G
H

seabed at will, but these holothurians would be suspended easily by strong nearbed currents. There is little doubt that the neutral buoyancy of B. funebris would aid the species to survive episodic catastrophes such as turbidity currents, events characteristic of steep continental slope areas (Heezen et al., 1955). This proposal is substantiated by other reports of Benthothuria in areas of steep topography, such as on a mid-oceanic ridge in the South Pacific (photograph p 85, Heezen and Hollister, 1971) and in the De Soto Canyon in the Gulf of Mexico (photographs pp 90, 95, Pequegnat et al., 1972).

The population size distributions for the samples in which B. funebris was common are plotted in Fig. 28. Specimens vary between 45 and 250mm long. There is no obvious relationship with depth except that those specimens at the bottom of the bathymetric range are generally smaller (e.g. St. 9640-1). In all the samples taken, specimens longer than 100mm are seldom found deeper than 4000m.

The biomass of B. funebris was determined directly from four epibenthic sledge samples (Table 7). The greatest biomass was recorded at the base of the continental slope (St. 51415-1), the area where B. funebris was most abundant, with an AFDW biomass of 589g per hectare. Walker et al., (1987a) calculated a total calorific value of 25.62 J/mg AFDW for B. funebris, producing a calorific biomass of 15090 KJ per hectare for this station. In this one sample B. funebris accounted for 71% of the total epibenthic invertebrate AFDW biomass.

Figure 28. The population size distributions of *Benthothuria funebris*. Length in 10mm size classes.

A) OT 51413-1, 30: 3:82, 2855m, n = 118.
B) BN 51415-1, 31: 3:82, 3490m, n = 16.
C) OT 9640-1, 13:11:77, 3753m, n = 40.
D) OT 51214-1, 27: 9:81, 3810m, n = 20.
E) OT 51216-4, 29: 9:81, 4035m, n = 19.

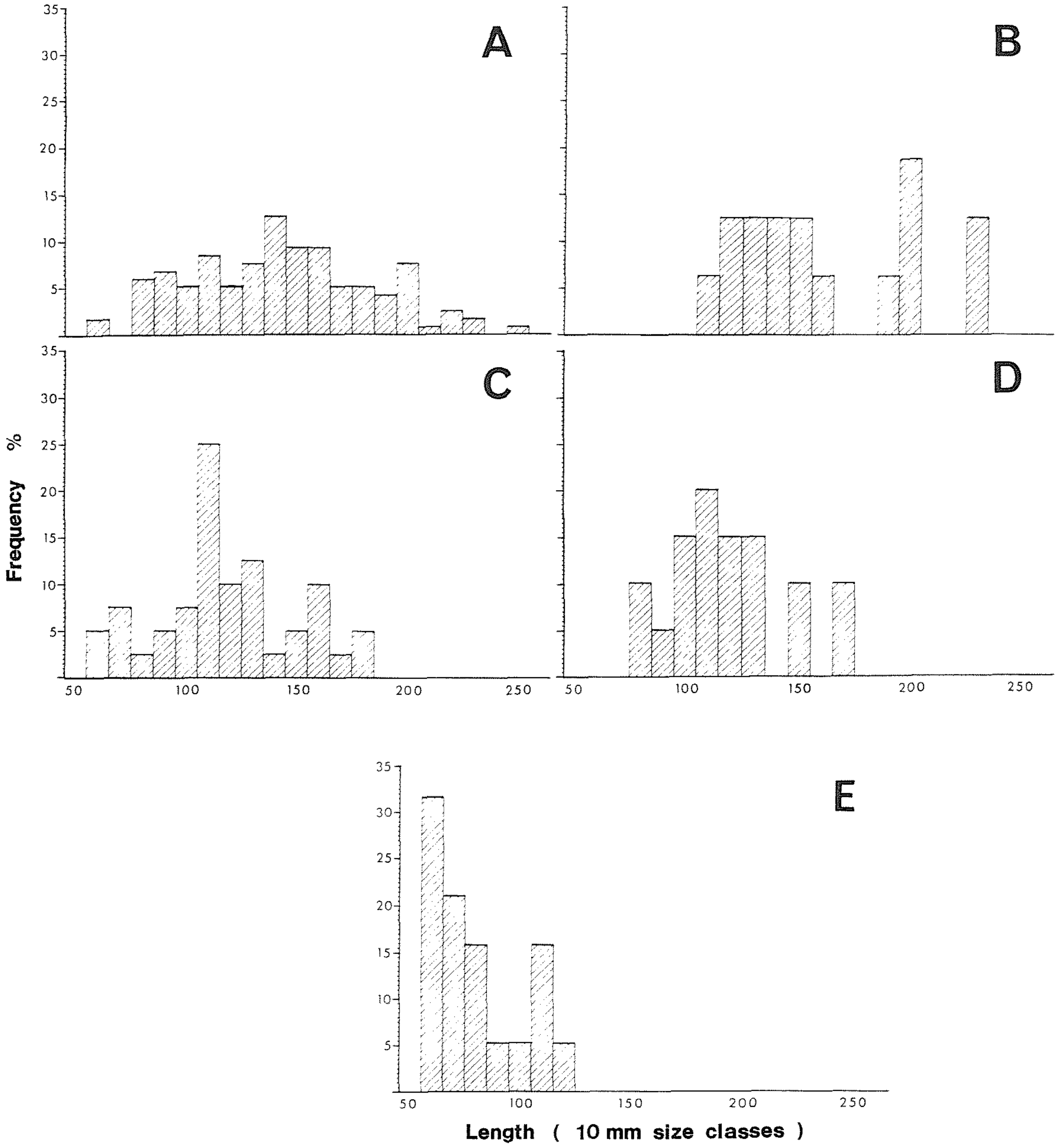

A
B
C
D
E
Frequency %
35
30
25
20
15
10
5
50
100
150
200
250
Length (10 mm size classes)

Table 7. The WW, DW, AFDW and calorific biomass of B. funebris from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 6.

Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51412-1	2775	2354 (88)	93 (50)	37 (41)	948
51415-1	3490	30055 (86)	1281 (67)	589 (71)	15090
51109-1	3950	3532 (50)	157 (23)	60 (23)	1537
51216-1	4070	1175 (19)	73 (12)	29 (13)	743

Both WW and DW are closely correlated with length, $r^2 = 0.89$ and 0.87 respectively. The relationship between DW and length is given by the equation :

$$\mathrm{Log}\ (DW) = \mathrm{Log}\ (\mathrm{Length}) \times 1.7243 - 2.4663$$

where $n = 18$ and the standard error = 0.0868. Similarly, DW is also closely correlated with volume, $r^2 = 0.75$. The relationship between the two is given by the equation :

$$\mathrm{Log}\ (DW) = \mathrm{Log}\ (\mathrm{Volume}) \times 0.3961 + 0.1313$$

where $n = 15$ and the standard error = 0.0783. The gradient of the regression of dry weight on volume is significantly different from the expected gradient of one. The disparity in the gradients is unlikely to be the result of difficulties in methodology. Rather, the singular form of Benthothuria, with its large dorsal mass of watery connective(?) tissue, allows it to increase its size substantially with only a minimum input of organic matter. Consequently, the proportion of water, ash and organic matter in B. funebris changes from about 89%, 4% and 7% respectively in small specimens to about 96%, 2.5% and

1.5% respectively in large specimens. The low organic content of B. funebris may allow this holothurian to reach a considerable size very rapidly thereby reducing predation.

The relationships of DW with both length and volume can be used to estimate the biomass of B. funebris from other samples, such as St. 51413-1. The 130 specimens at this station had a total DW of 2445g as determined from their lengths, or 2410g as determined from their volumes, giving a DW biomass of 313g per hectare. The true DW biomass of B. funebris at this station, however, could be much greater owing to the apparent inefficiency of the otter trawl in sampling epibenthic invertebrates. The samples show no evidence of seasonal recruitment. Tyler and Muirhead (1986) have suggested that there is periodic, but not seasonal, release of oocytes in batches, based on the analysis of oocyte sizes in the various tubules of the ovary. The maximum oocyte diameter of 1.5mm indicates either direct development or lecithotrophic larval development possibly with an extended larval phase since there are plenty of yolk reserves.

B. funebris, an epifaunal deposit-feeding holothurian, glides over the seabed leaving the barest trace of its passage across the sediment surface. Movement is probably effected by a double row of small, mid-ventral tubefeet. The gut of Benthothuria is of interest since it has a caecum attached to the stomach, but its role in the nutrition of the holothurian is unknown. Like several abyssal elasipodid species, B. funebris can be infested by sporozoan parasites.

Paelopatides grisea R. Perrier, 1902

BN 9753-7 (3), OT 9753-8 (1), BN 9754-3 (1),
OT 9774-1 (1), BN 9775-3 (72), BN 10106-1 (17),
BN 10111-8 (2), OT 50510-1 (80), OT 50517-1 (24),
BN 50602-2 (4), OT 50602-3 (52), OT 50703-1 (5),
OT 50715-1 (2), OT 50802-1 (1), OT 50810-1 (8),
OT 50822-1 (8), OT 50902-1 (8), OT 51010-1 (2),
OT 51011-1 (2), OT 51021-1 (3), OT 51022-1 (1),
BN 51105-3 (10), OT 51201-1 (75), OT 51213-1 (77),
OT 51308-1 (1), OT 51311-1 (7), BN 51408-1 (19),
OT 51409-1 (30), OT 51613-1 (115), BN 51717-2 (14),
OT 51801-1 (1), BN 52019-1 (1), BN 52211-1 (5).

Bathymetric range in PSB : 1484 to 2315m; generally 1650 to 2315m on both the Goban Spur and the main transect. *P. grisea* occurred in 29 of the 33 samples taken between 1600 and 2400m. The precise lower bathymetric limit is uncertain since few samples have been taken between 2100 and 2500m (Fig. 7, page 57).

Distribution : Northeast Atlantic, 1484 to 4060m (including the PSB material). It may occur throughout the north Atlantic if the synonymy with *P. gigantea* is correct (see Taxonomic remarks). Records from the PSB, the Rockall Trough (Gage *et al*., 1985; Harvey *et al*., in press) and the southern Bay of Biscay (Sibuet, 1977), indicate that *P. grisea* is usually found around the 2000m isobath in the northeast Atlantic, although Sibuet (1977) also recorded *P. grisea* (*P. gigantea*) from 3100m in the northern Bay of Biscay.

Taxonomic remarks : The species of *Paelopatides* are sometimes difficult to distinguish owing to the damage that the body suffers during sampling and preservation. Although Deichmann (1930) considered *P. grisea* to be synonymous with the northwest Atlantic species *P. gigantea* (Verrill, 1884), Heding (1940) believed that the two could be separated by the number of polian vesicles; the former species is reported to have one and the latter species two. The PSB specimens have 2 polian vesicles, one of which is large while the other is variable in size but generally small and could be overlooked. It is likely that the two species are indeed synonymous, but a detailed examination of material from the northwest Atlantic is needed.

Ecological remarks : The abundance of *P. grisea* in a few samples is very high (Table 8). 72 specimens were collected in one sledge sample from the centre of the PSB (St. 9775-3) despite the breakage of a weak link which holds the net in contact with the seabed (the weak link parts if the net is snagged by an obstacle on the seabed). It is possible, therefore, that a greater number of *P. grisea* could have been sampled. A second fault on this haul led to the loss of the centre net catch (for gear details see section 2.2). As a result, the abundance of *P. grisea* was estimated from the area sampled by the two outer nets only which are known to catch holothurians more effectively than the fine-mesh centre net. It would seem that holothurians bound for the centre net are deflected into the coarse-mesh nets to either side. Therefore, the abundance of *P. grisea* at St. 9775-3 (1125 individuals per hectare) is likely to be overestimated. Even assuming that all the specimens bound for the centre net were deflected into the outer nets, and therefore that the area swept should be calculated using the entire width of the sledge, an abundance of 786 individuals per hectare is still indicated.

The variation in the abundance of *P. grisea* indicates that its distribution is patchy as suggested by Sibuet (1977) from trawls made in the Bay of Biscay. A species of *Paelopatides* from the western Atlantic has been observed directly from submersibles to be aggregated in certain areas although the reasons for its patchy distribution were not immediately obvious (Pawson, 1982a). Despite the patchy distribution of *P. grisea*, it is evident from the abundance data that this species is common between 1650 and 2315m in the PSB, with a peak in abundance in the lower part of its bathymetric range (ca. 1900 to 2000m).

Table 8. The abundance of *Paelopatides grisea* in epibenthic sledge and otter trawl samples , expressed as number per hectare. Samples from the main transect unless otherwise indicated. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge hauls.				
a BN 9754-3	1484	1	2.1	
b BN 10111-8	1635	2	3.1	13.1
BN 52211-1	1716	5	15.4	35.4
BN 52019-1	1731	1	4.7	5.0
a BN 9753-7	1942	3	12.1	
BN 50602-2	1968	4	6.6	
BN 51717-2	1975	14	61.4	87.3
BN 51408-1	1998	19	41.5	104.0
a BN 9775-3	2016	72	71.8	1125.0 +
BN 51105-3	2025	10	19.6	71.4
BN 10106-1	2308	17	16.7	
Otter trawl samples.				
a OT 9774-1	1533	1	0.2	
b OT 50810-1	1650	8	1.8	
OT 50715-1	1678	2	0.5	
OT 51409-1	1684	30	6.7	
b OT 50517-1	1790	24	5.6	
OT 50902-1	1845	8	1.6	
OT 50602-3	1874	52	6.0	
b OT 50802-1	1884	1	0.3	
a OT 51213-1	1938	77	42.9	
a OT 9753-8	1942	1	0.3	
OT 50510-1	1943	80	14.3	
OT 51201-1	1975	75	23.5	
OT 50822-1	2123	8	0.7	
OT 51613-1	2220	115	13.7	

a northeast PSB
b Goban Spur

\+ weak link on bottom net bar broken centre net catch lost (see text).

The biomass of P. grisea was determined directly from the two stations sampled close to the 2000m isobath (Table 9). P. grisea accounts for over 60% of the total epibenthic invertebrate WW biomass. However, owing to its high water content (96%) the importance of this species is reduced when AFDW is considered (26 to 33% of the total biomass). A mean AFDW biomass of 725g per hectare is indicated for P. grisea at a depth of about 2000m. Walker *et al.* (1987a) estimated a calorific value for the body wall of P. grisea of 24.14 J/ mg AFDW leading to an average calorific biomass of 17500 KJ per hectare.

Table 9. The WW, DW, AFDW and calorific biomass of P. grisea from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 8.

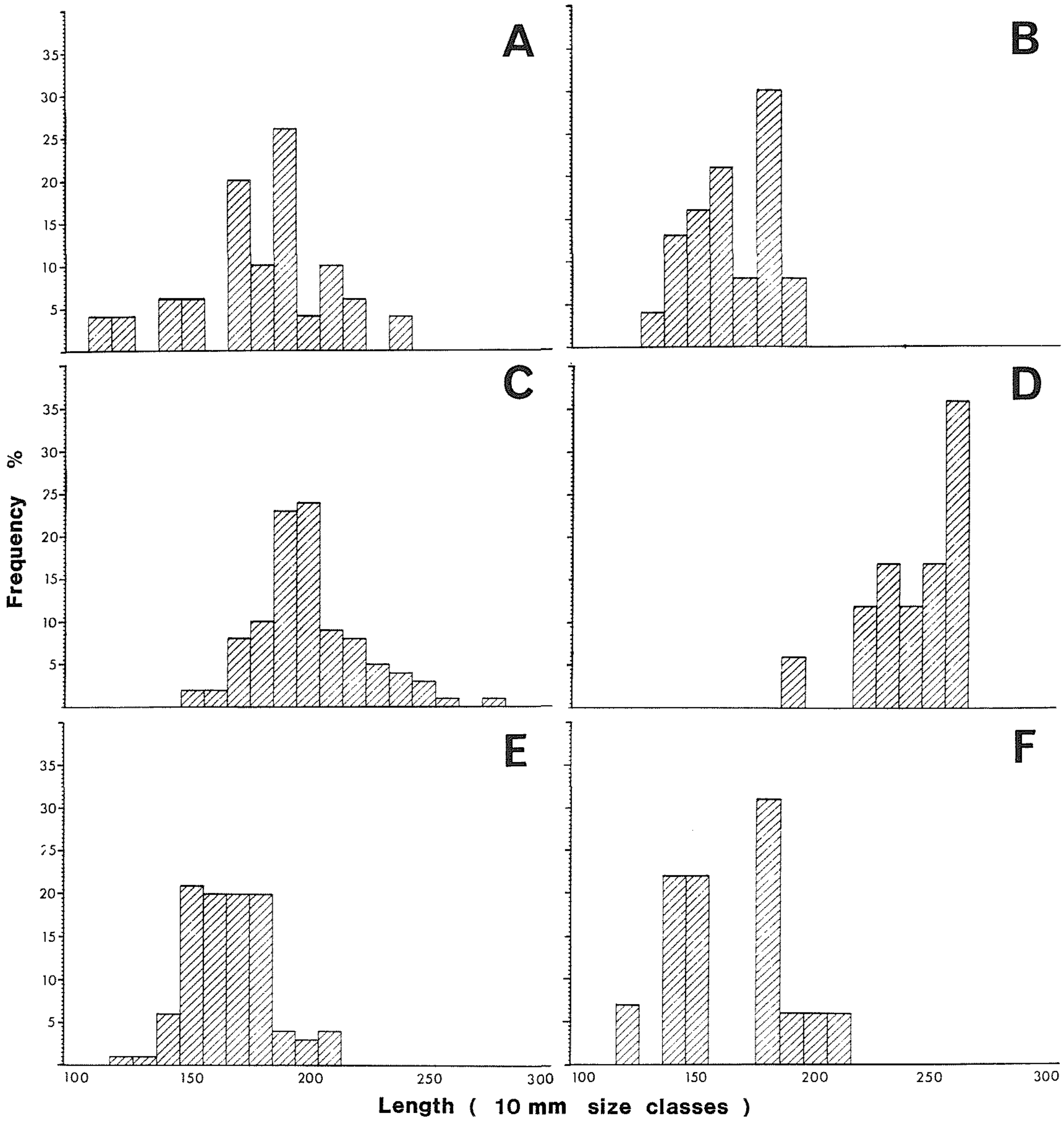
Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51408-1	1998	51567 (68)	2100 (30)	751 (33)*	18129
51105-3	2025	50692 (62)	1961 (19)	699 (26)	16873

* AFDW biomass estimated from DW using conversion factor calculated from St. 51105-3.

There are no differences in the population size distributions of the samples that are correlated with depth, although some samples such as Stas 51408-1 and 51409-1 indicate that the size of Paelopatides can vary significantly in various parts of the PSB (Fig. 29). There is no evidence of seasonal or periodic recruitment, even though the eggs are probably released in batches, as indicated by the similar size of all the eggs within individual tubules of the ovary (Tyler and Muirhead, 1986). P. grisea produces an egg with a maximum diameter of 1600μm indicative

Figure 29. The population size distributions of *Paelopatides grisea*. Length in 10mm size classes.

A) OT 51409-1, 28: 3:82, 1684m, n = 30.
B) OT 50517-1, 7: 6:79, 1790m, n = 24.
C) OT 51213-1, 26: 9:81, 1937m, n = 75.
D) BN 51408-1, 27: 3:82, 1998m, n = 17.
E) BN 9775-3, 22: 4:78, 2015m, n = 72.
F) BN 10106-1, 4: 9:79, 2308m, n = 14.


A
B
C
D
E
F
Frequency %
35
30
25
20
15
10
5
100
150
200
250
300
Length (10 mm size classes)

of direct development or possibly lecithotrophic larval development with an extended larval phase since the eggs have plenty of yolk reserves.

P. grisea is a large, flat holothurian (Fig. 27C). However, like *B. funebris* the body cavity occupies less than a third of the total body volume. The coelom lies along the centre axis of the body. To either side are areas of presumably collagenous connective tissue which, as in *B. funebris*, is quite firm when the holothurian is first sampled, but which breaks down into a gelatinous mass upon preservation. *Paelopatides* is almost neutrally buoyant and has been seen both in deep-sea photographs (Fig. 27C) and directly from submersibles (Pawson, 1976), to swim by passing waves along the sides of the body. These motions require considerable plasticity, in form not consistent with the stiff animals recovered by trawls. It is likely, therefore, that collagenous connective tissues, which regulate the body tone in holothurians (Motokawa, 1984), are particularly well developed in this species. Moreover, since the body musculature of *P. grisea* is poorly developed, the connective tissue may play an active role in the swimming of this species.

Paelopatides appears to spend most of its time on the seabed. While on the seafloor it creeps over the sediment surface using small mid-ventral tubefeet which leave only a faint imprint. *P. grisea* has 15 to 20 well developed tentacles which rake the topmost sediment layer.

Mesothuria candelabri Herouard, 1923

OT 9640-1 (1), OT 50515-1 (3), BN 50603-1 (1),
OT 50711-1 (3), BN 52216-8 (2).

Bathymetric range on PAP : 3757 to 4832m. More common on the abyssal plain away from the base of the continental slope.

Distribution : Possibly cosmopolitan; 3757 to 5440m (including the present records). All but one of the adults previously sampled have come from deeper than 4505m. In the present study the two specimens sampled shallower than 4500m are a large female (80mm long) from 3757 to 3794m (St. 9640-1) and a small juvenile (4mm long) from 4000m (St. 50603-1). Most of the records of M. candelabri come from the northeast Atlantic (Herouard, 1923; Madsen, 1953; Sibuet, 1977; Billett, 1987), but Hansen (1975) also records the species at abyssal depths in the Kermadec Trench in the Pacific. Sibuet (1977) reports the species as shallow as 2200 to 3100m in the Bay of Biscay, but these records need to be confirmed.

Ecological remarks : M. candelabri is not a common species. Only 10 specimens have been collected on the PAP. Its abundance at St. 52216-8 (4818m) is about 5 individuals per hectare. The adult specimens in the PSB ranged between 40 and 80mm long (preserved). Most of the specimens had eviscerated and were in poor condition. One female was found (80mm long) with a large ovary carrying eggs up to 500μm in diameter. If this is the maximum size to which eggs develop then either direct development or, considering the wide geographic distribution of the species, lecithotrophic larval development with an extended larval phase would be expected to occur.

Mesothuria lactea (Theel, 1886)

BN 9754-3 (9), OT 9774-1 (2), BN 9779-1 (6),
BN 10108-1 (2), BN 10111-8 (20), OT 50509-1 (33),
OT 50510-1 (7), OT 50519-1 (8), OT 50602-3 (39),
OT 50611-1 (11), OT 50703-1 (1), OT 50715-1 (4),
OT 50902-1 (1), OT 51009-1 (1), BN 51113-2 (10),
OT 51307-1 (1), OT 51308-1 (1), BN 51403-1 (7),
BN 51403-2 (3), BN 51403-3 (3), BN 51403-4 (14),
BN 51403-5 (2), BN 51403-6 (2), OT 51403-7 (6),
BN 51407-1 (48), OT 51409-1 (34), OT 51419-1 (83),
BN 51420-1 (6), BN 51420-2 (3), BN 51420-3 (1),
BN 51420-4 (2), BN 51708-2 (22), BN 51715-2 (12),
BN 52019-1 (4), BN 52203-1 (13), BN 52204-1 (2),
BN 52211-1 (22).

Bathymetric range in PSB : 1278 to 1960m, but most specimens occurred between 1430 and 1930m (83% of the specimens collected). The upper bathymetric limit coincides with the suspension-feeding community dominated by the sponge *Pheronema grayi* (see Section 5.2). A few specimens were collected on the Goban Spur (1385 to 1640m).

Distribution : Cosmopolitan, 694 to 5108m. The deepest record from the south Atlantic referred to as *M. lactea* var. *spinosa* by Heding (1940), should probably be assigned to *M. candelabri* Herouard, 1923. The deepest record would then become 4400m (Sibuet, 1977), but since most records in the northeast Atlantic come from around the 1500m isobath (e.g. Herouard, 1923), there is some doubt over these deep records of *M. lactea*.

Ecological remarks : The greatest abundance of *M. lactea* was found in the middle of its bathymetric range; around the 1500m isobath (Table 10). However, patches of *M. lactea* with an abundance of greater than 100 individuals per hectare were encountered at depths between 1320 and 1740m.

The WW, DW and AFDW biomass of *M. lactea* was determined directly at one station (St. 51113-2) (Table 11). The

Table 10. The abundance (A) of <u>Mesothuria lactea</u> in epibenthic sledge and otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise indicated. n = number of specimens taken. Number of juveniles (< 10mm long) and the abundance of <u>M. lactea</u> including these specimens are given in parentheses.

	Station	Mean Depth (m)	n	A/Posn	A/Odo	
	Epibenthic sledge samples.					
	BN 51420-4	1283	0 (2)	0.0 (12.3)	0.0 (22.0)	
	BN 51403-6	1287	2		21.2	
	BN 51403-5	1293	1 (1)	4.9 (9.8)	11.3 (22.7)	
	BN 51420-3	1296	1	8.6	11.1	
	BN 51403-1	1303	4 (3)	8.9 (15.6)	22.9 (40.0)	
	BN 52204-1	1303	2	21.7	28.2	
	BN 51420-2	1307	3	18.5	33.8	*
	BN 51403-2	1321	3	12.7	32.6	
	BN 51403-3	1322	3	19.2	28.6	
	BN 51403-4	1326	13 (1)	39.1 (42.1)	135.8 (146.0)	
	BN 51420-1	1327	6	35.0	64.4	
a	BN 10108-1	1388	2	4.2		
a	BN 9779-1	1401	6	8.6	31.3	
	BN 51708-2	1450	22	42.8	102.0	
b	BN 9754-3	1484	7 (2)	14.4 (18.6)		
	BN 51715-2	1493	12	18.1		
	BN 51407-1	1500	48	92.3	334.0	
	BN 52203-1	1526	13	68.6	88.0	
	BN 51113-2	1535	10		44.7	+
a	BN 10111-8	1635	15 (5)	23.5 (31.4)	98.5 (131.0)	
	BN 52211-1	1716	22	67.8	156.0	
	BN 52019-1	1731	4	18.9	20.1	
	Otter trawl samples.					
	OT 51403-7	1293	6	1.5		
	OT 50611-1	1388	11	1.8		
a	OT 50519-1	1448	8	1.6		
	OT 50509-1	1507	33	9.0		
	OT 51419-1	1509	83	18.6		
b	OT 9774-1	1533	2	0.5		
	OT 50715-1	1678	4	1.0		
	OT 51409-1	1684	34	7.6		
	OT 50902-1	1845	1	0.2		
	OT 50602-3	1874	39	4.5		
	OT 50510-1	1943	7	1.3		

a Goban Spur

b northeast PSB

\+ weak link broken on bottom net bar

* abundance estimated from outer nets only. Centre net catch discarded.

relationship of length to DW and AFDW was determined for these specimens in addition to a few specimens from Stas 51403 and 51420. Using these data the regression of AFDW on length was calculated ($r^2 = 0.69$). The relationship is given by the equation :

$$\text{Log (AFDW)} = \text{Log (Length)} \times 3.6208 - 7.6248$$

where n = 8 and the standard error = 0.1915. Using these data the biomass of M. lactea was estimated from a further 3 stations (Table 11). A maximum AFDW biomass of 230g AFDW per hectare was found at 1500m (St. 51407-1), accounting for some 13% of the total epibenthic invertebrate AFDW biomass. Walker et al. (1987a) report a calorific value of 26.24 J / mg AFDW for M. lactea producing a calorific biomass of 6085 KJ per hectare at the same station.

Table 11. The WW, DW, AFDW and calorific biomass of M. lactea from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. Data for St. 51113-2 were measured directly. DW and AFDW data for the other stations were estimated from length using the regression equations calculated. For the number of specimens in each sample see Table 10.

Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51113-2	1535	1808 (25)	103 (15)	35 (15)	918
51403-4	1326	1787 (5)	141 (2)	25 (3)	656
51708-2	1450	-	180	53	1391
51407-1	1500	14471 (29)	596 (13)	230 (13)	6035

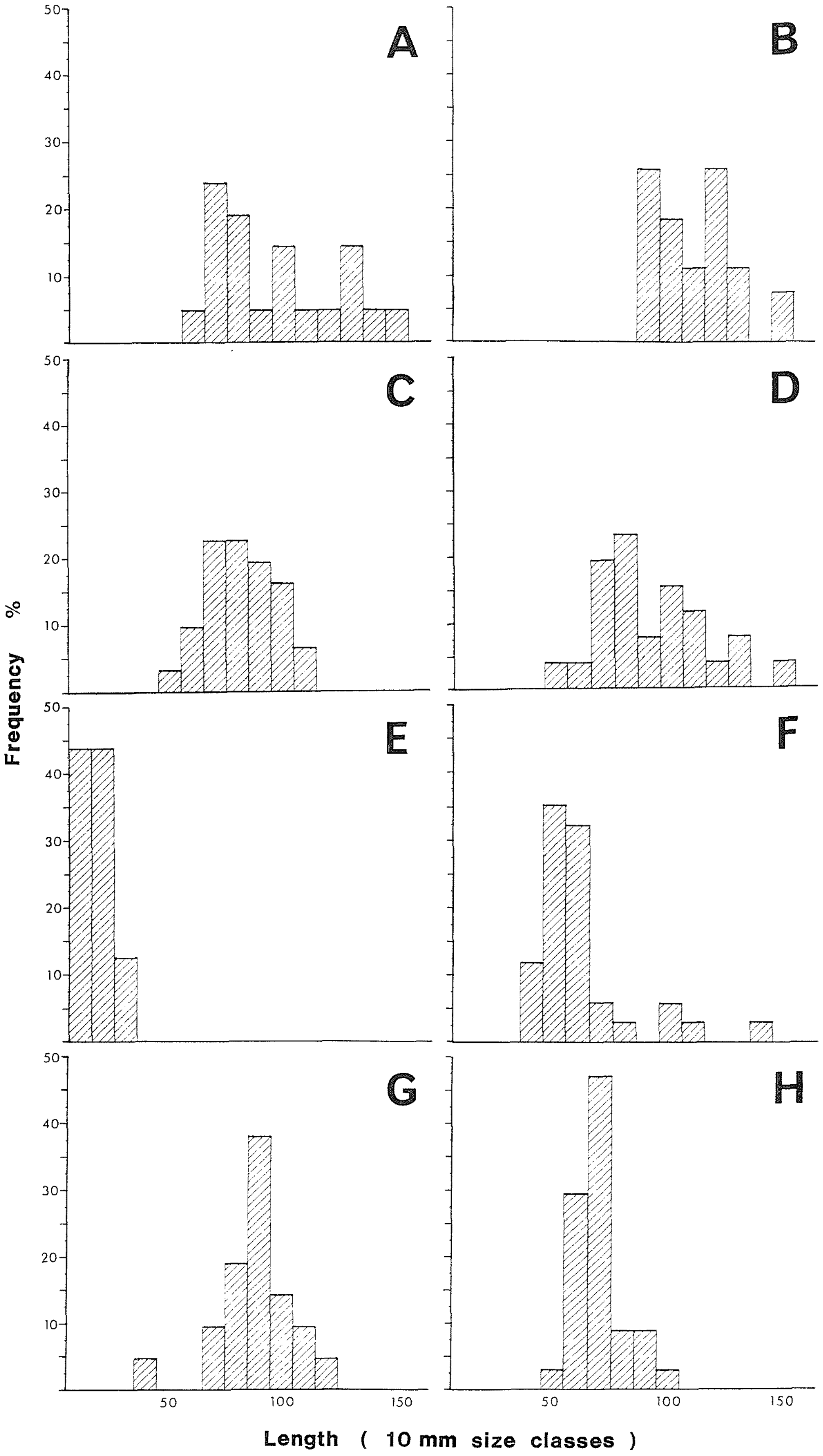
The sexes are separate although Tyler and Muirhead (1986) report two cases of hermaphroditism. M. lactea produces an egg with a maximum diameter of 400µm suggesting some form of lecithotrophic larval development

(Tyler and Muirhead, 1986). There is no evidence of seasonal or periodic reproduction and juveniles are likely to be recruited to the adult population continuously. However, the population size distributions for several samples of M. lactea show some remarkable differences (Fig. 30) not consistent with the scenario of slow, steady recruitment.

Most samples are dominated by large specimens but two, Stas 51409-1 and 10111-8 (Fig. 30), are composed mainly, or exclusively, of small specimens. No general relationship between specimen size and depth is apparent. Small juveniles only a few mm long occur in several samples that encompass almost all of the bathymetric range (Table 10). Patches of small individuals, therefore, occur within the wider adult population but the reasons for this are not clear. St. 10111-8 from the Goban Spur sampled by the epibenthic sledge contained, in addition to the small M. lactea, the rare occurrence of many small B. rosea, and over 2000 specimens of the small holothurian Elpidia. This combination of small holothurians in one sample indicates that the presence of small M. lactea is not related simply to the biology of this species, but to environmental features that favour the patchy and periodic recruitment of a number of species. These features are probably a combination of hydrography and topography but will be influenced also by the seasonal deposition of detritus.

Figure 30. The population size distributions of *Mesothuria lactea*. Length in 10mm size classes.

A) BN 51708-2, 13: 4:83, 1450m, n = 21.
B) BN 51407-1, 27: 3:82, 1500m, n = 27.
C) OT 50509-1, 3: 6:79, 1506m, n = 31.
D) OT 51419-1, 1: 4:82, 1508m, n = 26.
E) BN 10111-8, 9: 9:79, 1635m, n = 16.
F) OT 51409-1, 28: 3:82, 1684m, n = 34.
G) BN 52211-1, 18: 6:85, 1716m, n = 21.
H) OT 50602-2, 1: 7:79, 1968m, n = 34.


A
B
C
D
E
F
G
H
Frequency %
50
40
30
20
10
50
100
150
Length (10 mm size classes)

Mesothuria bifurcata Herouard, 1906

BN 10111-8 (1 fragment)

Distribution : Only known previously from two widely separated localities; the Antarctic Ocean (Herouard, 1906) and southeast of Greenland (Heding, 1942) (2137m).

Taxonomic remarks : Only a fragment of the species was found (4mm long), possibly a juvenile specimen. It is curious that so few specimens have been found over such a wide geographic distribution, but the ossicles are so characteristic that the fragment cannot be attributed to any other species. The ossicles are the same as those figured by Heding (1942). The fragment was found at the same station on the Goban Spur as many juvenile *M. lactea* and *B. rosea*.

Mesothuria cathedralis Heding, 1940

BN 9754-3 (1), BN 10113-1 (1), BN 50605-1 (1).

Bathymetric range in the PSB : 1484 to 2930m.

Distribution : Previously known only from the Gulf of Guinea, Cape Bojador, off southern Greenland (Heding, 1942) and the Rockall Trough (Gage *et al*., 1985a), all within the bathymetric range shown by the PSB material.

Taxonomic remarks : The three specimens from the PSB are all small, between 4 and 8mm long. The ossicles in the body wall, however, are quite distinctive and are unlike those found in juveniles of the other *Mesothuria* species from the PSB. The plate ossicles have 8 or more holes, arranged in a regular pattern with a quadriradiate spire in the centre bearing four long spiny arms. They are similar to those figured for the larger specimen (50mm long) collected by the "Ingolf" expedition (Heding, 1942). The similarities in the structure of the ossicles unite the various records of this species despite the wide separation of their localities.

Mesothuria maroccana Perrier, 1902

BN 10106-1 (1), OT 50518-1 (2), OT 50519-1 (10).

Bathymetric range in the PSB : 1431 to 2315m. The single specimen from the main transect (St. 10106-1) occurred between 2300 and 2315m, while the other 12 specimens were all sampled on the Goban Spur, between 1431 and 2110m.

Distribution : North Atlantic, both in the east from off Morocco to south of Iceland (Perrier, 1902; Heding, 1942) (1431 to 3120m, bathymetric range including the present records), and in the west in the Caribbean and the eastern Gulf of Mexico (914 to 2469m) (Miller and Pawson, 1984). *M. maroccana* bears a close affinity to *M. murrayi* (Theel, 1886a) and, indeed, Heding (1942) considered that the two species could be synonymous. If so, then this species is also found in the Pacific at similar depths (Theel, 1886a; Ohta, 1983).

Ecological remarks : *M. maroccana* is not a common species in the PSB, but the presence of 10 specimens in one sample indicates that its distribution is patchy. Similarly, in four samples taken by the "Ingolf" Expedition, three contained singleton *M. maroccana* while the fourth sample had 15 specimens (Heding, 1942). The size of the PSB specimens (30 to 95mm long) is similar to that reported previously (40 to 80mm long, Deichmann, 1954).

The largest egg size found in the PSB specimens was 200µm indicating either planktotrophic development or lecithotrophic development with a short larval phase.

Mesothuria intestinalis (Ascanius and Rathke, 1767)

OT 50503-1 (1), GT 50505-1 (1), OT 50519-1 (1),
OT 50704-1 (1), GT 50709-1 (3), OT 50801-1 (2),
GT 50809-1 (2), OT 50819-1 (1), OT 51025-1 (1),
GT 51313-1 (1), BN 51403-1 (2), BN 51403-5 (2),
OT 51403-7 (7), BN 51420-1 (1), BN 51420-4 (3),
BN 51707-1 (1).

Bathymetric range in the PSB : 460 to 1465m on the Goban Spur (but common only between 1225 and 1285m) and 500 to 1330m on the main transect but in this area only common within the Pheronema suspension-feeding community (1255 to 1330m) (see Section 5.2).

Distribution : Widely distributed in the northeast Atlantic from off NW Africa (Herouard, 1923) to the coasts of Norway, although nowhere in the deep sea does it appear to be very common. A few specimens are known from the Mediterranean (see Perrier, 1902; Koehler, 1927; Sibuet, 1974) and the western Atlantic (Deichmann, 1930). The species has a wide bathymetric range (c. 18 to 1445m) but reports of this species occurring as deep as 2000m appear to result from some confusion with M. verrilli. The shallowest records come only from the cold waters off Norway. In the Rockall Trough M. intestinalis is reported only from the upper Hebridean Slope (Harvey et al., in press).

Ecological remarks : M. intestinalis is not a particulary abundant species in the PSB (Table 12) contributing less than 1% of the total epibenthic invertebrate biomass in areas where it occurs. The greatest abundance (33 individuals per hectare) and biomass (193g DW - about 100g AFDW per hectare) was found within the Pheronema sponge area in the PSB (see Section 5.2).

Table 12. The abundance (A) of Mesothuria intestinalis in epibenthic sledge and otter trawl samples, expressed as number of specimens per hectare. Samples from the main transect unless otherwise stated. n = number of specimens taken.

Station	mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 51707-1	1218	1	1.1	
BN 51420-4	1283	3	18.5	33.0
BN 51403-5	1293	2	9.8	22.7
BN 51403-1	1303	2	4.5	11.4
BN 51420-1	1327	1	5.8	10.7
Otter trawl samples.				
OT 50819-1	506	1	0.3	
OT 50503-1	1017	1	0.3	
a OT 50801-1	1265	2	0.4	
OT 51403-7	1293	7	1.7	
a OT 50519-1	1448	1	0.2	

a Goban Spur

Although M. intestinalis is not abundant in the PSB, its presence in the sponge community is not without interest. M. intestinalis is one of four species that not only occur preferentially around the sponge patch but also occur much shallower in Scandanavian seas. The significance of this is discussed in Section 5.2.

Like shallow-water specimens, deep-sea individuals also cover their body with shell fragments (Fig. 27D, page 159) although this is not readily apparent in preserved specimens. The reasons for this behaviour are not known but the shell fragments could give M. intestinalis some protection from predators.

M. intestinalis is a hermaphroditic species producing large eggs (ca. 650μm in diameter) which Mortensen (1927) believed would lead to direct development of the holothurian. One small juvenile, 7.5mm long, was found at one station in the sponge patch (St. 51403-1).

Mesothuria verrilli (Theel, 1886)

BN 9754-3 (2), OT 9774-1 (3), BN 10108-1 (2),
OT 50509-1 (4), OT 50517-1 (1), OT 50519-1 (98),
OT 50611-1 (8), OT 50703-1 (2), GT 50713-1 (1),
OT 50810-1 (1), OT 51009-1 (6), OT 51023-1 (1),
OT 51307-1 (1), OT 51314-1 (1), BN 51403-1 (2),
BN 51403-2 (1), BN 51403-4 (3), BN 51403-5 (2),
BN 51403-6 (1), OT 51403-7 (1), BN 51407-1 (2),
OT 51419-1 (12), BN 51420-1 (3), BN 51708-2 (31),
BN 51715-2 (11), BN 52017-1 (16), BN 52204-1 (1).

Bathymetric range in PSB : 1255 to 1794m, but most common only between 1430 and 1530m (82% of the specimens collected). The bathymetric range is greater on the Goban Spur (1270 to 1794m) than on the main transect (1255 to 1535m).

Distribution : Widely distributed in the north Atlantic with some records from the Mediterranean. In the western Atlantic it is known from the Caribbean Sea, eastern Gulf of Mexico (Deichmann, 1930; Miller and Pawson, 1984) and off the Bahamas (Pawson, 1982a). In the eastern Atlantic it is recorded from off northwest Africa, the Canary Islands (Perrier, 1902), the Azores (Herouard, 1902,1923; Perrier, 1902), the Bay of Biscay (Sibuet, 1977) and as far north as the PSB (Mortensen, 1927). Its is now also known from the Rockall Trough (Harvey *et al*., in press).

The bathymetric range is not known with certainty, partly as a result of confusion with *M. intestinalis*. Hansen (1975) gives a wide range of 618 to 4165m for *M. verrilli* in the Atlantic and 280 to 1103m in the Mediterranean. With the aid of detailed bathymetric charts available today, it is possible to see that all the reliable records of this species deeper than 2000m come from areas where the seabed is particularly steep (e.g. on the continental slope off northwest Africa or in the vicinity of the King's Trough - see Perrier, 1902, for details of some stations). The accuracy of the depths recorded for such samples must be called into question. This also applies to a shallow sample of *M. verrilli* on the Magazan Escarpment (550m, Perrier, 1902). Mortensen (1927) gives a reduced range of c. 990 to 1765m for *M. verrilli* sampled in the vicinity of the PSB, a range almost identical to that of the present material. Samples from the Rockall Trough (Harvey *et al*., in press) and the majority of those sampled off the Azores (Marenzeller, 1893; Herouard, 1902, 1923; Perrier, 1902) all fall within this reduced bathymetric range.

The bathymetric range is greater in the western Atlantic, 699 to 3720m (Deichmann, 1954; Pawson, 1982a; Miller and Pawson, 1984; Suchanek, Williams, Ogden, Hubbard and Gill, 1985). The study of Suchanek *et al.* (1985) increased the lower bathymetric limit from 2141 to 3720m. Hansen (1975) cited *M. verrilli* from 618m in the Atlantic but this shallow record should be referred to material collected in the Mediterranean.

Ecological remarks : *M. verrilli* is abundant only within a restricted bathymetric range at mid-slope depths in the PSB (Table 13). The bathymetric range is almost identical to that of *Paroriza pallens*. A few small juveniles of

M. verrilli, only a few millimetres long, were found in the suspension-feeding community between 1100 and 1330m. In certain areas *M. verrilli* can be quite common with a maximum recorded abundance of 227 individuals per hectare (St. 52017-1). Data on the biomass of *M. verrilli* are not available.

Table 13. The abundance (A) of *Mesothuria verrilli* in epibenthic sledge and otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise stated. n = number of specimens taken including juveniles. Abundance values are given for 1) all specimens and 2) excluding juveniles.

	Station	mean Depth (m)	n	All specimens A/Posn	All specimens A/Odo	Adult specimens A/Posn	Adult specimens A/Odo
	Epibenthic sledge samples.						
	BN 51403-6	1287	1		10.6		10.6
	BN 51403-5	1293	2	9.8	22.7	0.0	0.0
	BN 51403-1	1303	2	4.5	11.4	0.0	0.0
	BN 52204-1	1303	1	10.9	14.1	10.9	14.1
	BN 51403-2	1321	1	4.2	10.9	0.0	0.0
	BN 51403-4	1326	3	9.0	31.3	0.0	0.0
	BN 51420-1	1327	3	17.5	32.2	11.7	21.5
	BN 10108-1	1388	2	4.2		0.0	
	BN 51708-2	1450	31	60.4	144.0	56.5	134.0
	BN 52017-1	1465	16	78.7	227.0	78.7	227.0
a	BN 9754-3	1484	2	4.1		4.1	
	BN 51715-2	1493	11	16.6		15.1	
	BN 51407-1	1500	2	3.9	13.9	3.9	13.9
	Otter trawl samples.						
	OT 51403-7	1293	1	0.2			
	OT 50611-1	1388	8	1.3			
b	OT 50519-1	1448	98	19.8			
	OT 50509-1	1507	4	1.1			
	OT 51419-1	1509	12	2.7			
a	OT 9774-1	1533	3	0.7			
b	OT 50810-1	1650	1	0.2			
b	OT 50517-1	1790	1	0.2			

a northeast PSB b Goban Spur

The population size distributions of M. verrilli are dominated by large specimens (Fig. 31). The differences apparent between the figured samples results from the contraction of the specimens during preservation, the sample at St. 50519-1 having been measured after prolonged preservation while the other two samples were measured at sea. Small juvenile specimens are present in several samples but there is no evidence of seasonal recruitment. Reproduction in this species is continuous (Tyler and Muirhead, 1986) with the production of eggs about 400µm in diameter, indicative of lecithotrophic larval development.

Paroriza pallens (Koehler, 1896)

OT 50509-1 (8), OT 50517-1 (2), OT 50519-1 (13),
OT 50703-1 (3), OT 50810-1 (3), OT 51022-1 (1),
BN 51708-2 (7), BN 51715-2 (4), BN 52017-1 (8),
BN 52019-1 (1), BN 52218-1 (6).

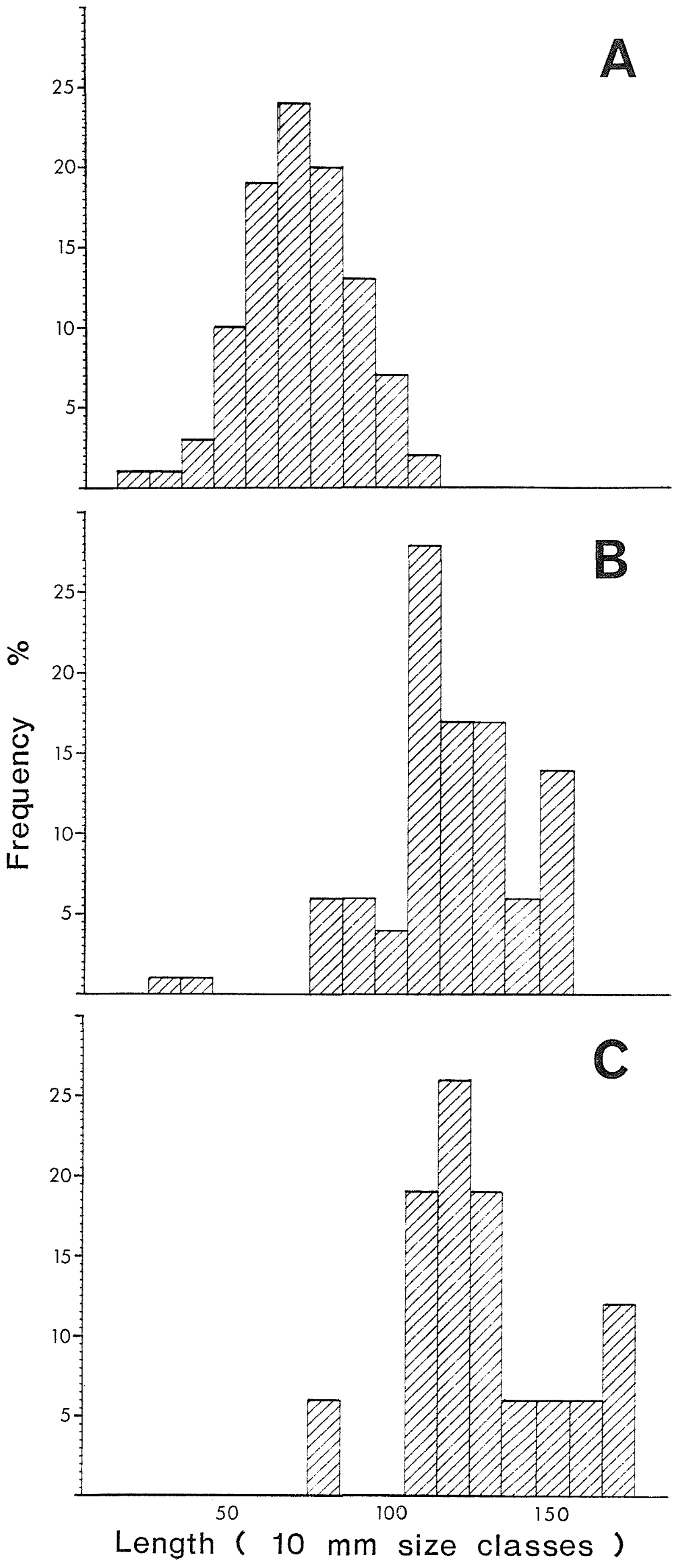
Bathymetric range in PSB : 1430 to 1794, but more prevalent between 1430 and 1525m (82% of the specimens collected) where it occurred in about half of the samples taken between these depths.

Distribution : Northeast Atlantic, from off northern Spain (1300 to 2100m) (Koehler, 1896; Sibuet, 1977), the northern Bay of Biscay (3100m) (Sibuet, 1977) to the PSB. The total range, therefore, is 1300 to 3100m although the deeper records need confirmation since P. prouhoi is apparently found in the same area.

Ecological remarks : P. pallens is not common in the PSB but in localized areas its abundance may exceed 100 individuals per hectare (Table 14). There are no data

Figure 31. The population size distributions of *Mesothuria verrilli*. Length in 10mm size classes.

A) OT 50519-1, 8: 6:79, 1448m, n = 98.
B) BN 51708-1, 13: 4:83, 1450m, n = 29.
C) BN 52017-1, 21: 8:84, 1465m, n = 16.


A
B
C
Frequency %
25
20
15
10
5
50
100
150
Length (10 mm size classes)

available on its biomass. The restricted bathymetric range of P. pallens in the PSB is almost identical to that of M. verrilli; in both cases the upper bathymetric limit lies just below the suspension-feeding community that forms a band round the PSB at about 1100 to 1330m (see Section 5.2). Most of the P. pallens sampled are large specimens, 200 to 270mm long, but at St. 50519-1 three small individuals (20, 40 and 90mm long) also occurred. Recruitment to the adult population appears to be a slow and continuous process, in keeping with the continuous production of gametes found in this hermaphroditic species (Tyler and Muirhead, 1986).

Table 14. The abundance (A) of Paroriza pallens in epibenthic sledge and otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise indicated. n = number of specimens taken.

	Station	Mean Depth (m)	n	A/Posn	A/Odo
	Epibenthic sledge samples.				
a	BN 52218-1	1440	6	13.9	25.8
	BN 51708-2	1450	7	13.6	32.4
	BN 52017-1	1465	8	39.3	113.0
	BN 51715-2	1493	4	6.0	
	BN 52019-1	1731	1	4.7	5.0
	Otter trawl samples.				
a	OT 50519-1	1448	13	2.6	
	OT 50509-1	1507	8	2.2	
a	OT 50810-1	1650	3	0.7	
a	OT 50517-1	1790	2	0.5	

a Goban Spur

P. pallens produces eggs with a maximum diameter of 250µm (Tyler and Muirhead, 1986). Eggs of a similar size in other holothurians, e.g. *Molpadia intermedia*, lead to the production of a doliolaria larva with a larval life of a few days (McEuen and Chia, 1985). It is possible that the larva produced by *P. pallens* undergoes planktotrophic development. However, this type of development seems unlikely since *P. pallens* has a restricted geographic distribution and a narrow bathymetric range. Lecithotrophic development with a short larval stage would be more probable in this particular case.

P. pallens is an epibenthic deposit-feeding holothurian which ploughs through the topmost few millimetres of the sediment. Khripounoff and Sibuet (1980) analyzed the gut contents of *P. pallens* and found that while nannoplankton, notably coccoliths, formed most of the particulate material ingested, it was organo-mineral aggregates, faecal matter and organic films in mineral particles that appear to form the nutritional sources. The organic content of sediment in the oesophagus of *P. pallens* was about 4 times greater than in sediment samples taken from the same locality, indicating that this species selects for particles with a higher organic content. The significance of this selectivity by deposit-feeding holothurians, including *P. pallens*, is discussed in Section 5.3. Feeding in *P. pallens* may be aided by the presence of commensal bacteria in its tentacles (Dr. D. Roberts, personal communication).

Paroriza prouhoi Herouard, 1902

OT 9756-3 (1), OT 50515-1 (2), OT 50711-1 (1),
OT 50811-1 (11), OT 50812-2 (1), OT 50910-1 (2),
OT 51309-1 (1), OT 51414-1 (2), OT 51608-1 (1),
BN 52216-8 (2).

Bathymetric range on PAP : 4035 to 4832m; more common in the middle of the abyssal plain than close to the continental slope, although it is not particularly abundant in any sample.

Distribution : Northeast Atlantic, 3100 to 4832m (depth range including the present records) from off the Azores, Bay of Biscay and Porcupine Abyssal Plain (Herouard, 1902, 1923; Sibuet, 1977).

Taxonomic remarks : Hansen (1956) noted that *Paroriza grevei* Hansen from the Banda Trench in the Pacific differed from *P. prouhoi* in having a curved body. This particular feature has been found in many specimens from the PAP that are contracted, particularly at the anterior end, but is not present in specimens that are relaxed. The two species differ, therefore, primarily in the shape of their tentacles.

Ecological remarks : The abundance of *P. prouhoi* is low, with a maximum abundance of 5 individuals per hectare recorded at St. 52216-8. Although data from the trawl also indicates that its abundance is low (Table 15), *P. prouhoi* is nevertheless a characteristic species of the area occurring in 8 of the 10 samples taken deeper than 4200m. There are no data on the biomass of this species. The specimens ranged between 115 and 270mm in length with no obvious correlation with location or depth.

P. prouhoi is a hermaphrodite with the testis lying posteriorly to the ovary. Eggs of an intermediate size up to about 400µm in diameter are produced indicating lecithotrophic larval development. A few eggs of this size are present in specimens sampled in August (St. 50811-1) but the gonads in all the specimens appeared to have spawned recently. In contrast, of two specimens sampled in

June (St. 50515-1) one had a well developed gonad with many yellow eggs, all of a similar size, while the gonad of the other, a small specimen only about 100mm long, was only just starting to develop. Gonads of specimens sampled in March appeared to be at an intermediate stage of development. Only a few specimens are available for examination but there is an indication that this hermaphroditic species spawns in July/August, a period that coincides with the annual deposition of detritus at abyssal depths (Billett *et al*., 1983; Lampitt, 1985; Rice *et al*., 1986). The detritus will be of little use to a lecithotrophic larva but there would be a greater supply of food for young juvenile specimens at this time of year which may aid their survival.

Table 15. The abundance (A) of *Paroriza prouhoi* in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge sample.				
BN 52216-8	4813	2	3.3	4.9
Otter trawl samples.				
OT 50812-2	4088	1	0.1	
OT 9756-3	4118	1	0.2	
OT 51414-1	4155	2	0.2	
OT 51309-1	4223	1	0.1	
OT 50910-1	4312	2	0.2	
OT 51608-1	4320	1	0.1	
OT 50811-1	4375	11	1.4	
OT 50515-1	4510	2	0.3	
OT 50711-1	4788	1	0.1	

All the specimens of *P. prouhoi* from St. 50811-1 carried commensal actiniarians, *Sicyonis commensalis* Gravier, as originally described by Herouard, 1923. A total of 66 *Sicyonis* were found on 11 *Paroriza* ranging from 2 to 11 actiniarians per holothurian. The actiniarians were situated mainly around the anterior and posterior ends of the holothurians. Evidence of a similar association can be seen in photographs taken from a submersible diving off Japan (Fujioka, Taira, Kobayashi, Ilyama, Cadet, Lallemand and Girard, 1987).

Pseudostichopus villosus Theel, 1886

OT 9638-2 (4), BN 10115-1 (1), OT 50514-1 (1),
OT 50515-1 (17), OT 50711-1 (9), OT 50811-1 (14),
BN 50812-1 (4), OT 50812-2 (4), OT 50907-1 (1),
OT 50910-1 (3), BN 51216-1 (1), OT 51309-1 (2),
OT 51414-1 (13), OT 51608-1 (2), BN 52216-8 (1).

Bathymetric range in PSB and PAP : 2850 to 4832m.

Distribution : Cosmopolitan, 2515 to 7000m but some small specimens have been recorded also off Guadeloupe at 896m (Deichmann, 1930). Likewise, in the PSB the two specimens sampled shallower than 4000m were both juveniles only 11 and 27mm long.

Taxonomic remarks : Although Heding (1940) revised the genus *Pseudostichopus*, placing both *P. atlanticus* and *P. villosus* in the genus *Molpadiodemas* and the family Gephyrothuriidae, several authors have continued to record these two species under the generic name *Pseudostichopus* in the family Synallactidae (Madsen, 1953; Hansen, 1956, 1975; Lemche *et al*., 1976; Sibuet, 1977). This latter scheme is more appropriate.

It is with some reservation that all the records cited above are attributed to this species. Some specimens are identical to Perrier's (1902) description of P. atlanticus which he considered to be synonymous with Theel's records of P. villosus from the north Atlantic. However, in the PAP material there is a gradation in form from typical P. atlanticus to some specimens that are comparable to P. villosus sampled by the "Challenger" Expedition in the Pacific (Theel, 1886a). These specimens were examined at the British Museum (Natural History). Only the smallest specimens (< 30mm long) can be said to be truly "villous" or hairy. These specimens usually have many foraminiferan tests attached to the body wall. Specimens about 70mm long may also have tubefeet crowded along the ventro-lateral ambulacra but their size is small relative to the body so that they do not give a hairy look to the specimens. In some cases the tubefeet occur only in patches together with foraminiferans. The rest of the body appears denuded and similar to P. atlanticus. These features would suggest the synonymy of P. atlanticus and P. villosus.

However, there are a few small specimens present (about 40mm long) that do not have any foraminiferans attached to the body wall and which appear to have only a few, very small tubefeet. It is not clear whether the skin has been abraded or whether the absence of these features is a real taxonomic feature. The former is possible for in larger specimens that appear denuded, areas of body wall with small tubefeet and foraminiferans can be found within folds of the skin. A detailed taxonomic study in future may be able to resolve the status of P. atlanticus and P. villosus.

Ecological remarks : P. villosus is a characteristic, though not very abundant, species on the PAP. A maximum abundance of 22 individuals per hectare (St. 50812-2) was calculated for one epibenthic sledge sample (Table 16).

Data from the otter trawl indicate that, like P. prouhoi, P. villosus is more prevalent in the centre of the abyssal plain than close to the base of the continental slope.

Table 16. The abundance (A) and biomass (B) of P. villosus in epibenthic sledge and otter trawl catches, expressed as number or g DW or AFDW per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo	DW A/Odo	AFDW B/Odo
Epibenthic sledge samples.						
BN 51216-1	4070	1	2.1	3.5	9.4	4.5
BN 50812-1	4090	4		22.4	19.2	9.2
Otter trawl samples.						
OT 50514-1	4056	1	0.1			
OT 50812-2	4088	4	0.4			
OT 51414-1	4155	13	1.3			
OT 51309-1	4223	2	0.2			
OT 50910-1	4312	3	0.3			
OT 51608-1	4320	2	0.3			
OT 50811-1	4375	14	1.8			
OT 50515-1	4510	17	2.5			
OT 50711-1	4788	9	1.0			

The biomass of only a few specimens from the otter trawls could be determined. Fortunately their size was similar to specimens taken in two epibenthic sledge samples allowing the biomass of P. villosus to be estimated at these stations (Table 16). The average body composition of P. villosus is 91% water, 4% skeletal material, and 5% organic tissue.

The specimens of P. villosus range between 15 and 170mm long. Most specimens are longer than 60mm except at St. 50515-1 where half of the specimens collected were between 40 and 60mm long. At this same station small individuals of P. longicauda, O. mutabilis and D. validum were notable by their abundance. Reproduction in P. villosus appears to be continuous since in any one specimen eggs of different sizes are found, and the eggs are similar in size in specimens collected at different times of the year. A maximum egg size of about 400µm is indicated by the PAP material.

P. villosus is an epibenthic deposit-feeding holothurian that ploughs its way through the upper layer of the sediment leaving behind a characteristic plough trail. Sibuet et al. (1982) and Briggs (1985) have described the feeding biology of P. villosus/ P. atlanticus (see section 1.1, page 6).

A few specimens of P. villosus from the PAP had actiniarians embedded in their skin, particularly near the anterior end. The association is the same as in P. prouhoi but it is not known whether the same species of actiniarian (Sicyonis) is involved.

Pseudostichopus sp.

OT 11116-1 (1), OT 11118-1 (1), OT 50515-1 (8),
OT 50711-1 (5), OT 50811-1 (1), BN 52215-1 (1),
BN 52216-8 (1).

Bathymetric range on PAP : 4350 to 4832m.

Distribution : Known only from the PAP. If this material proves to be synonymous with Pseudostichopus marenzelleri Herouard, 1923 (see below) then it occurs more widely in the northeast Atlantic.

Taxonomic remarks : Several specimens from the PAP resemble P. marenzelleri in having a coat of foraminiferan tests, principally Globigerina, and a series of larger pedicels along the ventro-lateral radii. These pedicels are not placed exactly along the border of the ventral and dorsal surfaces but a small distance dorsally from the border. In addition, the gonads have calcareous ossicles similar to those figured by Herouard (1902) (syn. *P. occultatus*). However, in every case there is also a double row of larger papillae along each of the dorsal ambulacra, a feature not noted in the original description of *P. marenzelleri*. Therefore, it is not possible for the present to refer the PAP material to this species. The presence of these papillae is not always readily apparent and it is possible that they were not evident in the original material of *P. marenzelleri*.

Several specimens of *Pseudostichopus* are present in the same samples from the PAP that are either completely naked or partially covered by foraminiferans. These specimens have exactly the same arrangement of pedicels as the specimens covered in foraminiferans. In addition, the ossicles in the gonad wall are similar . It is clear that the covering by foraminiferans in this species is variable casting some doubt on the use of adhering particles as diagnostic features.

Ecological notes : A variety of egg sizes are present in any one ovary and the egg size is similar in samples taken at different times of the year. The maximum egg size is about 300μm. Continuous reproduction with development via an abbreviated lecithotrophic larval stage is likely.

Order ELASIPODIDA

Family Deimatidae

Deima validum validum Theel, 1879

OT 9756-3 (1), BN 10113-1 (1), BN 10114-1 (1),
OT 11118-1 (2), OT 50515-1 (28), BN 50603-1 (1),
OT 50711-1 (1), OT 50811-1 (24), BN 50812-1 (2),
OT 50812-2 (3), OT 50907-1 (11), OT 50910-1 (7),
BN 51109-1 (1), BN 51216-1 (1), OT 51309-1 (1),
OT 51414-1 (2), BN 51414-2 (2), OT 51608-1 (2),
BN 52215-1 (1).

Bathymetric range in PSB/PAP : 2755 to 4795m, principally on the PAP at depths greater than 4000m. *D. validum* occurred in all but one of the samples taken deeper than 4200m and in half of the samples taken between 4000 and 4200m. The shallowest specimen was a single juvenile specimen (see below).

Distribution : Hansen (1975) has given many details of the distribution of this species which is found worldwide although it is absent from some regions, notably the northernmost part of the Atlantic. The bathymetric range of *D. validum* differs between its geographic localities. For instance, in the northeast Atlantic it is known from 2779 to 4795m (including the present records), but is found much shallower (1049 to 1783m) off the West Indies. Elsewhere *D. validum* has been recorded as shallow as 724m off Indonesia and as deep as 4820m in the western Indian Ocean.

Taxonomic remarks : Two juvenile specimens only 6.2 and 4.7mm long were found at Stas. 10113-1 (2755m) and 52216-8 (4818m) respectively. The specimens possessed plate ossicles that are typical for deimatid holothurians, and in the larger specimen the tentacles were retracted. It is believed, therefore, that the juveniles are deimatids and that the larger specimen, at least, is *D. validum*.

Ecological remarks : Although *D. validum* occurs fairly consistently in epibenthic sledge samples from the the PAP its abundance is low (only 3 to 11 individuals per hectare) (Table 17). The largest trawl samples were taken on the abyssal plain some distance from the base of the continental slope.

Table 17. The abundance (A) of *Deima validum* in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 10113-1	2775	1	3.2	7.9
BN 51109-1	3950	1	2.6	4.6
BN 50603-1	4000	1	1.3	
BN 10114-1	4050	1	3.7	9.0
BN 51216-1	4070	1	2.1	3.5
BN 51414-2	4080	2	3.5	6.7
BN 50812-1	4090	2		11.2
BN 52215-1	4563	1	1.5	2.9
Otter trawl samples.				
OT 50907-1	2975	11	1.3	
OT 50812-2	4088	3	0.3	
OT 9756-3	4118	1	0.2	
OT 51414-1	4155	2	0.2	
OT 51309-1	4223	1	0.1	
OT 50910-1	4312	7	0.8	
OT 51608-1	4320	2	0.3	
OT 50811-1	4375	24	3.0	
OT 50515-1	4510	28	4.1	
OT 11118-1	4565	2	0.2	
OT 50711-1	4788	1	0.1	

The biomass of D. validum was estimated directly at three stations (Table 18). The mean WW, DW, and AFDW biomass for these stations is 67.5g, 9.4g and 2.7g per hectare respectively. D. validum contributed some 1 to 7% of the total epibenthic invertebrate AFDW biomass at the three stations. Walker et al. (1987b) report a calorific content of 23.9 J per mg AFDW for the body wall of D. validum producing an average calorific biomass of 65 KJ per hectare for this species.

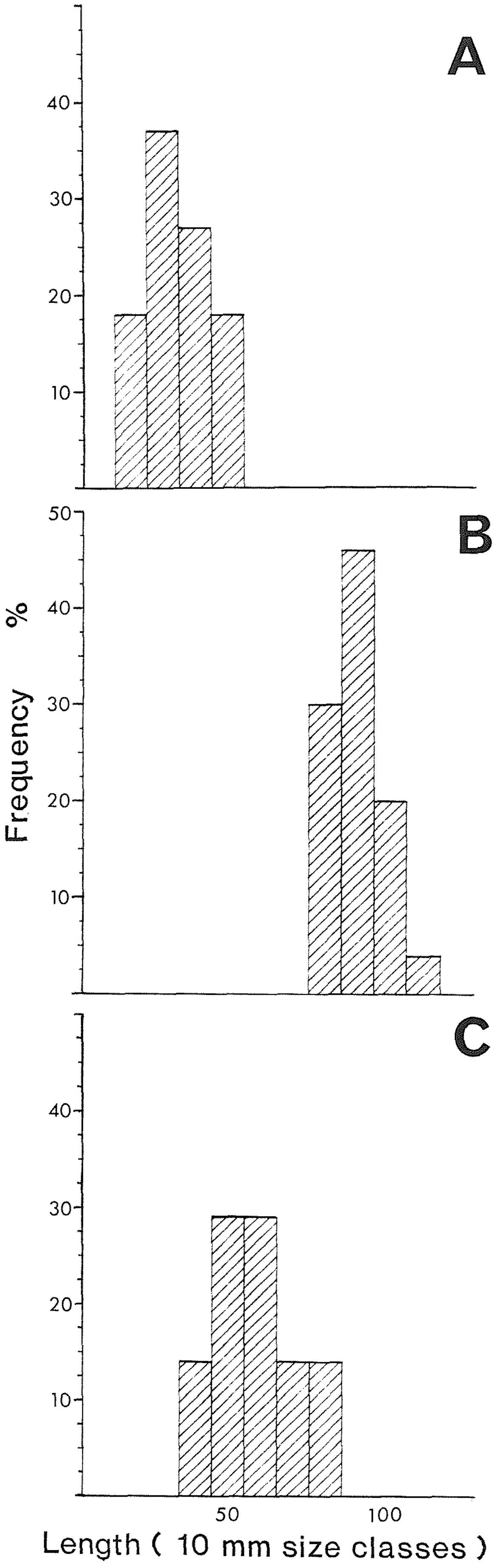
Table 18. The WW, DW, AFDW and calorific biomass of Deima validum from epibenthic sledge samples expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in a sample see Table 17.

Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51109-1	3950	43.3 (1)	6.0 (1)	1.7 (1)	41
51216-1	4070	68.3 (1)	8.0 (1)	2.3 (1)	55
51414-2	4080	90.8 (9)	14.1 (7)	4.1 (7)	98

The specimens of D. validum sampled on the continental slope were all small (Fig. 32) indicating that adult specimens are not normally found shallower than the edge of the abyssal plain. This is substantiated by data from the Rockall Trough since D. validum has not been taken in this region despite intensive sampling at depths shallower than 3000m (Gage et al., 1985a). On the abyssal plain there is no general correlation between length and location or depth although there is a remarkable difference between two samples from the PAP. This difference cannot be attributed to differential contraction during preservation since not only were the same preservation techniques used, but also the well-developed skeleton of D. validum does not allow any appreciable change in

Figure 32. The population size distributions of *Deima validum*. Length in 10mm size classes.

A) OT 50907-1, 10:11:80, 3025m, n = 11.
B) OT 50811-1, 2: 8:80, 4375m, n = 24.
C) OT 50515-1. 6: 6:79, 4510m, n = 28.


A
B
C
Frequency %
10
20
30
40
50
50
100
Length (10 mm size classes)

size. The smaller size of specimens of *D. validum* at St. 50515-1 is the same for the related species *Oneirophanta mutabilis* and is discussed in Section 5.5.

D. validum produces an egg with a maximum diameter of 800μm (Hansen, 1975; Tyler and Billett, in press) which would be expected to lead to direct development. In the related species *O. mutabilis*, which produces an egg of a similar size, one population sampled in the eastern Pacific and assigned to a separate sub-species was found to have intra-ovarian brooding (Hansen, 1968; 1975). In the same area *D. validum* also shows particular features that warrant characterization as a sub-species, *D. validum pacificum*, but no evidence of brooding has been found (Hansen, 1975). Similarly, brooding is not apparent in any specimen from the PAP. Rather, the presence of small *D. validum* at shallow depths in the PSB (St. 50907-1, Fig. 32), and the presence of a small juvenile at St. 10113-1 believed to be *D. validum*, indicate that there is a pelagic dispersal phase. Development may occur either through a lecithotrophic larval stage or through direct development in the pelagic realm, as found in several psychropotid species (Hansen, 1975; Billett *et al*., 1985). The almost worldwide geographic distribution of *D. validum* would also suggest development with a dispersal phase rather than either direct development on the seabed or brooding.

Hansen (1975) suggested that reproduction in *D. validum* could be periodic since all the specimens which he examined from the western Indian Ocean were at a similar stage of gametogenic development. Although samples have been taken on the PAP in different months of the year, no periodic reproduction has been noted in *D. validum*. However, periodic reproduction could occur on a timescale that is not evident from the IOS samples.

Hansen (1975) also noted that in all the samples of *D. validum* he examined worldwide the male specimens all appeared to be sexually inactive. A similar situation occurs with the PAP populations; about half of the specimens are sexually inactive, while oogenesis is evident in the rest of the population. The equal proportions of specimens with active and inactive gametogenesis has lead to the assumption that the inactive specimens are predominantly, or all, males (Hansen, 1975; Tyler *et al.*, 1985c). This is rather curious, for in other deep-sea echinoderms with continuous reproduction the males are usually always ready to spawn (Tyler *et al.*, 1985c). Many features of the reproductive strategy of *D. validum* are similar to those in *O. mutabilis* and are discussed in greater detail below.

D. validum is an epibenthic deposit-feeding holothurian that wanders over the seabed by using its ventro-lateral tubefeet. It appears to select for organically rich particles on the seabed and assimilates about 22% of the organic matter ingested (Sibuet *et al.*, 1982; Sibuet, 1984) (see Section 1.1).

The PAP material shows that *D. validum*, like several other deep-sea elasipodids (Massin, Jangoux and Sibuet, 1978; Massin, 1984), can be parasitized by sporozoans, particularly around the cloaca. In one specimen from St. 51608-1 a tanaidacean *Exspina typica* (Thurston, Billett and Hassack, 1987) was found inside the body cavity. This is not a chance occurrence since *E. typica* has been reported also from the body cavity of *Psychropotes semperiana*, *Molpadia blakei*, and *Amperima rosea* (Thurston *et al.*, 1987). 55 specimens of *D. validum* were also examined for the presence of an associated amphipod, a new species of *Valettia* (Mr. M.H. Thurston, personal communication), that is often found inside the cloaca of

O. mutabilis. Seven *Valettia* were found in three specimens of *D. validum* also within the cloaca or, in one instance, within the posterior intestine close to its junction with the cloaca. For further details see the ecological remarks on *O. mutabilis*. *D. validum* may be parasitized internally by the gastropod *Gasterosiphon deimatis* (Koehler and Vaney, 1903).

Oneirophanta mutabilis mutabilis Theel, 1879

OT 9638-2 (24), OT 9640-1 (1), OT 9756-3 (3),
OT 9756-5 (3), BN 9675-9 (2), BN 10114-1 (1),
OT 11116-1 (44), OT 50514-1 (22), OT 50515-1 (166),
BN 50603-1 (1), OT 50711-1 (65), OT 50811-1 (114),
BN 50812-1 (1), OT 50812-2 (9), OT 50907-1 (1),
OT 50910-1 (28), OT 51012-1 (1), OT 51214-1 (1),
BN 51216-1 (4), OT 51216-4 (5), BN 51216-5 (2),
OT 51309-1 (16), OT 51414-1 (17), BN 51414-2 (4),
OT 51608-1 (12), OT 51610-1 (1), OT 51803-1 (6),
BN 52215-1 (3), BN 52216-8 (17).

Bathymetric range in PSB/PAP : 2850 to 4832m, but only common below 3920m (Table 19).

Distribution : Cosmopolitan; the bathymetric range generally lies between 3200 to 6000m. Specimens have been taken as shallow as 1804m in the mid-north Atlantic (Herouard, 1923) and at 500m off the Andaman Islands, Indian Ocean (reported in Deichmann, 1930), although it should be noted that in the latter case the topography is particularly steep in this area. *O. mutabilis mutabilis* is found as far north as the Rockall Trough in the northeast Atlantic (Gage *et al*., 1985a).

Ecological remarks : Although *O. mutabilis* is found as shallow as 2850m in the PSB, and is considered to be fairly common in the Rockall Trough at depths of about 2900m (Gage *et al*., 1985a), the quantitative data from the

PSB/PAP indicate that this species is most abundant in the middle of the PAP rather than close to the base of the continental slope (Table 19). A maximum abundance of 42 individuals per hectare was calculated for the deepest epibenthic sledge sample (4818m). The most abundant samples taken by the otter trawl, with 14 and 24 individuals per hectare, came from depths of 4375 and 4510m respectively. The otter trawl is not very efficient in sampling epibenthic invertebrates and therefore it is likely that the true abundance of O. mutabilis exceeded 100 individuals per hectare at these stations.

The WW and DW biomass of O. mutabilis was calculated directly for 3 stations (Table 20). Specimens from these stations were combined with a further 28 specimens from two otter trawls (Stas. 51309-1 and 51414-1) to calculate the regression of DW on length ($r^2 = 0.71$). The relationship is given by the equation:

$$\mathrm{Log}\ (\mathrm{DW}) = \mathrm{Log}\ (\mathrm{Length}) \times 1.3437 - 2.3010$$

where n = 37 and the standard error = 0.0168. Using these data the DW biomass of O. mutabilis at Stas. 52215-1 and 52216-8, where it was most common, was estimated (Table 20). No data are available on the AFDW to DW relationship in O. mutabilis so the AFDW biomass has been estimated assuming that the relationship is the same as that for D. validum. A maximum AFDW biomass of 26g per hectare was calculated for St. 52216-8. Walker et al., (1987b) give a calorific content of 25.43 J per mg AFDW for O. mutabilis producing a maximum calorific biomass of 659 KJ per hectare for this station. O. mutabilis accounts for some 7 to 28% of the total epibenthic invertebrate AFDW biomass at abyssal depths around 4050m.

Table 19. The abundance (A) of *Oneirophanta mutabilis* in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 50603-1	4000	1	1.3	
BN 51216-5	4035	2	3.2	7.3
BN 10114-1	4050	1	3.7	9.0
BN 9756-9	4054	2	3.2	16.0
BN 51216-1	4070	4	8.6	13.9
BN 51414-2	4080	4	7.0	13.4
BN 50812-1	4090	1		5.6
BN 52215-1	4563	3	4.6	8.6
BN 52216-8	4813	17	28.1	42.0
Otter trawl samples.				
OT 50907-1	2975	1	0.1	
OT 51610-1	3485	1	0.1 +	
OT 9640-1	3753	1	0.1	
OT 51214-1	3810	1	0.2	
OT 51216-4	3985	5	0.8 +	
OT 9756-5	4016	3	0.4	
OT 50514-1	4056	22	2.7	
OT 9638-2	4074	24	5.0 *	
OT 50812-2	4088	9	0.9	
OT 9756-3	4118	3	0.6	
OT 51414-1	4155	17	1.7	
OT 51309-1	4223	16	1.6	
OT 50910-1	4312	28	3.0	
OT 51608-1	4320	12	1.5	
OT 50811-1	4375	114	14.3	
OT 50515-1	4510	166	24.2	
OT 50711-1	4788	65	7.1	
OT 11116-1	4800	44	4.2	

+ trawl doors found tangled on recovery. Abundance of *O. mutabilis* could be greater.

* *acoustic monitor* lost from trawl. Precise distance travelled by trawl unknown.

Table 20. The WW, DW, AFDW and calorific biomass of Oneirophanta mutabilis from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 19.

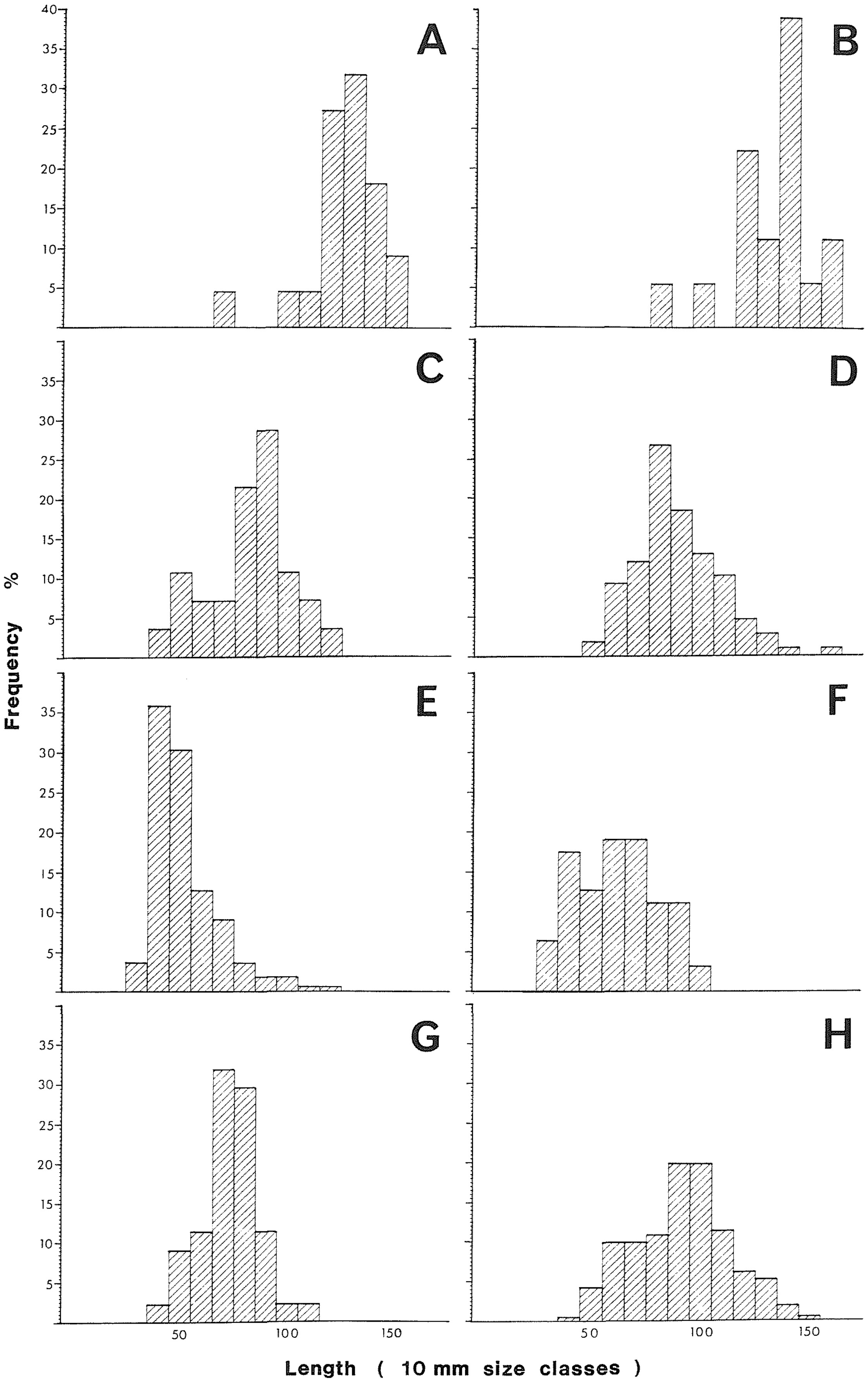
Station	mean Depth (m)	WW	DW	AFDW	Calorific biomass
51216-5	4035	210 (6)	37.3 (8)	10.6 (8)	270
51216-1	4070	523 (8)	58.7 (10)	16.7 (7)	425
51414-2	4080	498 (50)	55.3 (28)	15.7 (28)	399
52215-1	4563	-	17.1*	4.9	124
52216-8	4818	-	91.1*	25.9	659

* estimated from length / DW regression.

The size of O. mutabilis varies with location in the PSB/ PAP. All three specimens sampled shallower than 3800m were small (< 70mm long) indicating that O. mutabilis does not generally stray off the abyssal plain. Populations sampled between 3800 and 4100m, i.e. close to the base of the continental slope, were generally composed of large specimens (mean length ca. 140mm), while those sampled from depths greater than 4100m further out on the abyssal plain were smaller (mean length ca. 90mm) (Fig. 33). However, even on the PAP the specimens at some stations (e.g. St. 50515-1) were smaller than those at other stations, as detailed for D. validum. The reasons for the differences in population size distributions are not known, but they are not sampling or preservation artefacts. Samples taken with the otter trawl may underestimate the abundance of specimens < 40mm long owing to the large mesh of the otter trawl net, but no specimens as small as this have been taken by the sledge, so it seems unlikely that the trawl is missing many small specimens. Indeed, the samples with the greatest abundance of small specimens (> 25mm long) were taken by the otter trawl.

Figure 33. The population size distributions of *Oneirophanta mutabilis*. Length in 10mm size classes.

A) OT 50514- 1, 5: 6:79, 4056m, n = 22.
B) OT 9638- 2, 9:11:77, 4074m, n = 18.
C) OT 50910- 1, 10:11:80, 4312m, n = 28.
D) OT 50811- 1, 2: 8:80, 4375m, n = 190.
E) OT 50515- 1, 6: 6:79, 4510m, n = 165.
F) OT 50711- 1, 18:10:79, 4787m, n = 63.
G) OT 11116- 1, 24: 5:84, 4800m, n = 44.
H) OT 52403-13, 5:12:86, 4810m, n = 212.


A
B
C
D
E
F
G
H
40
35
30
25
20
15
10
5
Frequency %
50
100
150
Length (10 mm size classes)

Sexual development in O. mutabilis from the PAP starts in specimens about 70mm long. This means that the majority of the specimens from Stas 50515-1 and 50711-1 were juveniles. At St. 50515-1 more than 76% of the O. mutabilis collected were 30 to 40mm long. At this same station juvenile Deima validum, Psychropotes longicauda and Pseudostichopus villosus were also present indicating that recent successful recruitment had occurred in the area for a number of species (Section 5.5).

Reproduction in the deimatids is full of paradoxes. The gametogenic development of O. mutabilis on the PAP has been studied by Tyler et al. (1985c) and Tyler and Billett (in press) using specimens collected in different months of the calendar year over a period of a number of years. In each case about half of the adult population were females with well developed ovaries, while the other half were sexually inactive and were presumed to be males. The ovaries contain a variety of egg sizes and there is no evidence of seasonal changes in gametogenesis. There appears to be a continuous release of eggs about 950μm in diameter leading to slow but steady recruitment. With this scenario population size distributions like those for Stas 50514-1, 9638-2 and 50910-1 would be expected. The large egg size indicates direct development, possibly with brooding.

Hansen (1975) found that in one population of O. mutabilis from the Kermadec Trench (14 specimens) there was a surprising uniformity in the taxonomic characters, distinguishing this population from samples collected elsewhere. This local variation could have arisen from a single batch of young but, since the specimens ranged between 35 and 95 mm, Hansen thought that this explanation was unlikely. Rather, he believed that the local variation indicated limited dispersal of the eggs and that brood protection may occur.

Brood protection has been reported in *O. mutabilis* but only in one population from the Panama Basin (Hansen, 1968; 1975). The taxonomic features of the specimens from this area led to the recognition of a separate subspecies, *O. mutabilis affinis*. It is likely that all species of *Oneirophanta*, and the closely related genus *Deima*, reproduce in a similar manner. Hansen (1975) noted that where brooding occurred in *O. mutabilis affinis* all the brooded juveniles were at a similar stage of development indicating reproductive periodicity. Sampling occurred in an area noted for intense upwelling and at the end of the upwelling season. It is now known that the flux of particles to the seabed in the Panama Basin varies seasonally and that the amount of material deposited is correlated with primary productivity (Honjo, 1982). Reproduction of *O. mutabilis*, therefore, may depend on the seasonal flux of organic matter to the seabed, as proposed originally by Hansen (1975). A similar seasonal cycle in the flux of organic matter is known to occur in the northeast Atlantic (Billett *et al*., 1983) and could influence the reproductive cycle, or at least the recruitment, of *O. mutabilis* in this area.

A number of paradoxes still exist. First, periodic brooding does not seem to be an appropriate reproductive strategy for one of the few abyssal holothurians with a worldwide distribution. Second, the ovary of most specimens is large and contains many eggs, more in keeping with a species that broadcasts its eggs rather than broods them. Third, it is not clear how the eggs in the ovary are fertilised, particularly since the supposed male specimens are all in a sexually inactive state.

Several explanations may be proposed for the absence of spermatogenesis, but none are satisfactory. First, since O. mutabilis is a home for all sorts of associates (see below) including parasitic gastropods and sporozoans, it is possible that the males have been castrated. However, at least some active males should still be found. Hermaphroditism has not been noted in any specimen, but the periodic production of spermatozoa cannot be ruled out. However, if O. mutabilis were hermaphroditic it is not clear why half of the population should still be reproductively inactive. Analysis of over 200 specimens from St. 52403-13 showed that the size distributions of females and reproductively inactive specimens were almost identical, i.e. the development of testis and ovary is not related to specimen size.

A form of parthenogenesis seems most likely and could explain the extraordinary similarity of the specimens described by Hansen (1975) from the Kermadec Trench. However, in such a case one would expect a higher proportion of female specimens. Only one instance of natural parthenogenesis is known. The coral reef asteroid Ophidiaster granifer produces eggs about 600µm in diameter, some of which form a pelagic larva while others remain attached to rocks in the immediate vicinity of the adult population (Yamaguchi and Lucas, 1984). This variability in dispersal may also apply to deimatid holothurians explaining the similarity of specimens in some areas, but at the same time allowing the wide distribution of the species.

It is possible that O. mutabilis uses a combination of reproductive strategies, as found in other invertebrates (Hines, 1986). The use of a particular method could be dependent on the food supply. In this respect the geographic distribution of O. mutabilis may hold a few clues, for although the species occurs across the globe, it occurs primarily in areas where the flux of particulate matter to the seabed varies seasonally, such as in the northeast Atlantic, Panama Basin and in the Antarctic Ocean. No periodicity is obvious in the PAP material, but the quantity of detritus deposited in any one year and in any one area could affect the reproductive cycle of this species.

O. mutabilis is associated with a number of other organisms. Sporozoan parasites are found internally around the gut (Massin, 1984). O. mutabilis may be parasitized also internally by the gastropod Megadenus oneirophantae and externally by another gastropod Pisolamia brychia (Bouchet and Lutzen, 1976, 1980). Two cyclopoid copepods have been reported from the body cavity (Humes, 1974) while an amphipod, a new species of the genus Valettia (Mr. M.H. Thurston, personal communication), has been reported from the cloaca of O. mutabilis (Massin, 1984).

Over 500 specimens of O. mutabilis from the PAP were examined for the presence of Valettia in the cloaca and posterior intestine. In 130 of the specimens examined a total of 151 amphipods were found, 86% within the cloaca. All but one of the amphipods were orientated facing the posterior of the holothurian. Some amphipods occurred partly out of the anus but usually they were found tightly wedged inside the cloaca and occupying all the available space. In most cases the amphipods were free of sediment. Some specimens, generally small, occurred in the posterior intestine and in one instance four were found in a line. There were fourteen holothurians housing between 2 to 5 amphipods. The association appears to be commensal with no obvious deleterious effect on the holothurian. Presumably the amphipod vacates its house while the holothurian defaecates. The incidence of this association varies between stations. In some large samples no amphipods were found while in other samples 48% of the holothurians were host to an amphipod.

Family Laetmogonidae

Laetmogone violacea Theel, 1879

OT 9752-1 (3), OT 9776-1 (6), OT 9778-1 (16),
BN 9779-1 (45), BN 10108-1 (40), BN 10109-8 (14),
OT 50503-1 (1271), GT 50504-1 (30), GT 50505-1 (9),
GT 50507-1 (6), GT 50508-1 (12), OT 50509-1 (259),
OT 50519-1 (478), GT 50520-1 (10), OT 50522-1 (279),
OT 50524-1 (15), OT 50601-1 (14), BN 50606-1 (24),
OT 50606-2 (9), BN 50606-5 (15), OT 50607-1 (15),
BN 50607-2 (2), BN 50610-1 (65), OT 50611-1 (504),
OT 50702-1 (76), OT 50704-1 (32), GT 50707-1 (16),
GT 50708-1 (6), GT 50709-1 (14), GT 50713-1 (8),
GT 50714-1 (2), OT 50801-1 (240), OT 50808-1 (92),
GT 50809-1 (380), OT 50820-1 (6), OT 50821-1 (8),
OT 50903-1 (280), OT 50904-1 (305), OT 50905-1 (6),
OT 51003-1 (7), OT 51007-1 (51), OT 51008-1 (2),
OT 51009-1 (5), OT 51022-1 (1), OT 51023-1 (65),
OT 51026-1 (3), OT 51027-1 (73), BN 51103-4 (4),
BN 51103-5 (12), OT 51205-1 (20), OT 51206-1 (40),
BN 51208-1 (79), BN 51208-3 (63), OT 51304-1 (5),
OT 51305-1 (10), OT 51306-1 (40), OT 51307-1 (1),
GT 51312-1 (3), GT 51313-1 (40), OT 51314-1 (12),
GT 51315-1 (3), OT 51308-1 (10), BN 51403-1 (7),
BN 51403-2 (4), BN 51403-3 (2), BN 51403-4 (1),
BN 51403-5 (1), OT 51403-7 (41), OT 51404-1 (19),
BN 51406-1 (38), BN 51420-2 (3), BN 51420-3 (3),
BN 51420-4 (6), BN 51707-1 (15), BN 51708-2 (11),
BN 51715-2 (3), OT 51810-1 (11), OT 51811-1 (1),
BN 52009-1 (1), BN 52017-1 (2), BN 52204-1 (4).

Bathymetric range in the PSB : 510 to 1600m on the Goban Spur but mainly between 955 and 1490m (97% of the specimens collected); 700 to 1535m on the main transect with 95% of the specimens collected between 980 and 1300m.

Distribution : Almost a cosmopolitan distribution but not recorded from the western Atlantic or the eastern Pacific;

225 to 1804m. Hansen (1975) considered that the distribution may be dependent on the dispersal of its larvae by deep-sea currents. The records of *L. violacea* from the Rockall Trough come from a similar depth distribution, 940 to 1400m (Gage *et al*., 1985a; Harvey *et al*., in press). Two specimens have been sampled as deep as 3000m to the west of the Porcupine Bank at the base of the steep continental slope found in that area (Gage *et al*., 1985a).

Ecological remarks : Data on the abundance of *L. violacea* from the epibenthic sledge (Table 21) indicate that this species is most abundant on the main transect between 980 and 1200m, an area lying above the suspension-feeding community in the PSB (see Section 5.2). *L. violacea* is present in the suspension- feeding community but unlike other holothurians, such as *E. hispida*, *Y. talismani*, *B. natans*, and *M. intestinalis*, its abundance is reduced in this area. The abundance of *L. violacea* in the sledge samples is low below the suspension feeders (at depths greater than 1300m) on the main transect but it is common at comparable depths on the Goban Spur. Data from the otter trawl (Table 22) show that the paucity of *L. violacea* from sledge samples deeper than 1300m on the main transect, is a sampling artefact since patches of *L. violacea* with a high abundance can be found down to 1520m (St. 50509-1), as on the Goban Spur. A maximum abundance of 860 individuals per hectare was recorded from around 1000m on the main transect (St. 50610-1). A particularly large catch was taken at a similar depth by the otter trawl (St. 50503-1) with an abundance that probably exceeded 1000 individuals per hectare, taking into account the inefficiency of the trawl in sampling epibenthic invertebrates.

Table 21. The abundance (A) of *Laetmogone violacea* in epibenthic sledge samples, expressed as number per hectare. Samples from the main transect unless otherwise indicated. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
b BN 50607-2	700	2	4.3	13.6
BN 51103-5	940	12	30.7	48.5
BN 51103-4	955	4	14.7	27.5
BN 50610-1	980	65	212.5	859.8
BN 51406-1	1082	38	151.5	256.9
b BN 50606-1	1115	24	54.2	174.7
a BN 10109-8	1125	14	17.2	
b BN 50606-5	1130	15	35.9	35.8
BN 51208-3	1178	63	261.0	788.5
BN 51208-1	1185	79	151.1	616.2 o
BN 51707-1	1218	15	15.8	
BN 52009-1	1221	1	3.2	6.4
BN 51420-4	1283	6	36.9	66.0
BN 51403-5	1293	1	4.9	11.3
BN 51420-3	1296	3	25.6	33.2
BN 51403-1	1303	7	15.6	40.0
BN 52204-1	1303	4	43.4	56.3
BN 51420-2	1307	3	18.5	33.8 +
BN 51403-2	1321	4	17.0	43.4
BN 51403-3	1322	2	12.8	19.1
BN 51403-4	1326	1	3.0	10.4
a BN 10108-1	1388	40	84.4	
a BN 9779-1	1401	45	64.3	234.7
BN 51708-2	1450	11	21.4	50.9
BN 52017-1	1465	2	9.8	28.4
BN 51715-2	1493	3	4.5	

a Goban Spur
b southern part of Porcupine Bank

\+ Abundance estimated from outer nets only.
o weak link, on bottom net bar broken during haul.

Table 22. The abundance (A) of Laetmogone violacea in otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise indicated. n = number of specimens taken.

	Station	Mean Depth (m)	n	A/Posn
	OT 50820-1	720	6	1.1
	OT 51404-1	750	19	4.6
	OT 50905-1	788	6	1.2
a	OT 9776-1	804	6	1.6
c	OT 50601-1	849	14	2.8
a	OT 50522-1	983	279	72.9
	OT 50503-1	1017	1271	347.0
	OT 50904-1	1028	305	59.8
	OT 51306-1	1218	40	13.2
a	OT 50801-1	1265	240	50.2
	OT 50611-1	1388	504	81.1
a	OT 50519-1	1448	478	96.7

a Goban Spur
b southern part of Porcupine Bank
c northeast PSB

The WW biomass of L. violacea was measured directly from 6 samples (Table 23). Three of these samples were then used to determine DW and AFDW biomass as detailed in Section 2.2. Using these samples a mean conversion factor was estimated so that the DW and AFDW biomass at the other stations could be calculated. In addition, 46 specimens were used to calculate the length/DW regression for L. violacea. The DW and AFDW biomass were then estimated from the population size distributions for a further 6 sledge samples (Table 23). The relationship between DW and Length is given by the equation :

$$\text{Log (DW)} = \text{Log (Length)} \times 1.7271 - 3.2140$$

where n = 46 and the standard error = 0.1222 (r^2 = 0.72).

Table 23. The WW, DW, AFDW and calorific biomass of _Laetmogone violacea_ from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 21.

Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51103-4	955	2043 (4)	135 (1)	58 (1)	1431
51406-1	1082	5490 (11)	477 (4)	226 *(7)	5578
51208-3	1178	7059 (6)	423 *(1)	212 *(4)	5232
51208-1	1185	6353 (2)	413 *(1)	179 *(2)	4418
51420-4	1283	2101 (2)	165 *(1)	78 *(2)	1925
51403-1	1303	716 (2)	82 (1)	43 (3)	1061
51103-5	940	-	75 +	35 *	864
50610-1	980	-	488 +	230 *	5676
50606-1	1115	-	22 +	10 *	247
50606-5	1130	-	34 +	16 *	395
9779-1	1401	-	391 +	185 *	4566
51708-2	1450	-	136 +	64 *	1580

* estimated using a conversion factor; DW from WW, AFDW from DW
+ estimated from length / DW regression.

The greatest biomass of _L. violacea_ on the main transect occurred between 940 and 1200m. A similar AFDW biomass was found at three stations between 980 and 1178m (212 to 230g AFDW per hectare). The equivalent calorific biomass ranges between 5232 and 5676 KJ per hectare for the same stations, using a calorific value of 24.68 J per mg AFDW (Walker _et al_., 1987b). Although _L. violacea_ is fairly abundant at Stas 50606-1 and 50606-5, most of the specimens are small (see below) producing a low biomass. Data from St. 9779-1 (1400m) show that the abundance of _L. violacea_ can be high even at the bottom of its bathymetric range. The greatest proportion that _L. violacea_ contributed to the total epibenthic invertebrate AFDW biomass was 7%.

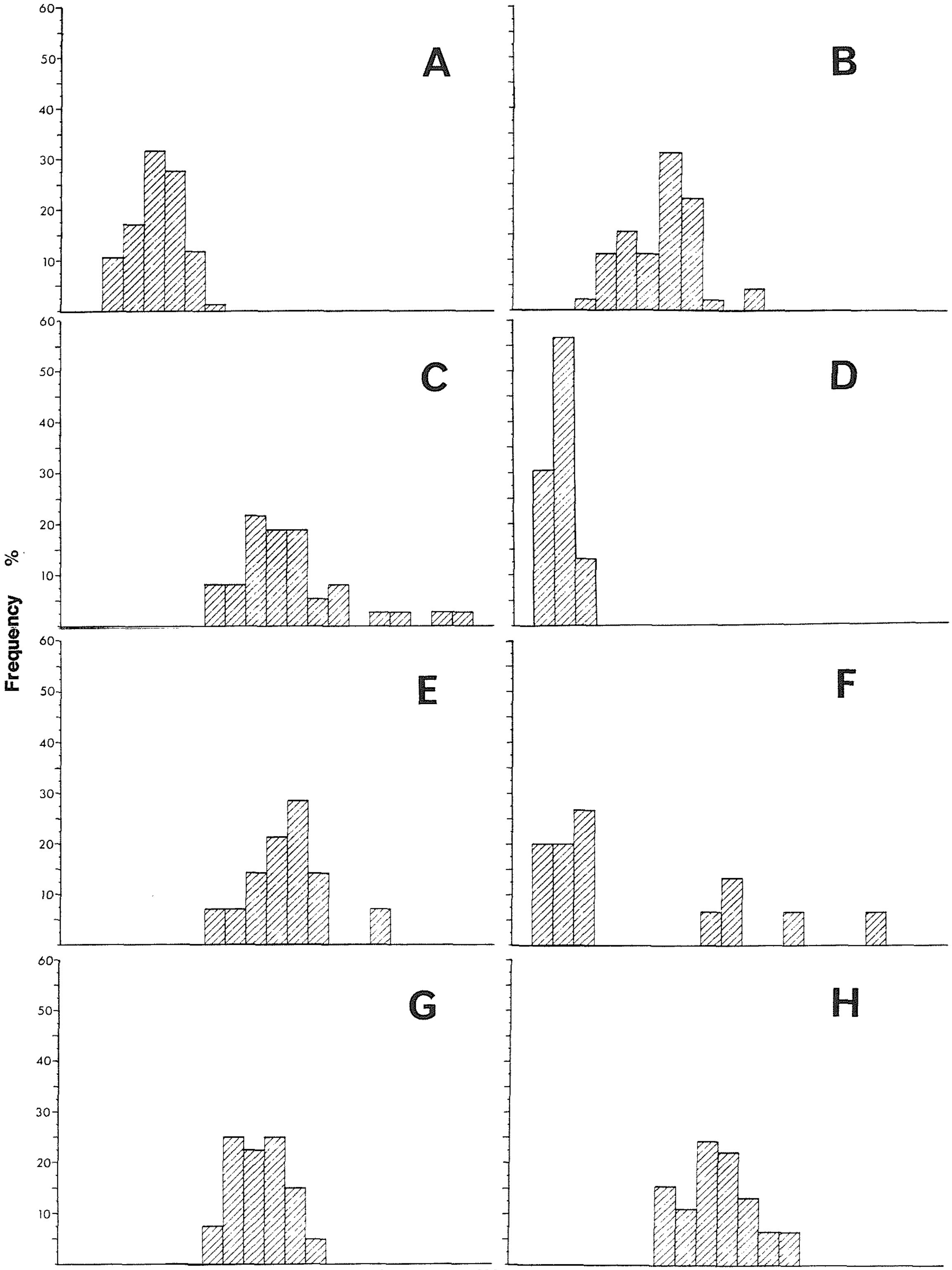
The population size distributions for 7 epibenthic sledge and 1 otter trawl samples are presented in Fig. 34. Most samples show a well established adult population with a mean length of about 95mm. Similar size distributions were obtained for a number of other stations not included in Fig. 34. No relationship between specimen size and depth was found. However, two areas of the PSB proved to be unusual.

First, St. 50702-1 (Fig 34) from an area on the eastern slopes of the PSB had a large population of small specimens (mean length 40mm). Similarly at St. 50601-1, from the same area, only small specimens were present. A similar prevalence of small individuals was found for another deposit-feeding holothurian, Stichopus tremulus, in these samples. The area is dominated by suspension feeders, such as the corals Lophelia pertusa and Madrepora oculata and the holothurian Psolus squamatus, and it is possible that the deposit-feeders are unable to reach their full size in an area more suited to suspension feeders. Alternatively, recent recruitment of the two species may have occurred in the area.

Second, samples from the southern part of the Porcupine Bank in July 1979, Stas 50606-1 and 50606-5 (Fig 34), have many small juveniles only 10 to 30mm long in addition to several adult specimens in the latter sample. In this case it is evident that recruitment has taken place only recently. There is no seasonal periodicity in egg production in L. violacea (Tyler et al., 1985a) and so the success of recruitment in this area in July 1969 could be in response to the annual deposition of detrital material which occurs in summer months (Billett et al., 1983). Similar seasonal changes in the success of recruitment have been proposed for the ophiuroid Ophiomusium lymani (Gage and Tyler, 1982).

Figure 34. The population size distributions of *Laetmogone violacea*. Length in 10mm size classes.

A) OT 50702-1, 13:10:79, 785m, n = 76.
B) BN 50610-1, 8: 7:79, 980m, n = 45.
C) BN 51406-1, 27: 3:82, 1082m, n = 37.
D) BN 50606-1, 6: 7:79, 1115m, n = 23.
E) BN 10109-8, 7: 9:79, 1125m, n = 14.
F) BN 50606-5, 6: 7:79, 1130m, n = 15.
G) BN 10108-1, 5: 9:79, 1388m, n = 40.
H) BN 9779-1, 24: 4:78, 1401m, n = 45.


A
B
C
D
E
F
G
H
60
50
40
30
20
10
Frequency %
50
100
150
200
Length (10 mm size classes)

L. violacea produces eggs up to 400um in diameter. Eggs of this intermediate size probably lead to abbreviated lecithotrophic larval development (Tyler *et al*., 1985a).

L. violacea is an epibenthic deposit-feeding holothurian that wanders over the seabed by using its ventro-lateral tubefeet. Photographs of *L. violacea* in situ (Fig. 27E) show that contractions pass down the body in a similar fashion to *Scotoplanes globosa* (Hansen, 1972, 1975). These contractions regulate the turgidity of the tubefeet by alternately forcing fluid from the intra-dermal water-vascular cavities into the tubefeet and then relaxing to allow fluid back into the cavities. The contractions also appear to pull the tubefoot from a position pointing forwards to a position pointing backwards (Fig. 27E) at the same time as forcing the fluid into the tubefoot. The tubefeet, therefore, are used actively in locomotion, rather than acting merely as stilts while the body moves forward by muscular contractions, as in *B. rosea* (Fig. 27F). The use of the tubefeet in locomotion by *L. violacea* leaves a characteristic tramline track (Fig. 27E) rather than the series of pinpoint marks made by *B. rosea*.

There is little information on the feeding of *L. violacea*. The gut is normally full of sediment skimmed off the surface of the seabed. Data on chloropigments (see Section 5.3) show that, like *B. rosea* and other holothurians, *L. violacea* is able to select for detrital particles on the seabed. Using chloropigment concentrations as an indicator of organic concentration it is found that chloropigments are some 14 times greater in the oesophagus of *L. violacea* than in surficial sediment from the same locality. Feeding in *L. violacea* may be aided by the presence of commensal bacteria in its tentacles (Dr. D. Roberts, personal communication).

Many of the specimens collected bore red scars on their ventral surface, made by a commensal polychaete, *Eunoe laetmogonensis* (Kirkegaard and Billett, 1978). This polychaete was found still attached to a few *L. violacea* and in some samples the scars made by the polychaete occurred on over 90% of the holothurians. A similar association was found in populations of *L. violacea* from off the coast of north-west Africa.

Benthogone rosea Koehler, 1896

OT 9753-4 (16), BN 9753-7 (25), OT 9753-8 (21),
BN 9754-3 (17), OT 9774-1 (31), BN 9775-3 (131),
BN 9779-1 (219), BN 10108-1 (118), BN 10111-8 (140),
OT 50509-1 (313), OT 50510-1 (464), OT 50517-1 (309),
OT 50518-1 (28), OT 50519-1 (924), BN 50602-2 (66),
OT 50602-3 (507), OT 50611-1 (164), OT 50703-1 (86),
OT 50710-1 (9), OT 50715-1 (109), OT 50802-1 (152),
OT 50810-1 (540), OT 50822-1 (124), OT 50902-1 (590),
OT 51009-1 (111), OT 51010-1 (15), OT 51011-1 (7),
OT 51021-1 (38), OT 51022-1 (48), BN 51104-1 (2),
BN 51105-3 (53), BN 51105-4 (26), BN 51113-1 (17),
OT 51201-1 (273), OT 51205-1 (50), OT 51213-1 (271),
OT 51307-1 (6), OT 51308-1 (8), OT 51311-1 (105),
OT 51314-1 (32), BN 51403-1 (4), BN 51403-2 (1),
BN 51403-3 (2), BN 51403-4 (9), BN 51403-5 (2),
BN 51403-6 (3), OT 51403-7 (6), BN 51407-1 (58),
BN 51408-1 (77), OT 51409-1 (496), OT 51419-1 (209),
BN 51420-2 (1), BN 51420-3 (1), BN 51420-4 (1),
OT 51613-1 (5), BN 51708-2 (109), BN 51715-2 (81),
BN 51717-2 (29), OT 51801-1 (7), BN 52017-1 (39),
BN 52019-1 (71), BN 52203-1 (18), BN 52211-1 (78),
BN 52218-1 (206).

Bathymetric range in PSB : 1255 to 2240m on the main transect, but principally between 1365 and 2150m. A similar depth range occurs on the Goban Spur (1385 to 2110m). The lower bathymetric limit is uncertain since few samples have been taken between 2100 and 2500m (Fig. 7, page 57). *B. rosea* occurred in every sample taken between 1400 and 2200m.

Distribution : Eastern Atlantic, southwest Pacific and western Indian Ocean, 1103 to 2480m. Although the lower bathymetric limit was increased to 4100m by Sibuet (1977) from material taken at "Biogas" St. 3, Bisol, Costa and Sibuet (1984) state that *B. rosea* was taken only at "Biogas" St. 1 (1800 to 2200m). Recent records from the Rockall Trough (Gage *et al.*, 1985a; Harvey *et al.*, in press) have extended the northward limit of *B. rosea* in the northeast Atlantic, and confirm that the species is often found around the 2000m isobath.

Ecological remarks : The zone of suspension feeders found between about 1100 and 1330m in the PSB marks the upper bathymetric limit of *B. rosea*. A few specimens do occur in the suspension-feeding community (see Section 5.2), but generally the abundance of *B. rosea* in this region is low. Below this zone the abundance of *B. rosea* is particularly high in nearly all the samples, ranging up to 2047 individuals per hectare (St. 9775-3) (Table 24). However, this estimate may be rather high since the abundance of holothurians at this station was based on the area sampled by only the outer two nets of the epibenthic sledge (see ecological remarks on *Paelopatides grisea*). An abundance of about 1000 individuals per hectare is indicated at several epibenthic sledge stations. Abundances are lower in the otter trawl catches, as expected; up to 187 individuals per hectare (Table 25). However, owing to the inefficiency of the trawl in sampling epibenthic invertebrates it is likely that the true abundance is some 5 times greater.

Table 24. The abundance (A) of *Benthogone rosea* in epibenthic sledge samples, expressed as number per hectare. Samples from the main transect unless otherwise indicated. Number of juveniles only a few mm long and abundance estimates including these specimens are given in parentheses. n = number of specimens taken.

	Station	Mean Depth (m)	n		A/Posn		A/Odo		
	BN 51420-4	1283	1		6.2		11.0		
	BN 51403-6	1287	3				31.8		
	BN 51403-5	1293	2		9.8		22.7		
	BN 51420-3	1296	0	(1)	0.0	(8.6)	0.0	(11.1)	
	BN 51403-1	1303	4		8.9		22.9		
	BN 51420-2	1307	1		6.2		11.3		+
	BN 51403-2	1321	1		4.2		10.9		
	BN 51403-3	1322	2		12.8		19.1		
	BN 51403-4	1326	9		27.1		94.0		
	BN 51104-1	1380	2		5.1		14.1		
a	BN 10108-1	1388	118		248.9				
a	BN 9779-1	1401	219		312.8		1142.4		
a	BN 52218-1	1440	206		478.5		887.2		
	BN 51708-2	1450	109		212.3		505.6		
	BN 52017-1	1465	39		191.7		553.2		
b	BN 9754-3	1484	14	(3)	28.9	(35.1)			
	BN 51715-2	1493	81		122.0				
	BN 51407-1	1500	58		111.5		403.3		
	BN 52203-1	1526	18		94.9		121.9		
	BN 51113-2	1535	17		26.3		76.1		o
a	BN 10111-8	1635	132	(8)	207.2	(219.7)	866.7	(919.2)	
	BN 52211-1	1716	78		240.5		552.0		
	BN 52019-1	1731	71		335.5		356.4		
b	BN 9753-7	1942	25		101.2				
	BN 50602-2	1968	66		109.6				
	BN 51717-2	1975	29		127.2		180.9		
	BN 51105-4	1989	26		86.7				
	BN 51408-1	1998	77		168.1		421.9		
b	BN 9775-3	2016	131		130.6		2046.9		+
	BN 51105-3	2025	53		103.8		378.0		

a Goban Spur
b northeast PSB

\+ weak link on bottom net bar broken, abundance estimated from outer nets only. Centre net catch discarded.
o weak link on bottom net bar broken.

Table 25. The abundance (A) of Benthogone rosea in otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise stated. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn
OT 51403-7	1293	6	1.5
OT 50611-1	1388	164	26.4
a OT 50519-1	1448	924	187.0
OT 50509-1	1507	313	85.4
OT 51419-1	1509	209	46.9
b OT 9774-1	1533	31	7.0
a OT 50810-1	1650	540	121.1
OT 50715-1	1678	109	27.3
OT 51409-1	1684	496	111.2
a OT 50517-1	1790	309	71.8
OT 50902-1	1845	590	119.4
OT 50602-3	1874	507	58.9
a OT 50802-1	1884	152	39.7
b OT 51213-1	1938	271	151.1
b OT 9753-8	1942	21	6.3
OT 50510-1	1943	464	83.2
b OT 9753-4	1945	16	2.9
OT 51201-1	1975	273	85.6 +
a OT 50518-1	2078	28	4.3
OT 50822-1	2123	124	11.5
OT 51613-1	2220	5	0.6

a Goban Spur
b northeast PSB

\+ trawl doors found tangled on recovery. Abundance could be higher.

The WW, DW and AFDW biomass of B. rosea was estimated directly at three stations (Table 26) as detailed in section 2.2. Using these data the DW and AFDW biomass of three further stations were calculated from the WW biomass measured at these stations (Table 26). In addition, 38 specimens between 15 and 225mm long were used to determine the relationship between length and AFDW. Using the regression of AFDW on length the AFDW biomass of a further 10 samples was calculated from their population size distributions (Table 26). The relationship between AFDW and length is given by the equation :

$$\text{Log (AFDW)} = \text{Log (Length)} \times 2.4030 - 4.8587$$

where n = 38 and the standard error = 0.2238 ($r^2 = 0.87$). Some contraction of the specimens in these samples will have occurred during preservation so the biomass of B. rosea at these stations have been underestimated.

Table 26. The WW, DW, AFDW and calorific biomass of Benthogone rosea from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 24.

Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51403-1-5	1310	1769 (2)	147 (1)	72+(2)	1760
51104-1	1380	1225 (34)	80 (11)	39 (21)	953
51407-1	1500	23971 (47)	1881 (30)	932+(43)	22778
51113-2	1535	4254 (58)	262 (38)	118 (51)	2884
51408-1	1998	15633 (21)	1227 (18)	612+(27)	14957
51105-3	2025	11327 (14)	1175 (11)	657 (24)	16057
9779-1	1401	-	-	776 *	18965
52218-1	1440	-	-	1093 *	26713
51708-1	1450	-	-	497 o	12147
52017-1	1465	-	-	560 *	13686
52203-1	1526	-	-	186 *	4546
10111-8	1635	-	-	368 *	8994
52211-1	1716	-	-	480 *	11731
52019-1	1731	-	-	231 *	5646
51717-2	1975	-	-	399 o	9752
9775-3	2016	-	-	1761 *	43039

+ Estimated using a conversion factor : DW from WW, AFDW from DW.
Estimated from length / AFDW regression :
* preserved specimens.
o fresh specimens.

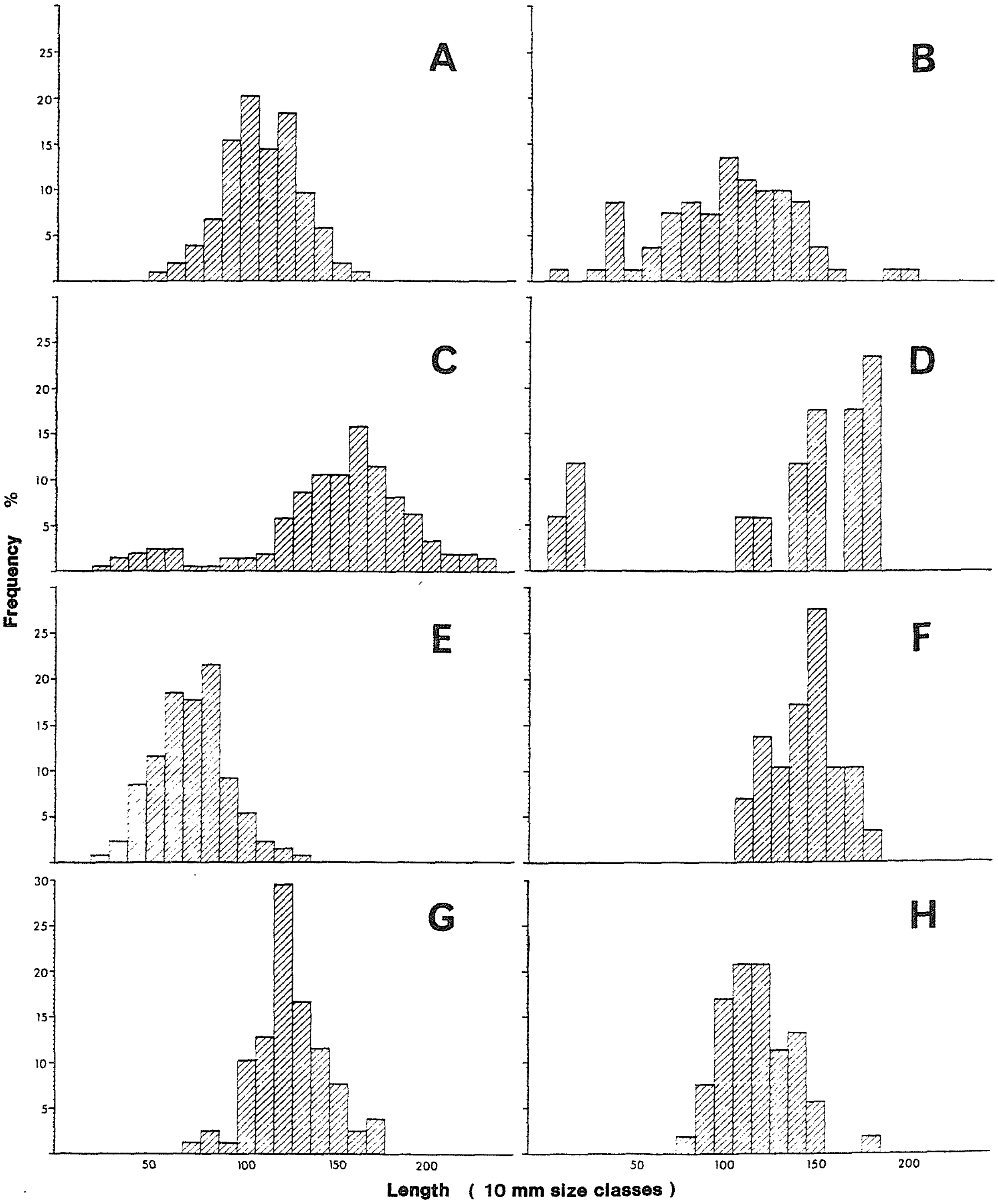
As the data on abundance suggest, *B. rosea* is an important member of the benthic community at mid-slope depths, accounting for some 25 to 50% of the total epibenthic invertebrate AFDW biomass. The AFDW biomass of *B. rosea* varies between 118 and 1761g (mean 620g) per hectare at depths between 1400 and 2100m. For the same depth range the calorific biomass varies between 2884 and 43039 (mean 15150) KJ per hectare, using a calorific value of 24.44 J per mg AFDW for *B. rosea* (Walker *et al*., 1987b).

Sibuet and Lawrence (1981) report calorific biomass values of 973 and 1114 Kcal per hectare (4070 and 4662 KJ per hectare) for two different populations of *B. rosea* in the Bay of Biscay. These estimates were based on the abundance of *B. rosea* in trawls which Sibuet and Lawrence (1981) considered underestimated the true biomass of *B. rosea* by about one-half, based on photographic observations at the same sites. Therefore, calorific biomass values approaching 10,000KJ per hectare might be more appropriate for *B. rosea* in the Bay of Biscay. This is similar to many stations sampled in the PSB, although the present data indicate that in some areas the biomass of *B. rosea* can be some 2 to 4 times greater.

All the population size distributions of *B. rosea* (Fig. 35) are unimodal with a mean length of about 120mm (measured from fresh specimens). There is some reduction in length with preservation so that the mean length of preserved samples is 70 to 90 mm long (e.g. St. 10118-1). The size distributions are similar for the sledge and otter trawl samples, except for St. 51419-1 (Fig. 35) which had a wide range of sizes and a greater proportion of large specimens. There is no obvious correlation of specimen size with depth or location. Small juvenile specimens less than 30mm long are present in only a few samples. Generally they are very rare, but in some samples,

Figure 35. The population size distributions of *Benthogone rosea*. Length in 10mm size classes.

A) BN 51708-2, 13: 4:83, 1450m, n = 78.
B) BN 51715-2, 18: 4:83, 1493m, n = 81.
C) OT 51419-1, 1: 4:82, 1409m, n = 209.
D) BN 51113-2, 30: 5:81, 1535m, n = 17.
E) BN 10111-8, 9: 9:79, 1635m, n = 130.
F) BN 51717-2, 18: 4:83, 1975m, n = 29.
G) BN 51408-1, 27: 3:82, 1998m, n = 104.
H) BN 51105-3, 22: 5:81, 2025m, n = 53.


A
B
C
D
E
F
G
H
5
10
15
20
25
30
Frequency %
50
100
150
200
Length (10 mm size classes)

for example Stas 10111-8 and 51113-2 (Fig. 35), several may occur together. This appears to be the result of patchy recruitment since St. 10111-8 also had many juvenile *M. lactea* and small *Elpidia*.

B. rosea produces eggs continuously up to a diameter of about 750μm (Tyler *et al*., 1985c) suggesting that development occurs directly on the seabed or via lecithotrophic larvae. A pelagic phase is also indicated by the wide geographic distribution of this species.

B. rosea moves over the seabed using its tubefeet as stilts and muscular contractions to move the body forward (Fig. 27F). This type of locomotion leaves a double track of pinpoint marks where the tubefeet have alighted on the seabed (Fig. 27F). Apart from these marks, *B. rosea* leaves the seabed remarkably undisturbed.

Feeding in *B. rosea* is discussed in Section 5.3. with reference to its apparent ability to wander over the seabed selecting for particles with a high organic content.

Family Psychropotidae

Benthodytes typica Theel, 1882

OT 51610-1 (1).

Bathymetric range in the PSB : 3310 to 3660m.

Distribution : Worldwide, 1873 to 4700m (Hansen, 1975) although it is also reported from much shallower depths, 315 to 1401m, in the northwest Atlantic (Deichmann, 1954).

Taxonomic remarks : The specimen is 190mm long and in poor condition. The brim is well developed and the pigmented tubefeet canals can be seen within it. There are 18 tentacles with a structure as described by Hansen (1975) except that the discs are not retracted into the stalks. Circum-oral papillae are present but no ossicles could be found in the body wall.

Ecological remarks : B. typica produces a large egg up to 3mm in diameter (Hansen, 1975) which, as in other psychropotids, leads to the pelagic, direct development of juveniles. Grieg (1921, syn. B. glutinosa) reported a 13mm long juvenile from a depth of 1400m (some 1600m above the seabed) in a pelagic trawl from the northeast Atlantic. Four other juveniles have now been found in IOS midwater samples, one (7mm long) from off the coast of Ghana at a depth of 1205 to 1300m (some 3400m above the seabed) and three others (4.9 to 13mm long) from between 910 and 2700m (over 3000m above the seafloor) over the Madeira Abyssal Plain. The significance of the large egg size found in psychropotids is discussed in Section 5.5.

Benthodytes sordida Theel, 1882

OT 9638-2 (1), OT 9640-1 (5), OT 9756-3 (1),
OT 9756-5 (1), BN 9756-14 (2), OT 11118-1 (4),
OT 50514-1 (4), OT 50515-1 (1), BN 50603-1 (1),
BN 50604-1 (1), OT 50711-1 (1), OT 50811-1 (4),
OT 50812-2 (2), OT 50910-1 (2), OT 51012-1 (1),
OT 51214-1 (2), BN 51216-1 (1), OT 51216-4 (3),
BN 51216-5 (1), OT 51414-1 (1), BN 51415-1 (2),
OT 51608-1 (1), OT 51610-1 (14), OT 51803-1 (2).

Bathymetric range in PSB/PAP : 3310 to 4795m (Theel, 1882; von Marenzeller, 1893, syn. B. janthina; present records). This species may be synonymous also with B. lingua (see below) known from the South and North Atlantic, 860 to

4700m, including a record of *B. janthina* (Grieg, 1921) which Hansen (1975) considered to be synonymous with *B. lingua*.

Taxonomic remarks : Hansen (1975) was unable to place a few species of *Benthodytes* taxonomically since the forms of their body wall ossicles were unknown. These species included *B. sordida* and *B. janthina* von Marenzeller, 1893 which Perrier (1902) considered to be synonymous. At the same time Perrier (1902) described a new species, *B. lingua*, which he considered to be close to, but distinct from, *B. sordida*/*B. janthina*. The PAP material has permitted a reappraisal of the criteria used to distinguish the species and indicates that the species may indeed be synonymous.

The major feature used to characterise *B. lingua* was the shape of the dorsal papillae which are filiform (long and thin throughout their length) rather than short and conical, as drawn for *B. sordida* and *B. janthina*. The papillae of the PAP specimens in most cases are retracted within deep pits. For some large papillae the base of the tentacle is large and forms a distinct mound. The tentacle is retracted inside the body within this mound, often making it look conical. However, in some cases the tip of the tentacle, which is filiform, protrudes outside the body by a length of 10mm or so. It is evident that the papillae of the PAP specimens adopt a variety of forms depending on the degree of contraction. Long, filiform papillae were not found in the PAP specimens but they could appear so if found in an uncontracted state. A photograph of a dark-bodied *Benthodytes* from 3980m off northwest Africa (Fig. 27G) shows that although the papillae are filiform at their end, the largest papillae also have a broad base. It is likely that there would be considerable variation in the form of these papillae on contraction during capture and preservation. The use of the shape of the papillae to characterise *B. lingua*, therefore, does not appear to be valid.

The papillae, however, are important taxonomic characters, for their relative size and their position on the dorsal ambulacra is similar in all three species and quite unlike that described for any other *Benthodytes*. The PAP specimens usually have three pairs of papillae that are larger than the others. These larger papillae are not always obvious on external inspection, but when the body wall is viewed from the inside some large water-vascular cavities, corresponding to the large papillae, are easily seen owing to their purple pigmentation. The same observation was made by Perrier (1902) for *B. lingua* and it is clear from the drawings of *B. sordida* and *B. janthina* that three, or possibly four, pairs of papillae in these species are larger than the rest. This is a remarkable similarity for the three species and points towards their synonymy.

Other features used to characterise *B. lingua* are also of dubious validity in the light of the PAP specimens. First, tentacle number is variable (14 or 15) and not consistently 15. Second, fresh specimens are usually dark purple when freshly caught but they lose their colour rapidly upon preservation. The alcohol preservative becomes discoloured and any other organism in the same container becomes pigmented. In preserved specimens the dorsal surface is light violet, in some cases almost white, while the ventral surface remains dark purple. The drawings of *B. sordida* and *B. janthina* made from fresh specimens on board ship are dark purple while the preserved specimens of *B. lingua* are light pink (Perrier, 1902). This colour difference does not appear to be diagnostic. Third, the constriction of the body behind the anterior end is variable in the PAP specimens and may not be important.

Large primary cross ossicles with a bipartite apophysis are described for B. lingua. These ossicles are also present in some of the PAP specimens, but in many cases the ossicles are completely lacking, as Perrier (1902) reported for B. lingua. Ossicles were not found in B. sordida or B. janthina but Theel (1882) did indicate that B. sordida could have cross-shaped ossicles since these were present, although nearly dissolved, in B. abyssicola, a species with a close affinity to B. sordida and sampled at the same station. The presence of cross-shaped ossicles may thus be used to substantiate an identification, but their absence cannot be used to distinguish between species.

Since the PAP specimens share features found in B. lingua, B. sordida and B. janthina, the synonymy of these three species is proposed. It is shown below that the large egg size produced by B. sordida leads to direct development of juveniles in the pelagic realm allowing the wide dispersal of the species. Other psychropotids with this type of development have worldwide distributions and this is probably true also for B. sordida. It is odd that B. lingua should be reported to have such a wide geographic distribution but only within the Atlantic Ocean.

Ecological remarks : Although B. sordida is not a common holothurian on the PAP, it is certainly characteristic, occurring in 18 of the 20 otter trawls from depths greater than 3400m. Data from the trawls indicate that B. sordida is more common close to the base of the continental slope (Table 27), but it occurred in abundance in only one trawl.

Table 27. The abundance (A) and biomass (B) of *Benthodytes sordida* in epibenthic sledge and otter trawl samples, expressed as number or g DW per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo	B/Odo
Epibenthic sledge samples.					
BN 51415-1	3490	2	4.9	6.9	204
BN 50604-1	3520	1	1.2		
BN 9756-14	3689	2	2.0	13.8	
BN 50603-1	4000	1	1.3		
BN 51216-5	4035	1	1.6	3.7	127
BN 51216-1	4070	1	2.1	3.5	102
Otter trawl samples.					
OT 51610-1	3485	14	1.4 *		
OT 9640-1	3753	5	0.5		
OT 51214-1	3810	2	0.4		
OT 51216-4	3985	3	0.5 *		
OT 9756-5	4016	1	0.1		
OT 50514-1	4056	4	0.5		
OT 9638-2	4074	1	0.2 +		
OT 50812-2	4088	2	0.2		
OT 9756-3	4118	1	0.2		
OT 51414-1	4155	1	0.1		
OT 50910-1	4312	2	0.2		
OT 51608-1	4320	1	0.1		
OT 50811-1	4375	4	0.5		
OT 50515-1	4510	1	0.1		
OT 11118-1	4565	4	0.4		
OT 50711-1	4788	1	0.1		

* trawl doors found tangled on recovery. Abundance could be higher.

\+ acoustic monitor lost from trawl. Precise distance travelled by trawl unknown.

The DW biomass of *B. sordida* was determined directly at 3 stations (Table 27), producing a mean DW biomass of 144g per hectare for this species. The body wall accounts for some 90% of the total weight with an average ash content of 44%. Using these data a mean AFDW biomass of 81g per hectare can be calculated. A further conversion can be made to a calorific biomass of 2016 KJ per hectare using a calorific value of 24.89 J per mg AFDW for this species (Walker *et al*., 1987b).

In the three samples used for biomass analysis *B. sordida* contributed some 11 to 28% of the total epibenthic invertebrate biomass. *B. sordida* is a particularly large holothurian and therefore contributes substantially to the total biomass when it is present. The specimens from the PSB/PAP measured between 115 and 540mm in length. Most specimens were 300 to 400mm long.

B. sordida, like other psychropotids, produces particularly large eggs, in excess of 1.2mm (Tyler and Billett, in press) and probably as large as 2.0mm (Hansen, 1975 - *B. lingua*). As in other psychropotids this size of egg leads to the direct, pelagic development of juveniles. A juvenile of *B. sordida* has been found in pelagic nets in the northeast Atlantic "Discovery" St. 11121-10, 3485 to 3515m) some 600m above the seafloor (syn. *B. lingua*, Billett *et al*., 1985). The importance of this type of development is discussed in Section 5.5.

Psychropotes depressa (Theel, 1882)

BN 9753-7 (1), RMT 9756-2 (1), BN 10106-1 (157),
OT 50511-1 (126), OT 50518-1 (1), BN 50613-1 (35),
OT 50907-1 (3), OT 51015-1 (5), OT 51310-1 (6),
OT 51411-1 (1), OT 51610-1 (1), OT 51613-1 (2),
OT 51805-1 (1).

Bathymetric range in PSB : 1942 to 3660m, but principally in a narrow depth range of 2300 to 2440m (94% of the specimens collected).

Distribution : Probably cosmopolitan, ranging over the deeper bathyal and upper abyssal zones, 957 to 4060m.

Ecological remarks : Despite the wide geographic range of *P. depressa*, it is common only in patches in the PSB within a narrow bathymetric range in the centre of the Seabight (Table 28). The bathymetric range of this species is similar in the Rockall Trough (Gage *et al*., 1985a). A maximum abundance of 156 individuals per hectare was found at St. 10106-1, similar to the abundance of *P. depressa* calculated from submersible transects in the northwest Atlantic (Pawson, 1982a). These submersible transects showed that *P. depressa* has a very patchy distribution and that in some localised areas its abundance can be over an order of magnitude greater (2980 individuals per hectare). Unfortunately, no data are available from the PSB on the biomass of this species.

Table 28. The abundance of *Psychropotes depressa* in epibenthic sledge and otter trawl samples, expressed as number per hectare. Samples from the main transect unless otherwise stated. n = number of specimens taken.

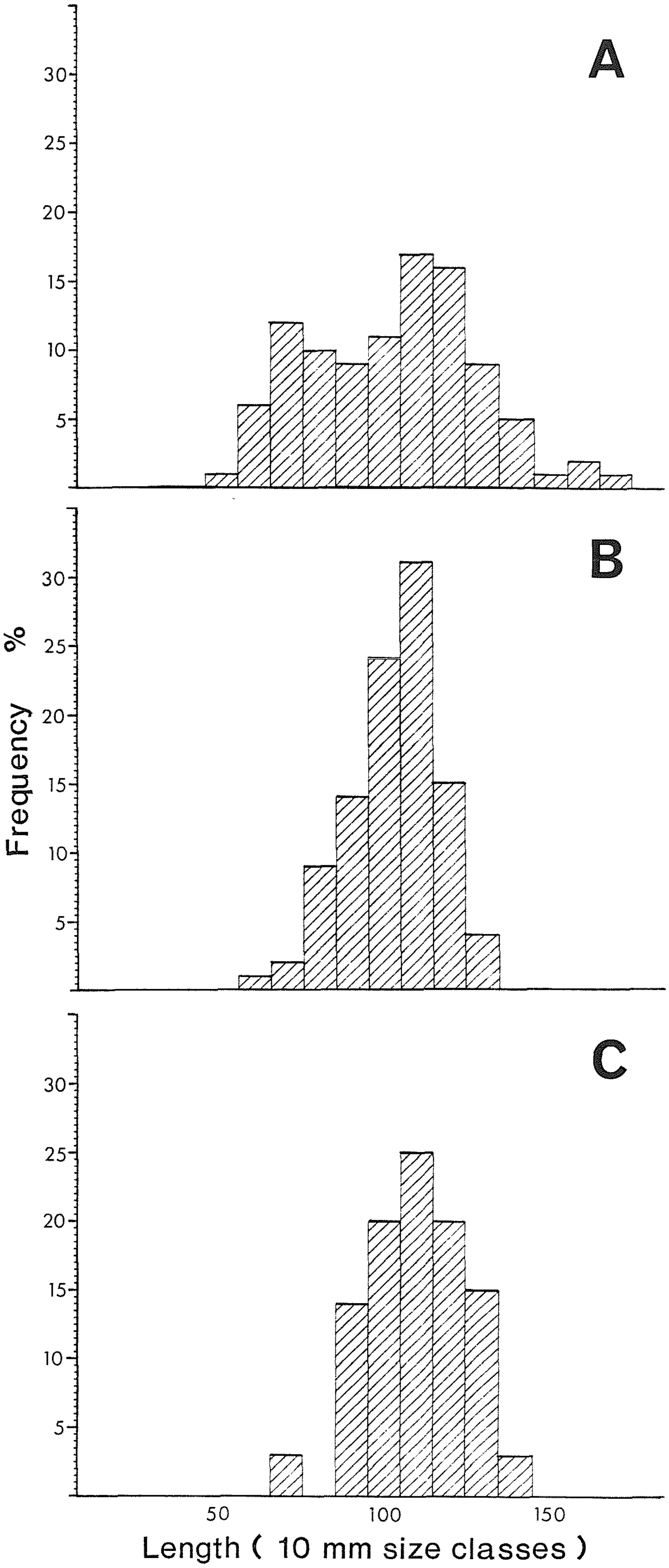
	Station	Mean Depth (m)	n	A/Posn
	Epibenthic sledge samples.			
b	BN 9753-7	1942	1	4.1
	BN 10106-1	2308	159	155.9
	BN 50613-1	2440	35	73.8
	Otter trawl samples.			
a	OT 50518-1	2078	1	0.2
	OT 51613-1	2220	2	0.2
	OT 50511-1	2420	126	19.3
	OT 51411-1	2485	1	0.1
	OT 50907-1	2975	3	0.3
	OT 51610-1	3485	1	0.1 +

a Goban Spur
b northeast PSB

+ trawl doors found tangled on recovery of net. Abundance could be greater.

Figure 36. The population size distributions of *Psychropotes depressa*. Length in 10mm size classes.

A)	BN 10106-1,	4: 9:79,	2308m,	n = 157.
B)	OT 50511-1,	4: 6:79,	2420m,	n = 126.
C)	BN 50613-1,	9: 7:79,	2440m,	n = 35.


A
B
C
Frequency %
30
25
20
15
10
5
50
100
150
Length (10 mm size classes)

The population size distributions for the three large samples of *P. depressa* are similar, showing a population dominated by adults with a mean length of 110mm (Fig. 36). Apart from these specimens, only a few other small *P. depressa*, 35 to 75mm long, were sampled in the PSB. The shallowest specimen was 7mm long (St. 9753-7). This specimen had probably only just settled on the seabed after developing in the water column, since a specimen of a similar size, 9.6mm long, was sampled in a pelagic trawl at the mouth of the PSB (St. 9756-2) at a depth of 1000 to 1500m and some 2500m above the seafloor.

This planktonic juvenile is the first record of pelagic development in *P. depressa* but its presence in a mid-water sample is not surprising. Juveniles of other psychropotids, such as *B. sordida* and *P. longicauda* have also been taken pelagically. This type of development is related to the large egg size found in psychropotids, which in *P. depressa* reaches a diameter of 1.9mm, and is a feature of those deep-sea holothurians with a wide geographic distribution (see Section 5.5).

Psychropotes longicauda Theel, 1882

OT 9638-2 (28), OT 9640-1 (7), OT 9756-3 (14),
OT 9756-5 (7), BN 9756-9 (1), BN 10114-1 (1),
OT 11116-1 (9), OT 11118-1 (3), OT 50514-1 (19),
OT 50515-1 (66), BN 50603-1 (2), OT 50711-1 (13),
OT 50811-1 (70), BN 50812-1 (4), OT 50812-2 (23),
OT 50910-1 (14), BN 51109-1 (1), OT 51214-1 (7),
BN 51216-1 (4), OT 51216-4 (10), BN 51216-5 (1),
OT 51309-1 (15), OT 51414-1 (18), BN 51414-2 (2),
OT 51608-1 (10), OT 51610-1 (3), OT 51803-1 (4),
BN 52215-1 (15), BN 52216-8 (1).

Bathymetric range in PSB/PAP : 3310 to 4832m, but principally at depths greater than 3800m. *P. longicauda* occurred in all but two samples taken deeper than 4000m.

Distribution : Cosmopolitan, 2210 to 5173m. *P. longicauda* is more common at higher latitudes, though not in the Arctic Ocean, or in tropical areas where there are large seasonal fluctuations in the supply of organic matter to the seabed, such as in the Panama Basin (Honjo, 1982). In tropical areas of the Atlantic it is replaced by *P. semperiana*. The distribution of *P. longicauda* appears to be dependent on the seasonal deposition of detritus or, at least, on the total amount of detritus that is deposited on the seabed.

Ecological remarks : *P. longicauda* is the most consistently abundant holothurian from the PAP with a maximum abundance of 43 individuals per hectare (Table 29). At most stations, however, the abundance of this species is less than 20 individuals per hectare, similar to the abundance of *P. longicauda* in the Bay of Biscay (Sibuet and Lawrence, 1981). Data from the trawl indicate a similar abundance, allowing for the inefficiency of the trawl in sampling epibenthic invertebrates. There is little variation in the abundance of *P. longicauda* throughout its depth range.

Biomass data are available for three samples only (Table 30). It was not possible to calculate the regression of DW on length since so few specimens were available for analysis. Consequently, the biomass of *P. longicauda* in the area where it was most common (St. 52215-1) is unknown. Data from a single specimen at St 51109-1 had to be used to estimate AFDW from the DW of *P. longicauda* at the other two stations. A mean AFDW biomass of 49g per hectare was found from the three stations (3950 to 4080m) which is equivalent to a calorific biomass of 1196 KJ per hectare using a calorific value of 24.26 J per mg AFDW for *P. longicauda* (Walker *et al*., 1987b). This calorific biomass is similar to that calculated for *P. longicauda* in

Table 29. The abundance (A) of *Psychropotes longicauda* in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 51109-1	3950	1	2.2	4.6
BN 50603-1	4000	2	2.6	
BN 51216-5	4035	1	1.6	3.7
BN 10114-1	4050	1	3.7	9.0
BN 9756-9	4054	1	1.6	8.0
BN 51216-1	4070	4	8.6	13.9
BN 51414-2	4080	2	3.5	6.7
BN 50812-1	4090	4		22.4
BN 52215-1	4563	15	23.0	42.9
BN 52216-8	4813	1	1.7	2.5
Otter trawl samples.				
OT 51610-1	3485	3	0.3 *	
OT 9640-1	3753	7	0.7	
OT 51214-1	3810	7	1.4	
OT 51216-4	3985	10	1.6 *	
OT 9756-5	4016	7	0.9	
OT 50514-1	4056	19	2.3	
OT 9638-2	4074	28	5.9 +	
OT 50812-2	4088	23	2.2	
OT 9756-3	4118	14	2.6	
OT 51414-1	4155	18	1.8	
OT 51309-1	4223	15	1.5	
OT 50910-1	4312	14	1.5	
OT 51608-1	4320	10	1.3	
OT 50811-1	4375	70	8.8	
OT 50515-1	4510	66	9.6	
OT 11118-1	4565	3	0.3	
OT 50711-1	4788	13	1.4	
OT 11116-1	4800	9	0.9	

+ trawl doors found tangled on recovery of net. Abundance could be greater.

* acoustic monitor lost from trawl. Precise distance travelled by trawl unknown.

the Bay of Biscay, 820 to 1900 KJ per hectare (Sibuet and Lawrence, 1981).

Table 30. The WW, DW, AFDW and calorific biomass of Psychropotes longicauda from epibenthic sledge samples, expressed as g or KJ per hectare. The proportion of the total epibenthic invertebrate biomass is expressed as a percentage in parentheses. For the number of specimens in each sample see Table 29.

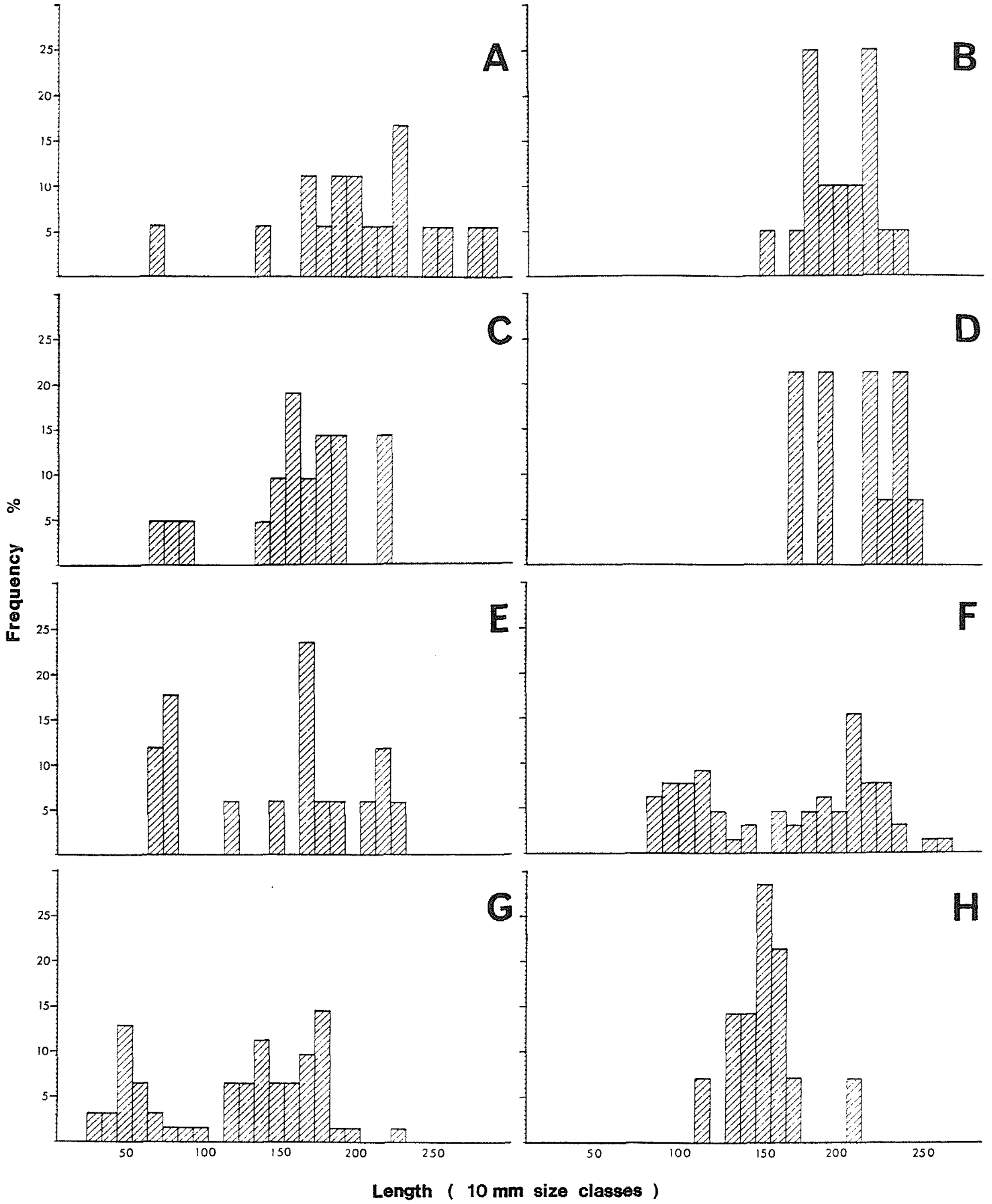
Station	Mean Depth (m)	WW	DW	AFDW	Calorific biomass
51109-1	3950	1712 (24)	102 (22)	50 (19)	1213
51216-5	4035	1397 (37)	72 (20)	35 (26)	849
51216-1	4070	1790 (28)	129 (22)	63 (28)	1528

The population size distributions for P. longicauda show that most samples are dominated by large adults with the gradual recruitment of a few small specimens (Fig. 37). Other samples not plotted in Fig. 37 show this same general structure. There is no relationship between specimen size and location or depth. Two size distributions, however, both from large samples, show a distinctly bimodal population (Stas 50515-1 and 50811-1). These appear to arise from patchy recruitment, for at St. 50515-1 a number of other species, Pseudostichopus villosus, Deima validum and Oneirophanta mutabilis, also show a preponderance of small juvenile specimens.

Data on gametogenesis in P. longicauda (Tyler and Billett, in press) show that this species reproduces continuously, releasing a slow trickle of eggs. As few as 8 eggs in the ovary may approach full development at any one time. The eggs of P. longicauda are the largest known for any holothurian, 4.4mm in diameter (Hansen, 1975), and probably lead to direct development without a larval stage. However, this development takes place pelagically

Figure 37. The population size distributions of *Psychropotes longicauda*. Length in 10mm size classes.

A) OT 50514-1, 5: 6:79, 4056m, n = 18.
B) OT 9638-2, 9:11:77, 4073m, n = 20.
C) OT 50812-2, 3: 8:80, 4090m, n = 21.
D) OT 50514-1, 5: 6:79, 4155m, n = 17.
E) OT 50910-1, 10:11:80, 4312m, n = 13.
F) OT 50811-1, 2: 8:80, 4375m, n = 65.
G) OT 50515-1, 6: 6:79, 4510m, n = 62.
H) BN 52215-1, 22: 6:85, 4563m, n = 14.


A
B
C
D
E
F
G
H
25
20
15
10
5
Frequency %
50
100
150
200
250
Length (10 mm size classes)

and not on the seabed.

Several juvenile P. longicauda have also been sampled in pelagic nets. Belyaev and Vinogradova (1969, syn. Nectothuria translucida) reported a specimen (35 mm long, excluding the large unpaired dorsal appendage) sampled between 4940 and 5930m in the Kurile-Kamchatka Trench, some 2000 to 3000m above the seabed. A further 8 specimens have now been found in IOS pelagic trawls in the northeast Atlantic (Table 31). The specimens ranged between 13 and 23mm in length and although one specimen was collected close to the seabed, the rest were sampled over 600m above the seafloor. The size of the largest juveniles sampled by the pelagic trawls corresponds to the smallest size of P. longicauda found in benthic trawls.

Table 31. Juvenile Psychropotes longicauda sampled by pelagic trawls in the northeast Atlantic. For station details see Billett et al., 1985).

Station	Depth m	Height above the seabed	Number of specimens
8509-27	3500 - 4000	1000 - 1500	1
11121- 1	3470 - 3580	510 - 620	1
11121- 2	3470 - 3565	525 - 620	1
11121- 8	3490 - 3530	560 - 600	2
11121- 9	3485 - 3580	510 - 605	1
11121-18	3480 - 3520	570 - 610	1
11121-21	3988 - 4008	17 - 37	1

Five of the trawls cited in Table 31 came from a series of 15 trawls investigating the variability in abundance of abysso-pelagic fauna. Using the total volume of water sampled by these trawls it is possible to calculate an abundance of about 1 individual per 100,000 m^3. At first, this abundance appears to be particularly low but when one considers the vast space of the deep sea it is apparent that over any one square kilometre of seabed some 500 juvenile *P. longicauda* may be developing.

The length of time the juveniles remain in the plankton is unknown, but all the psychropotids that produce large eggs have exceptionally wide geographic distributions and are often cosmopolitan. In the deep sea, where food is often limiting, the production of large eggs that lead to direct development is a distinct advantage but restricts the dispersal of a species. This has been overcome by producing large yolky eggs which provide not only buoyancy but also an independent food source for development in the abyssopelagic and bathypelagic zones. The guts of these juveniles are always empty and there is no evidence that they feed in the plankton, although some nutrition may be derived from dissolved organics. This type of development is discussed further in Section 5.5.

Deming and Colwell (1982) estimated that each specimen of *P. longicauda* (syn. *P. buglossa*) processes about 105g sediment WW per day. Assuming that the water content of the sediment is about 55% (Khripounoff, 1979) this amounts to a DW of 47.25g. Using a mean abundance of 10 individuals per hectare, then a feeding rate for *P. longicauda* of 17.25g DW sediment per square metre per year can be calculated. This is a similar rate to that estimated for *S. tremulus* from a depth of 500m even though this species is 10 times more abundant than *P. longicauda*. These data suggest that either abyssal holothurians process the sediment more rapidly than species from shallower water,or that the feeding rate of *P. longicauda* has been overestimated, or that the feeding rate of *S. tremulus* has been underestimated.

Psychropotes semperiana Theel, 1882

OT 50515-1 (2).

Bathymetric range on PAP : 4505 to 4515m.

Distribution : Generally the sub-tropical and tropical areas of the Atlantic and Indian Oceans. 3465 to 5600m (Hansen, 1975). The PAP record is the most northerly for this species in the North Atlantic. However, it is clear that *P. semperiana* is not an abundant species on the PAP.

Ecological remarks : Although *P. semperiana* (Fig. 27A, page 159) occurred in the same sample as many juvenile *Pseudostichopus villosus*, *Oneirophanta mutabilis*, *Deima validum* and *Psychropotes longicauda*, both specimens were adults, 85 and 95mm long. Their presence on the PAP, therefore, is not the result of recent recruitment of juveniles from the plankton, but demonstrates that *P. semperiana* is able to survive to adulthood outside its preferred geographic range.

Hansen (1975) noted a maximum egg diameter of only 0.8mm for *P. semperiana*, but it is evident from samples taken from the Madeira Abyssal Plain by IOS that eggs reach a diameter of at least 3.5mm and are therefore comparable in size to those of other species of *Psychropotes*. As with *P. longicauda*, pelagic, direct development is indicated although no pelagic juveniles have been found. With pelagic development the presence of *P. semperiana* as far north as the PAP is not unexpected.

Family Pelagothuriidae

Enypniastes diaphana (Gilchrist, 1920)

RMT 9756-10 (1).

Bathymetric range on PAP : 3000 to 3500m (in pelagic trawl 500 to 1000m above the seabed).

Distribution : Eastern Atlantic from the Cape of Good Hope (Gilchrist, 1920) to the PAP. The species may occur also in the northwest Atlantic if it proves to be synonymous with a larger form found at shallower depths, E. eximia Theel, 1882 (Pawson, 1976, 1982a). E. diaphana has a wide bathymetric range, 995 to 4980m, and on one occasion has been sampled at the surface (syn. Pelagothuria bouvieri Herouard, 1923).

Ecological remarks : E. diaphana is a benthopelagic holothurian that floats in nearbed currents close to the seabed, descending to the sediment surface to feed. One small specimen, 10mm long, was sampled at the mouth of the PSB, but many more specimens, 4 to 50mm long, have been caught in IOS pelagic trawls throughout the northeast Atlantic (Table 32).

The highest incidence of E. diaphana in pelagic trawls and its greatest abundance occur close to the seabed. Abundance was calculated as described in Section 2.2. from both pelagic trawls and wide-area survey photography (Table 32). The highest abundance of E. diaphana in a mid-oceanic area came from survey-camera data from the Madeira Abyssal Plain (up to 62 individuals per 100,000m^3). A lower abundance was found in similar data from the Azores-Biscay Rise; up to 7 individuals per 100,000m^3. A still lower abundance was calculated from pelagic trawls in the

Table 32. The sample details and abundance (A), expressed as number per 100,000 m^3, of *Enypniastes diaphana* in pelagic trawls and photographed close to or on the seabed in the northeast Atlantic. The abundance in pelagic trawls has been calculated only where replicate hauls have been made at the same depth and locality. n = number of specimens taken.

Station	Range Depth (m)	Height above seabed m	n	A
RMT 1 pelagic trawl.				
9131-19	3500 - 3760	250 - 500	1	
9541-19	3970 - 4040	0 - 20	1	6
9541-30	995 - 1500	2500 - 3000	1	9
RMT 8 pelagic trawl.				
8509-27	3500 - 4000	100 - 1500	2	
9541-18	3945 - 4020	0 - 20	8	4
9541-19	3970 - 4040	0 - 20	19	11
9541-24	3520 - 3490	100 - 500	2	
9541-30	995 - 1500	2500 - 3000	4	3
9541-31	1515 - 2000	2000 - 2500	1	
9756-10	3000 - 3500	500 - 1000	1	
9801-89	3500 - 3710	1800 - 2000	1	
9801-90	3300 - 3500	2000 - 2200	1	
9801-92	Net failed to close at depth		1	
10379-36	2840 - 2980	0 - 175	1	2
10379-37	2960 - 2985	0 - 55	3	7
10651- 2	4970 - 4980	80 - 100	1	
11121-10	3485 - 3515	575 - 605	1	
11121-20	4006 - 4021	4 - 19	3	5
11121-21	3988 - 4008	17 - 37	1	2
11121-23	4004 - 4021	4 - 21	3	4
11261-65	5410 - 5430	1 - 31	3	
11262- 3	2310 - 2700	2740 - 313	1	
11262-25	5340 - 5375	51 - 0	1	
11262-27	5415 - 5430	10 - 25	1	
Photosledge.				
10890- 2	2140 - 2200		157	100000
Wide-area survey camera.				
10656	3737	0 - 17	4	4
10664	3720	0 - 17	20	7
10669	3700	0 - 17	5	2
10678	5422	0 - 17	19	62
10693	5433	0 - 17	49	22

same area but this is not surprising for the RMT net does not sample adequately the 3 metres or so closest to the seabed, the preferred habitat for many Enypniastes (Pawson, 1976). Only one E. diaphana was sampled in 15 trawls made some 600m above the seabed on the Azores-Biscay Rise, but 7 specimens were sampled in 3 out of 6 trawls made within 50m of the seabed in the same area, demonstrating that E. diaphana is more common close to the seabed.

The greatest abundance of E. diaphana is known from an epibenthic sledge trawl from the continental slope off northwest Africa ("Discovery" St. 10890-2). A photo-transect over a distance of about 1600m was undertaken using the epibenthic sledge camera system. From 274 frames, each covering an area of 2.2 m^2 , a total of 157 E. diaphana were counted, producing an estimated abundance of one individual per m^2. Despite this high abundance another haul made at the same site (St. 10890-1) failed to collect any E. diaphana, indicating either a highly patchy distribution for this species, or that feeding by E. diaphana, and hence its presence on the seabed, is dependent on (?tidal) changes in current velocity.

These observations, together with those made from submersibles (Pawson, 1976, 1982a) and deep-sea photography (Ohta, 1983, 1985), indicate that Enypniastes generally lives close to the seabed However, a few specimens have have been taken in the open ocean as much as 3000m above the seabed (Table 32). These specimens are generally small, 5 to 10mm long. Ohshima (1915) found that E. eximia from the Pacific Ocean produced eggs up to 3.5mm in diameter. The maximum egg diameter in the present material is also 3.5mm, although the majority of eggs in the ovary are much smaller. Therefore, the smallest specimens taken in the RMT net, 4mm long, apparently represent recently metamorphosed individuals. This suggests that in most cases the presence of _E. diaphana_ high above the seafloor results from its reproductive strategy, in which either the eggs or the juveniles undertake an upward ontogenetic migration. Pelagic direct development is indicated, as found in psychropotid species that produce eggs of a similar size.

Adult _E. diaphana_ may also undertake migrations up the water column although these journeys appear to be rare. One large specimen, 40mm long, was collected some 2100m above the seabed (St. 9801-90), while another has been reported at the sea surface in an area overlying the mid-Atlantic Ridge (Herouard, 1923). In general, however, large specimens are more common within 500m of the seabed.

These apparent migrations and the production of buoyant eggs that rise up through the water column are important for they represent two processes by which organic matter is transported up the water column in the open ocean. Many micro-nektonic animals in the upper 1000m of the water column undertake large diurnal vertical migrations but below this depth the pathways of upward transport are less well defined. Some abyssal fish produce buoyant eggs, often enmeshed in a large mucous sheet, which rise to the surface of the sea, where they complete their development (Merrett, 1978; Bertelsen, 1980). Other fish release eggs that sink to the seabed and the resulting larvae then rise back up to the adult's normal habitat (Robison and Lancraft, 1984). Some species of abyssal gastropods produce planktotrophic larvae that rise to the surface waters (Bouchet and Waren, 1979), while the small egg size of some deep-sea asteroids suggests that they also produce feeding larvae that probably migrate to surface waters (Tyler _et al._, 1982).

Microscopical analysis of the gut contents of specimens from St. 9541 shows that *E. diaphana* does indeed feed on surficial sediment. The contents include foraminiferans, coccoliths and diatoms and sand grains. The intestines of specimens greater than 175m above the seabed are completely empty, suggesting that this species does not feed on suspended material in the water column.

Family Elpidiidae

Peniagone diaphana (Theel, 1882)

OT 9638-2 (4), OT 9640-1 (4), BN 9753-7 (1),
OT 9756-3 (7), OT 9756-5 (8), BN 9756-9 (1),
RMT 9756-11 (1), BN 10115-1 (1), OT 11116-1 (3),
OT 11118-1 (3), OT 50511-1 (1), OT 50515-1 (339),
BN 50603-1 (12), RMT 50603-2 (39), RMT 50603-3 (12),
BN 50604-1 (3), RMT 50605-2 (1), OT 50711-1 (6),
OT 50811-1 (5), BN 50812-1 (2), OT 50812-2 (11),
OT 50813-1 (2), OT 50910-1 (5), BN 51109-1 (1),
OT 51216-4 (1), OT 51309-1 (1), OT 51310-1 (1),
OT 51414-1 (1), BN 51414-2 (1), OT 51608-1 (23),
OT 51803-1 (2), BN 52215-1 (6), BN 52216-8 (9).

Bathymetric range in PSB/PAP : 1942 to 4832m, but most common at depths greater than 3500m (i.e. beyond the base of the continental slope.)

Distribution : Described originally from a specimen taken in the Australian Bight by the "Challenger" Expedition (Theel, 1882), several more specimens were sampled later in the northeast Atlantic (Herouard, 1902, 1923). More recently, specimens have been observed from submersibles in the western Atlantic (Pawson, 1976) and the north-eastern Pacific (Barnes *et al*., 1976). The wide separation of these records is probably the result of difficulties in sampling benthopelagic fauna in the deep sea. This species has a cosmopolitan distribution, from about 1900 to 5600m.

Ecological remarks : *P. diaphana* is a benthopelagic holothurian that swims close to the seabed and descends to the seafloor to feed on the surficial sediment. The epibenthic sledge and otter trawl are unsuitable for estimating the abundance of pelagic holothurians although the trawl can give some indication of their relative abundance between samples. However, the IOS midwater trawl (RMT) has been adapted to fish within a few metres of the seabed (see Section 2.2) and have been used to provide reliable data on the abundance of swimming holothurians on the PAP and elsewhere in the northeast Atlantic.

The samples show a greater incidence and a greater abundance of *P. diaphana* in trawls taken close to the seabed (Table 33). *P. diaphana* has been found up to 1500m above the seabed (Table 33) but still within the abyssopelagic zone. It has not been recorded from depths shallower than 1900m, unlike *Enypniastes diaphana*, and at these bathyal depths is always found close to the seabed.

The greatest abundance of *P. diaphana* was found on the PAP (St. 50603-2, 101 individuals per 100,000 m^3) although many of these specimens were juveniles less than 10mm long. Excluding these specimens the abundance falls to 39 individuals in an equivalent volume of water. This is a similar abundance to that found in the area of the Azores-Biscay Rise (Stas 11121-20 to 25) (Table 33). An average abundance of 19 individuals per 100,000 m^3 was calculated from these 5 samples taken within 40 metres of the seabed, which compares with an abundance of only 1 individual in the equivalent volume in samples taken 600m above the seabed in the same area. The distribution of *P. diaphana* has been observed from submersibles to be patchy in the northeast Pacific (Barnes *et al*., 1976). Such patchiness is not readily apparent from the PAP midwater trawl data, but the presence of 339 specimens in one otter trawl (St.

50515-1) indicates that the distribution of *P. diaphana* can be patchy in this area too. The area sampled at St. 50515 is not associated with any particular topographic features but the sample is unique in other respects, for it also contained many juveniles of a number of benthic holothurians (see Section 5.5).

Table 33. The sample details and abundance (A), expressed as number per 100,000 m^3, of *Peniagone diaphana* in pelagic trawls in the northeast Atlantic. The abundance has been calculated only where replicate hauls have been made at the same depth and in the same area. n = number of specimens taken.

Station	Range Depth (m)	Height above seabed m	n	A
RMT 1 pelagic trawl.				
8509-43	1500 - 4560	>450	1	
9131-18	3760 - 3920	100 - 250	1	9
RMT 8 pelagic trawl.				
8509-27	3500 - 4000	1000 - 1500	1	
9131-18	3760 - 3920	100 - 250	6	5
9541-22	3740 - 3870	20 - 100	1	
9756-11	4000 - 4012	5 - 20	1	
9801-91	4300 - 4520	1000 - 1200	1	
50603- 2	3720 - 3940	60 - 260	39	101
50603- 3	3700 - 3900	50 - 250	12	33
50605- 2	2640 - 2750	5 - 25	1	
11121- 8	3490 - 3530	560 - 600	1	2
11121- 9	3485 - 3580	510 - 605	1	2
11121-11	3480 - 3515	575 - 610	1	1
11121-17	3490 - 3520	570 - 600	1	2
11121-18	3480 - 3520	570 - 610	6	9
11121-20	4006 - 4021	4 - 19	7	12
11121-21	3988 - 4008	17 - 37	11	20
11121-22	3976 - 3991	34 - 39	16	33
11121-23	4004 - 4021	4 - 21	18	26
11121-24	3991 - 4007	18 - 34	4	6
11121-25	3941 - 3991	34 - 84	1	-

In many hauls the abundance of *P. diaphana* is too low to allow a detailed analysis of population structure. However, data from a few RMT hauls, 2 from the PAP and another 4 from the Azores-Biscay Rise, show that small specimens usually dominate the population (Table 34). Patchiness in population structure is indicated by the two samples from the PAP, Stas 50603-2 and 3, for while specimens less than 20mm long dominate one sample, they are absent from the other. Fifteen of the 39 specimens sampled at St. 50603-2 were less than 4.5mm long, the nominal mesh size of the RMT8 net (see Section 2.2). As a result, the abundance of small specimens may have been underestimated. However, data from a fine mesh net (RMT1, 320µm mesh) taken concurrently with the RMT8 sample, indicates that the latter net did not miss a large population of minute *P. diaphana*.

Table 34. *Peniagone diaphana*. Length frequency distributions *in 10mm size classes* where 10 = 1 to 10mm, 20 = 11 to 20mm, etc. Samples from midwater trawls. See Table 33 for details of depths of samples. Number in each size class given.

	Size classes (mm)										
Station	10	20	30	40	50	60	70	80	90	100	110
50603- 2	22	3	4	2	1	3			1		
50603- 3			3	2	2	3		1			1
11121-20	4	2							1		
11121-21	3	5	1	1							
11121-22	9	4	1		1		1				
11121-23	7	8	1				1				

P. diaphana produces eggs up to 300µm in diameter indicative of lecithotrophic larval development with a short larval phase (Tyler *et al*., 1985b). This type of development has the advantage of producing the greatest number of eggs without the need for a feeding larval stage.

Planktotrophic development would necessitate a hazardous migration to the surface waters and back. The short larval stage would lead to limited dispersal, but this is scarcely a problem for a benthopelagic species.

The guts of most specimens observed by Barnes *et al.* (1976) from submersibles were distended with material that appeared to be of sedimentary origin. However, because *P. diaphana* was never seen to be in contact with the sediment, the authors suggested that this benthopelagic holothurian fed on suspended detritus. The guts of specimens from the PAP, and those collected from off the coast of northwest Africa, were examined microscopically and were found to contain surficial sediment including coccoliths, foraminiferans and diatoms. The stomach contents were almost identical to phytodetrital material collected from the surficial layer lying on the seabed (Billett *et al.*, 1983). In most specimens sampled by pelagic nets the anterior part of the gut was devoid of sediment, while the hind gut was often full. In contrast, the anterior gut was full and the hind gut empty in specimens collected on or close to the seabed in benthic trawls. These data suggest that *P. diaphana*, like *Enypniastes*, feeds at the sediment surface and in the PAP *P. diaphana* has been photographed in a feeding posture on the seabed. The rapid feeding rate of *Enypniastes* witnessed by Pawson (1982a) led him to believe that the holothurian spent only a short time on the seabed. *P. diaphana* seems to behave in a similar way.

Peniagone azorica von Marenzeller, 1893

OT 50511-1 (1), OT 50906-1 (5), BN 51110-4 (1),
OT 51411-1 (3), BN 51412-1 (1), OT 51611-1 (1).

Bathymetric range in PSB : 2405 to 2800m.

Distribution : *P. azorica* has a rather curious distribution. It is present in the northeast Atlantic between 1385 and 4020m but has been found also in the Kermadec Trench between 2640 and 8210m (Hansen, 1975). It has been photographed in other deep-sea trenches (Lemche *et al*., 1976) and possibly within the Romanche Trench in the mid-Atlantic (Heezen *et al*., 1964). This species is common from 2000 to 3000m in the northeast Atlantic (Herouard, 1923; Le Danois, 1948; Gage *et al*., 1985a; Harvey *et al*., in press).

Ecological remarks : The most notable feature of *P. azorica* in the PSB is its rarity. *P. azorica* is the most abundant holothurian between 2000 and 3000m in the Rockall Trough (Gage *et al*., 1985a) and is also common further south (Herouard, 1923) yet only 12 specimens have been collected at comparable depths in the PSB. The reasons for the scarcity of *P. azorica* is not clear. The area in the centre of the PSB, between 2200 and 3400m, is notable for its lack of deposit feeders apart from *Psychropotes depressa* between 2300 and 2440m and the occasional enigmatic appearance of herd of *Kolga hyalina*.

Amperima rosea (R. Perrier, 1896)

OT 9638-2 (14), OT 9756-3 (8), OT 9756-5 (1),
BN 10114-1 (1), OT 50515-1 (8), OT 50711-1 (3),
OT 50811-1 (9), OT 50910-1 (2).

Bathymetric range on PAP : 4012 to 4795m.

Distribution : Northeast Atlantic, 4012 to 5005m (Perrier, 1902; Herouard, 1923; Hansen, 1975; present records).

Ecological remarks : An abyssal species that is not particularly common on the PAP. It occurred in about half of the otter trawls taken deeper than 4000m. One specimen from the PAP had a tanaidacean, *Exspina typica* (Thurston *et al*., 1987) in its coelomic cavity. This association is not the result of a chance occurrence for *E. typica* has been reported also from other holothurians (Thurston *et al*., 1987).

Kolga hyalina Danielssen and Koren, 1879.

BN 9754-3 (1), BN 9756-9 (14639), BN 9756-14 (21527),
BN 10113-1 (6512), BN 10114-1 (4950), BN 10115-1 (50),
BN 50603-1 (4049), BN 50604-1 (152), BN 50605-1 (6320),
BN 50823-1 (568), BN 50913-1 (3222), BN 50914-1 (59),
RMT 52403-21-23 (204).

Bathymetric range in PSB/PAP : 1484 to 4815m.

Distribution : *K. hyalina* is known principally from the Arctic Ocean and the Norwegian Sea, but it has also been collected in the northwest Atlantic, the Rockall Trough, off Japan and in the Antarctic Ocean. This monotypic genus has a cosmopolitan distribution and a wide bathymetric range, 1484 to 4850m (Billett and Hansen, 1982).

Ecological remarks : *K. hyalina* is an enigmatic holothurian with many peculiar features to its biology. At some stations it is by far the most abundant species encountered in the PSB, but in the vast majority of samples it is absent. In many cases these latter samples have come from areas where *K. hyalina* has been abundant at one time.

The abundance of *K. hyalina* has been calculated from both catch and photographic data (Table 35), as detailed in Section 2.2., page 63. Unfortunately, the odometer failed to work at Stas 50603-1 and 50605-1, but two particularly long hauls at these stations did result in a long series of photographs from which an accurate estimate of the abundance was obtained. The precision of the value was further enhanced by the small variation in the abundance of *K. hyalina* between photographs. At stations where *K. hyalina* was aggregated, the standard error reflects, in part, the effect of the spatial pattern on the estimate of mean abundance. The influence of spatial pattern was particularly important at St. 10114-1 where the photographic mean abundance could have risen to 10 individuals per m^2 had the two aggregations photographed fallen within the analysed area.

Table 35. The abundance of *Kolga hyalina* in epibenthic sledge samples, expressed as number per hectare. n = number of specimens taken. Standard error of mean photographic abundance for each station is given in parentheses. For the number of specimens in each sample see station details on page 261.

Station	Mean Depth (m)	A/Posn	A/Odo	A/Photo	S.E.
a BN 9754-3	1484	7			
BN 10113-1	2758	70972	174118	93231	20523
BN 50914-1	2800			30723	2718
BN 50823-1	2830		9189		
BN 50605-1	2875	22657		119209	3739
BN 50913-1	3020	17047		82336	8007
BN 50604-1	3520	601			
BN 9756-14	3689	70658	501701	500200	169814

The greatest abundance of *K. hyalina* occurred at two stations sampled close to the base of the continental slope in the mouth of the PSB in April 1978 (Stas 9756-9 and 14). Abundances of 33.8 and 50.0 individuals per m^2 respectively were calculated from the photographic data (Table 35). The photographs showed also that the holothurians were not distributed evenly across the seabed but were aggregated, in some cases in groups of several hundred specimens (see Section 5.4). *K. hyalina* was found in the same area again in July and September 1979 (Stas 50603-1 and 10114-1) but its abundance was about one tenth of that found previously. During the same cruises another area lying above the steep terrain at the mouth of the PSB (ca. 2800m) was explored and another large population of *Kolga* was found (more than 10 individuals per m^2). Further sampling in August and November 1980 at these two sites failed to locate *K. hyalina* at the deeper station while its abundance at depths of about 2800m was much reduced. Sampling since 1980 in both these areas has failed to find any trace of the species. It appears, therefore, that the presence of *Kolga* in any one area is ephemeral and that following mass recruitment the population declines. This is substantiated by other observations in the PSB and in the Rockall Trough detailed below.

First, in July 1982 during an epibenthic sledge phototransect between 1505 and 1535m on the Porcupine Bank (St. 51619-1) many holothurians that appeared to be *Kolga* were encountered roaming across the seabed. Unfortunately, no net was attached to the sledge during this haul and so the identification could not be confirmed. This area was sampled subsequently in April 1983 but no trace of *Kolga*, or any holothurian that could be mistaken for it, could be found. *K. hyalina* has never been collected in any of the samples taken at upper slope depths in the PSB except for a single individual in the northeast of the PSB from a depth of 1484m.

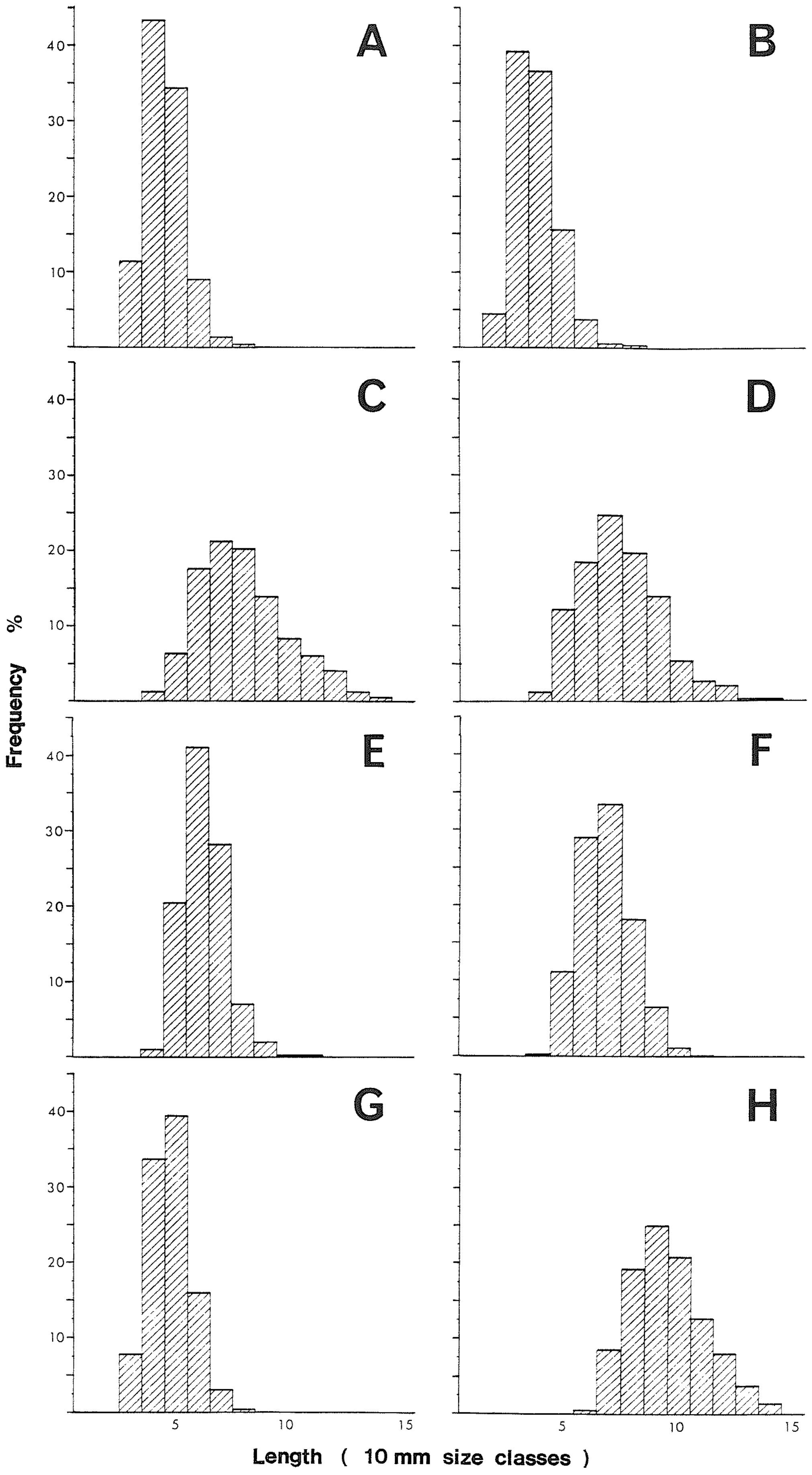
Second, in the summer of 1984 a time-lapse camera system, "Bathysnap" (Lampitt and Burnham, 1983), was deployed at a depth of 2025m in the centre of the PSB. This site has been sampled many times since 1978 but *K. hyalina* has never been collected. However, twice during a 123 day deployment of the camera system an aggregation of small holothurians, believed to be *K. hyalina*, passed over the area of seabed being photographed (ca. 2 square metres) (Dr. R.S. Lampitt, personal communication). The time interval between photographs was 8 and a half hours and in both instances the aggregation passed through the field of view within 17 hours. All the holothurians were travelling in the same direction and left behind numerous faecal casts. The abundance of *K. hyalina* in one of these aggregations was about 200 individuals per m^2.

Third, at a site in the Rockall Trough (ca. 2900) sampled repeatedly by the Scottish Marine Biological Association since 1975 (Gage *et al*., 1980), *K. hyalina* has been collected just once (May 1980) even though other samples were taken in the same year at this site (Gage *et al*., 1985a). The authors also noted that the specimens were all small and of a similar size (4 to 5mm long).

Precisely the same population structure occurs in the PSB, with size distributions that are unimodal and narrow (Fig. 38). In April 1978 the specimens of *K. hyalina* ranged in length between 2 and 9 mm after preservation, although the photographs indicate that the animals were slightly larger *in vivo*. Smaller specimens occurred at St. 9756-14 (mean length 4.3mm) than at St. 9756-9 (mean length 5.0mm). The specimens collected in July 1979 were longer, ranging between 4 and 15mm with a mean length of

Figure 38. The population size distributions of *Kolga hyalina* from the Porcupine Seabight. Length in 1mm size classes.

A) BN 9756- 9, 13: 4:78, 4054m, n = 14623.
B) BN 9756-14, 15: 3:78, 3688m, n = 21522.
C) BN 50603- 1, 2: 6:79, 4000m, n = 4024.
D) BN 50605- 1, 5: 6:79, 2875m, n = 6320.
E) BN 10114- 1, 10: 9:79, 4050m, n = 4923.
F) BN 10113- 1, 10: 9:79, 2757m, n = 6419.
G) BN 50913- 1, 12:11:80, 3020m, n = 59.
H) BN 50823- 1, 8: 8:80, 2830m, n = 212.


A
B
C
D
E
F
G
H
40
30
20
10
Frequency %
5
10
15
Length (10 mm size classes)

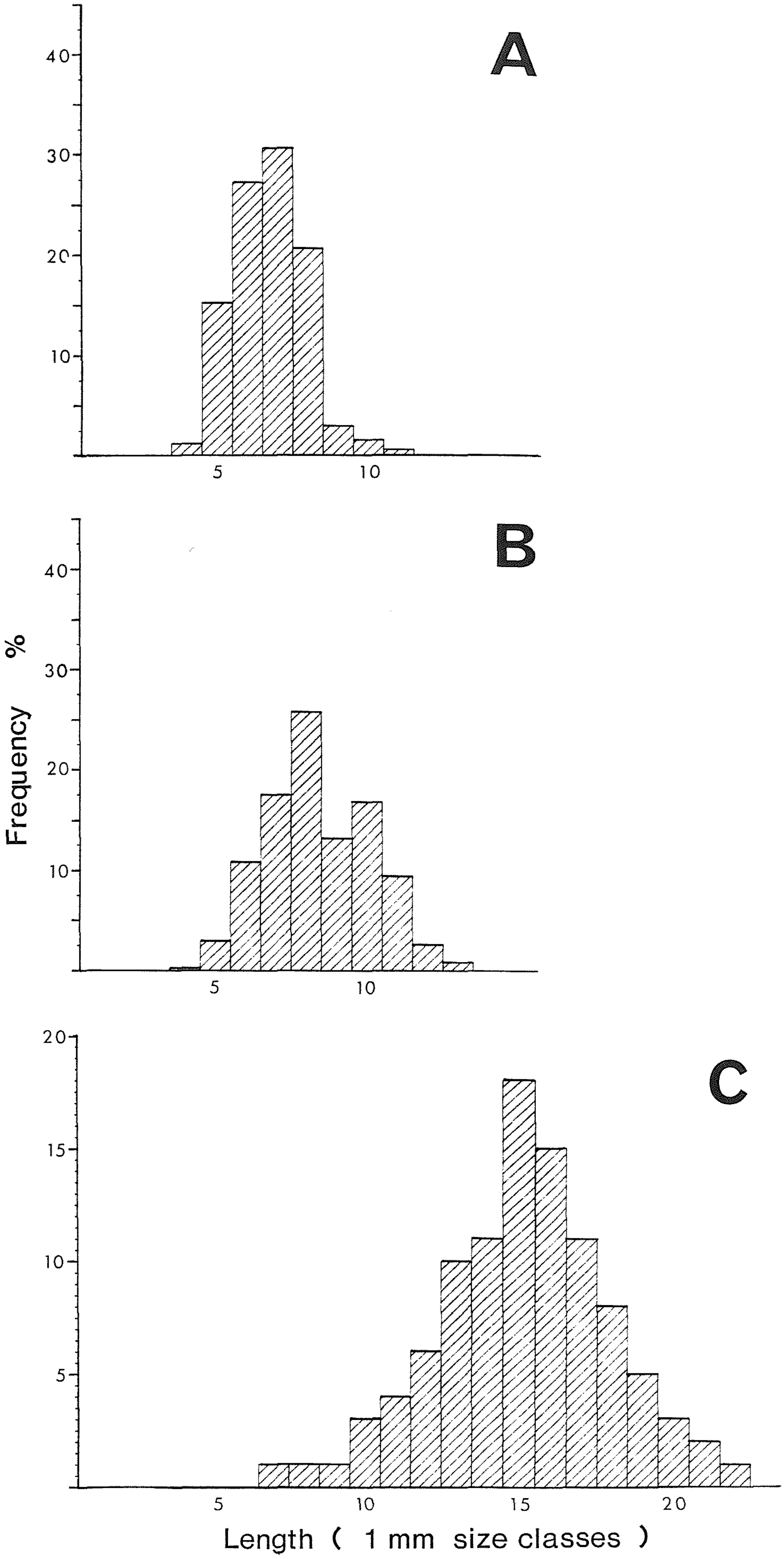
8.7mm at St. 50603-1 and 8.1mm at St. 50605-1. The two catches were in poor condition, however, probably the result of the sieving technique, leading to a long tail in the population size distribution and hence an overestimation of the mean length. No doubt the samples should have resembled the narrower distributions derived from samples taken in September 1979 which were in excellent condition. The length of K. hyalina at the latter stations varied between 4 and 12mm with a mean of 7.5mm and 7.0mm at Stas 10113-1 and 10114-1 respectively. The few specimens taken at Stas 50604-1 and 10115-1 were of a similar size.

The following year (August 1980) a further increase in mean size was noted at St. 50823-1 (mean length 9.5mm). Assuming that the same population has been sampled over the period of 1978 to 1980 then slow growth rates of this deep-sea holothurian are indicated. However, when the same area was sampled again in November 1980 a mean length of only 4.7mm was found. This, coupled with the more recent evidence of the fickle appearance of K. hyalina cited above, means that it is by no means certain that the same population was sampled in the same area in succeeding years.

Similar unimodal, narrow size distributions have been found in populations of K. hyalina from other localities. Two samples from the mouth of the Rockall Trough (Fig. 39) show populations of a similar size to those sampled in August 1980. Hansen (in Billett and Hansen, 1982) found larger specimens in material collected by the "Ingolf" and "Godthaab" Expeditions but still with a unimodal population structure. One population from Baffin Bay was made up solely of large specimens, with a mean length of 37.2mm, and only a few specimens were shorter than 27mm. In contrast, few specimens longer than 27mm, and none

Figure 39. The population size distributions of *Kolga hyalina* from the Rockall Trough and the Porcupine Abyssal Plain. Length in 1mm size classes.

A) "Discovery" St. 7711-62, 28: 5:71, 2725m, n = 22065.
B) "Discovery" St. 7711-85, 1: 6:71, 2639m, n = 992.
C) BN 52403-21, 8:12:86, 4815m, n = 186.


A
40
30
20
10
5
10
B
Frequency %
40
30
20
10
5
10
C
20
15
10
5
5
10
15
20
Length (1 mm size classes)

greater than 30mm, were found at the stations sampled by the "Ingolf" Expedition. *K. hyalina* was abundant at three of these stations sampled within about 100 miles of eachother in the Norwegian Sea. The mean length of the holothurians at two of these stations was about 17mm and at the third about 13mm. The difference in size between the "Ingolf" and "Godthaab" material is unlikely to be the result of geographic location, as specimens up to 50mm long were taken in the Norwegian Sea by the Norwegian North-Atlantic Expedition (Danielssen and Koren, 1882).

A recent sample from the PAP (St. 52403-21-23) contained specimens with a mean length of 15.1mm (Fig. 39), similar in size to those *Kolga* taken by the "Ingolf" Expedition and demonstrating that the small size of many PSB *K. hyalina* is also not the result of geographic location. This sample, although taken by a midwater trawl, came from the seabed when the trawl inadvertently struck the bottom in atrocious weather conditions.

The profusion of small, similarly sized *K. hyalina* over a wide area of the Porcupine Seabight is indicative of a highly synchronized reproductive event. Although no annual recruitment is evident in the population size distributions (Figs 38,39) it is still possible that *K. hyalina* breeds seasonally like some other deep-sea echinoderms (Tyler *et al.*, 1982). To determine whether a seasonal reproductive cycle occurs in *Kolga*, gonads were examined from specimens collected from six different calendar months of the year between April and December, albeit over an eight year period. Ovaries were cleared in lactic acid and the diameters of the oocytes were measured. In addition, about 20 specimens from each sampling period were embedded in paraffin wax, sectioned at 7µm and stained with Mayers haemalum and eosin to determine the general histology and to examine the maturity of the testes.

The histological sections showed that even in the smallest specimens collected, 3 to 4mm long, the gonad was developing, indicating that K. hyalina matures at a very early stage. Mature testes were found in both summer and winter samples. A maximum egg size of 240µm was measured from a specimen collected in August 1980, but in most specimens the eggs did not exceed 180µm and the vast majority were no larger than 80µm irrespective of the sampling date. In small specimens, sampled in both April 1978 and November 1980, 70 to 90% of the oocytes were 20 to 40µm in diameter, and only 2% were greater than 70µm (max. 110um). Oocytes of a similar size dominated in specimens collected in July 1979 but a greater proportion of larger eggs were present (ca. 10% were greater than 70µm in diameter, max. 180µm). Similar egg size distributions occurred in specimens sampled in July 1979, although 70 to 80% of the oocytes were 30 to 60µm in diameter.

Larger K. hyalina sampled in August 1980 and December 1986 showed a greater spread of oocyte sizes, but there was not a large number of eggs proceeding to maturity at the same time. Several specimens collected in December 1986 appeared to be spent, but otherwise there was little evidence of seasonality in oogenesis or spermatogenesis. The evidence suggests that K. hyalina reproduces periodically but not with an annual cycle.

The maximum egg size of about 240µm is similar to that in other elpidiid holothurians and suggests lecithotrophic larval development. However, it is by no means certain that all the eggs attain this size before spawning and some form of feeding larva could be formed. In this particular case the initial high abundance of K. hyalina within a circumscribed area of the PSB suggests that development would be demersal, feeding on detrital particles rather than in surface waters.

With the apparent irregular periodicity in reproduction, the broad depth range, the wide geographic distribution, and, in particular, the development of the gonad in even the smallest of the specimens examined (3mm long), it is clear that *K. hyalina* exhibits life-history traits consistent with physically controlled, or *r*-selected, fauna (Sanders, 1979). In the deep sea, species with these characteristics would be expected to be found in unstable sedimentary environments such as trenches and canyon systems. In the latter case, turbidity currents, although augmenting the organic content of the sediments, also periodically annihilate whole faunal assemblages (Heezen *et al*., 1955). In such an environment, where adult survival is unpredictable, early maturity would be a distinct advantage. Unstable conditions in the PSB might occur within and around the Gollum Channel System. The prevalence of *K. hyalina* in areas of the PSB under the influence of the channels supports the hypothesis that holothurian clumps are characteristic of canyon systems (Rowe, 1971), although Haedrich *et al*., (1975, 1980) were unable to confirm the presence of a specialized canyon fauna. The presence of *Kolga* in areas of the PSB away from the channel systems, i.e. on the eastern slope of the Porcupine Bank, indicates also that this species is not restricted to unstable areas.

K. hyalina may exist in the canyons on the continental slope of the northwest Atlantic where clumps of "*Peniagone*-like" holothurians have been photographed (Rowe, 1971). These may well be *K. hyalina* which is similar to some species of *Peniagone* in external appearance. Indeed, while no species of *Peniagone* have been reported in the northwest Atlantic, apart from the benthopelagic species *P. diaphana*, *Kolga* has been collected in the area (Theel, 1882).

The narrow, monomodal size distributions of *K. hyalina* are typical of the species over a wide geographic area and size range. Once a population is established, therefore, further recruitment does not appear to take place. The reasons for this are not readily apparent. As an *r*-strategist *K. hyalina* may be semelparous, but in view of its length at first maturity (3mm), the longest known individual (50mm), and the apparent slow growth rates of deep-sea fauna, iteroparity is to be expected. For an opportunistic species a larval dispersal phase is a necessity and would lead to the separation of the parent and sibling populations. The egg size found could lead to either planktotrophic development or to lecithotrophic development with a short dispersal phase. The mono-modal size distributions appear to result from factors affecting larval dispersal and settlement. A variable current regime would lead, therefore, to a mosaic of populations with different mean sizes.

Mono-modal size-frequency distributions of abundant, small specimens of the anemone *Actinoscyphia aurelia* Stephensen have also been attributed to unstable sedimentary conditions although larger, reproductively viable individuals also occurred in the samples (Aldred, Riemann-Zurneck, Thiel and Rice, 1979). On a smaller scale, Jumars (1978) noted a complex dispersion pattern for the polychaete *Polyophthalmus sp*. in which patches of individuals of a similar size occurred, but the causes of the pattern were not identifiable.

The early maturity of *K. hyalina* coupled with its complete disappearance from areas in the PSB where it was at one time super-abundant, suggests that specimens that reach the size noted by the "Godthaab" Expedition in Baffin Bay (up to 50mm long) are probably the exception rather than the rule.

Elpidia sp.

BN 9753-7 (117), BN 9754-3 (503), BN 10111-8 (2002),
BN 10112-1 (4), BN 10112-2 (1), BN 10112-3 (1),
BN 50602-2 (494), BN 50603-1 (2), BN 50604-1 (3),
BN 50913-1 (111), BN 52019-1 (58).

Bathymetric range in PSB : 1484 to 4000m, but generally shallower than 3040m.

Distribution and taxonomic remarks : The taxonomy of the species of *Elpidia* in the North Atlantic is imperfectly known and no specific identification can be given to the PSB material. Perrier (1896) described a few specimens of *Elpidia* from off northwest Africa as *Tutela echinata* but he later synonymised the material with *Elpidia glacialis* Theel, 1876 (Perrier, 1902). These specimens were in a poor condition but three pairs of dorsal papillae could be discerned. Belyaev (1971), in his revision of the genus *Elpidia*, referred to the northwest Africa specimens as *Elpidia sp*.2 because of the uncertainty over its taxonomic position.

Hansen (1975) followed Belyaev's (1971) classification but was able to describe the body wall ossicles of specimens collected by the "Valdivia" off northwest Africa. These ossicles are similar to those of the PSB specimens in having a slender axis of about 20µm. However, the maximum length of the ossicles in the PSB material is 800µm as opposed to 1000µm in the "Valdivia" specimens, and the apophyses of the ossicles of the former are tall and slender, 25 to 45% of the length of the ossicles, as opposed to 10 to 25% in the latter. These features indicate a specific difference between the PSB and northwest Africa specimens but more data on the total variation in these characters are needed.

Ecological remarks : The abundance of *Elpidia* in the PSB is variable (Table 36). In one sample from the Goban Spur *Elpidia* was very abundant (ca. 44,000 individuals per hectare), similar to the abundance of *E. glacialis* in the Norwegian Sea (Dahl *et al*., 1976). The abundance of *E. glacialis* and other species of *Elpidia* varies considerably between hauls (Belyaev, 1971; Dahl *et al*., 1976) suggesting that some species of the genus have a patchy distribution.

Table 36. The abundance (A) of *Elpidia sp*. in epibenthic sledge samples, expressed as number per hectare. n = number of specimens taken.

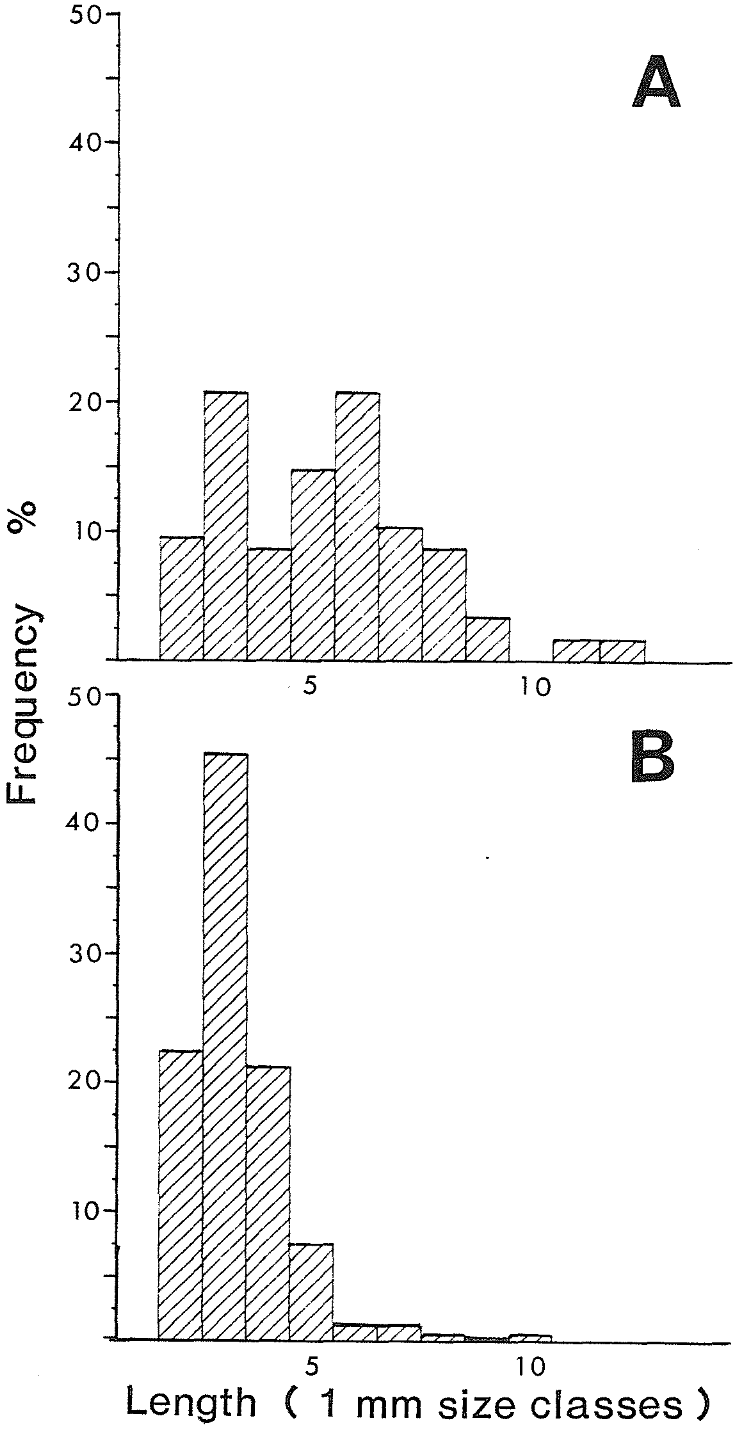
Station	Mean depth (m)	n	A/Posn	A/Odo
BN 9754-3	1484	503	3474	
a BN 10111-8	1635	2002	10507	43949
BN 52019-1	1731	58	916	973
BN 9753-7	1942	117	1584	
BN 50602-2	1968	494	2742	
BN 10112-2	2645	1	16	47
BN 10112-1	2650	4	15	
BN 10112-3	2748	1	6	26
BN 50913-1	3020	111	583	
BN 50604-1	3520	3	12	
BN 50603-1	4000	2	9	

a Goban Spur

The population size distributions of *Elpidia* from two samples taken within a day of each other in the PSB (Fig 40), Stas 9753-7 and 9754-3, show that although both samples cover the same size range of specimens, one sample is heavily skewed to the small specimens. This suggests that, like *K. hyalina*, there is at least periodic and spatially variable recruitment of juveniles. The maximum egg size of *Elpidia sp*. is about 200µm, similar to *Kolga*, suggesting that the reproductive strategy may be similar for the two genera. For *K. hyalina* it has been proposed

Figure 40. The population size distributions of *Elpidia sp*. Length in 1mm size classes.

A) BN 9753-7, 8: 4:78, 1942m, n = 117.
B) BN 9754-3, 9: 4:78, 1484m, n = 413.



A
B
Frequency %
50
40
30
20
10
5
10
Length (1 mm size classes)

that the species leads an opportunistic lifestyle with early maturity and mass recruitment in certain areas, suitable for environments with unstable sedimentary conditions.

Hansen (1975) noted that *Elpidia* species had a peculiar distribution pattern that could be related to ecological factors, in particular nutritive conditions. Belyaev (1971) had already pointed out that *Elpidia* occurred primarily in highly productive areas, especially close to the continental slope. High abundances of *Elpidia* are found in hadal trenches, in the Arctic and the Antarctic Oceans, and possibly off northwest Africa. This led Hansen (1975) to suggest that the distribution of *Elpidia* could be related to areas where there was a periodic accumulation of organic matter either from the seasonal deposition of detritus or from periodic turbidity currents. The evidence suggests that *Elpidia*, like *Kolga*, has a life-history strategy that is suited to physically-controlled environments.

Order MOLPADIIDA

Family Molpadiidae

Molpadia blakei (Theel, 1886)

OT 9638-2 (20), OT 9640-1 (2), BN 10112-3 (1),
BN 10114-1 (3), BN 10115-1 (6), OT 50514-1 (17),
OT 50515-1 (22), BN 50603-1 (3), BN 50604-1 (2),
OT 50711-1 (13), OT 50712-1 (1), OT 50811-1 (32),
OT 50812-2 (2), OT 50906-1 (3), OT 50907-1 (9),
OT 50910-1 (5), OT 51015-1 (1), BN 51106-1 (1),
BN 51109-1 (2), BN 51109-2 (1), BN 51111-1 (1),
BN 51216-5 (2), OT 51411-1 (1), BN 51412-1 (2),
OT 51414-1 (2), BN 51417-1 (1), OT 51608-1 (3),
OT 51610-1 (6), OT 51803-1 (1), OT 51805-1 (1),
BN 52215-1 (1), BN 52216-8 (1).

Bathymetric range in PSB/PAP : 2470 to 4795m, but appears to be more common on the PAP.

Distribution : North Atlantic, 1747 to 5270m. Sibuet (1977) reports that *M. blakei* is particularly abundant in the Bay of Biscay at depths of around 3100 and 4100m, similar to the PSB.

Ecological remarks : *M. blakei* occurred in over half of the samples taken deeper than 3400m. A maximum abundance of 44 individuals per hectare was recorded for St. 10115-1 (Table 37) but the true abundance of *M. blakei* is likely to be much higher, since neither the sledge nor the otter trawl sample large, infaunal animals efficiently.

The relative abundance of *M. blakei* may be discerned by estimating the abundance of cone-shaped mounds on the sediment surface (see section 1.1, page 3). The cones can be seen in photographs of the seabed but it is not possible to determine how many are actually active. Young *et al*., (1985) counted the number of such cones, some 10

Table 37. The abundance of Molpadia blakei in epibenthic sledge and otter trawl samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Posn	A/Odo
Epibenthic sledge samples.				
BN 51106-1	2515	1		7.0
BN 51111-1	2665	1		4.8
BN 10112-3	2748	1	1.7	7.7
BN 51412-1	2775	2	2.7	5.8
BN 51417-1	2780	1	3.2	6.7
BN 50604-1	3520	2	2.4	
BN 10115-1	3925	6	15.3	44.0
BN 51109-1	3950	2		9.1
BN 51109-2	3985	1		4.5
BN 50603-1	4000	3	3.9	
BN 51216-5	4035	2	3.2	7.3
BN 10114-1	4050	3	11.2	27.0
BN 52215-1	4563	1	1.5	2.9
BN 52216-8	4813	1	1.7	2.5
Otter trawl samples.				
OT 51411-1	2485	1	0.1	
OT 50906-1	2645	3	0.4	
OT 50712-1	2738	1	0.2	
OT 50907-1	2975	9	1.1	
OT 51610-1	3485	6	0.6 *	
OT 9640-1	3753	2	0.2	
OT 50514-1	4056	17	2.1	
OT 9638-2	4074	20	4.2 +	
OT 50812-2	4088	2	0.2	
OT 51414-1	4155	2	0.2	
OT 50910-1	4312	5	0.5	
OT 51608-1	4320	3	0.4	
OT 50811-1	4375	32	4.0	
OT 50515-1	4510	22	3.2	
OT 50711-1	4788	13	1.4	

* trawl doors found tangled on recovery. Abundance could be higher.

\+ acoustic monitor lost from trawl. Precise distance travelled by trawl unknown.

to 25 cm in diameter and about 5cm high, on three different types of sediment in the Venezuela Basin. The cones were most abundant on a hemipelagic sediment with an abundance of about 9000 per hectare. Similar cone shaped mounds were found on the Madeira Abyssal Plain (MAP) (Billett, 1987) with an abundance of about 1000 cones per hectare. Photographs from the PAP were examined for *M. blakei* cones. Very few were seen close to the continental slope but at deeper depths on the PAP a similar abundance of cones was found as on the MAP. An average abundance of about 1000 cones per hectare was found at St. 52215-1.

An examination of population size structure is not possible since *M. blakei* is not very abundant in any one sample and there is no confidence that the sampling equipment collected a representative sample of the population. Smaller specimens will live closer to the sediment surface and therefore the samples will be biased towards the smaller sizes. The specimens from the PSB ranged between 3 and 125mm long. There is no evidence of seasonal recruitment.

M. blakei produces an egg with a maximum diameter of about 200µm (Tyler *et al.*, 1987). This is similar in size to the eggs produced by many other molpadiid species including *M. intermedia* (McEuen and Chia, 1985). Development in this species progresses via a doliolaria larva which remains in the plankton for about 3 days (temp. 11 ° C). A similar planktonic larva is expected for *M. blakei*, although its residence time in the plankton may be much longer in water with a temperature of only 3 ° C. Development of the gonad in *M. blakei* starts when the holothurian is about 18mm long and breeding appears to be continuous for the population as a whole, although spawning may be periodic in each individual (Tyler *et al.*, 1987).

Cherbonniera utriculus Sibuet, 1974

BN 9756-9 (5), BN 9756-14 (172), BN 10114-1 (95),
BN 10115-1 (215), BN 50603-1 (45), BN 50604-1 (256),
BN 50605-1 (1), BN 50812-1 (83), BN 50913-1 (43),
BN 52214-1 (20).

Bathymetric distribution in PSB/PAP : 2820 to 4140, but a principally 3500 to 4000m.

Distribution : Northeast Atlantic, Bay of Biscay to the Rockall Trough, 2039 to 4251m (Sibuet, 1974, 1977; Gage *et al*., 1985a; Harvey *et al*., in press).

Ecological remarks : Abundance of *C. utriculus* is greatest close to the base of the continental slope, up to about 5000 individuals per hectare (Table 38). This is not surprising, for it is an infaunal species with limited locomotion and will be dependent on detrital material deposited on the bottom in its immediate vicinity. The base of the continental slope will be an area of deposition for downslope processes and also lies close to the shelf break where productivity is often high. The latter will lead to a greater deposition of detritus.

The population size distributions for *C. utriculus* on the PAP are similar to those reported by Tyler *et al*. (1987) for populations in the Rockall Trough. Each sample has a single mode but the position of the mode varies slightly (Fig. 41). The differences between the samples may result from periodic recruitment possibly allied to a seasonal change in gametogenesis. The latter is indicated since females appear to be less well developed in summer months (Tyler *et al*., 1987).

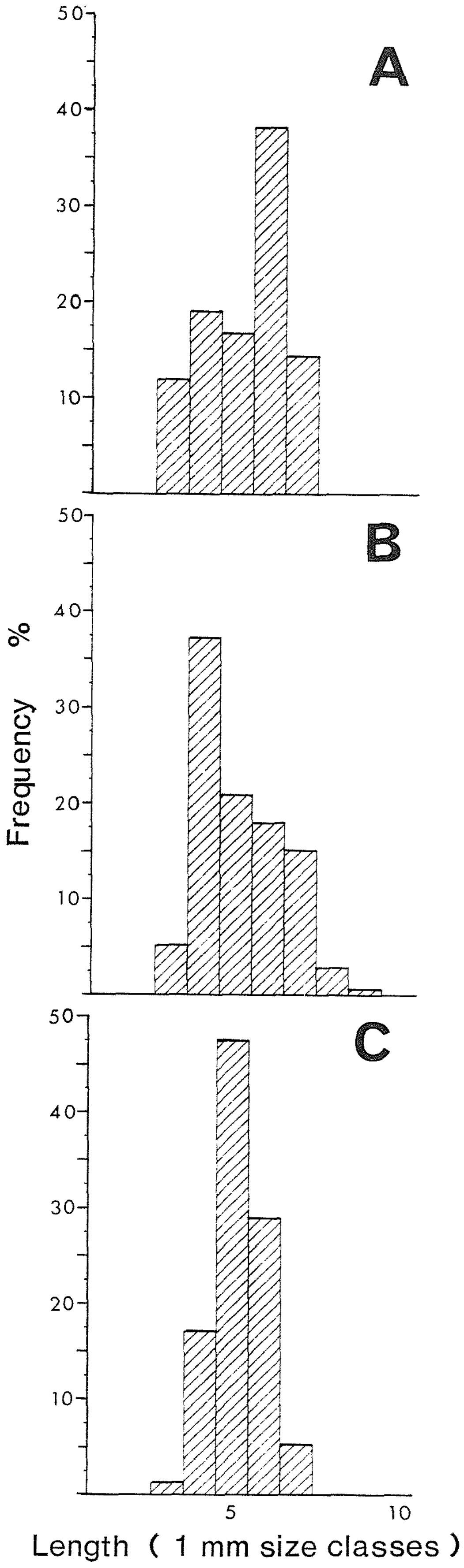
Table 38. The abundance (A) of Cherbonniera utriculus in epibenthic sledge samples, expressed as number per hectare. n = number of specimens taken.

Station	Mean Depth (m)	n	A/Area	A/Odo
BN 50605-1	2875	1	4	
BN 50913-1	3020	43	226	
BN 50604-1	3520	256	1005	
BN 9756-14	3689	172	560	3979
BN 10115-1	3925	215	1838	5275
BN 50603-1	4000	45	193	
BN 10114-1	4050	95	1185	2860
BN 9756-9	4054	5	27	134
BN 52214-1	4063	20	48	147
BN 50812-1	4090	83		1553

Like M. blakei, Cherbonniera has a maximum egg size of about 200µm (Tyler et al., 1987) indicative of either planktotrophic development or abbreviated lecithotrophic larval development with a short larval stage. The latter is more likely since the distribution of C. utriculus appears to be quite restricted.

Figure 41. The population size distributions of *Cherbonniera utriculus*. Length in 1mm size classes.

A) BN 50913- 1, 12:11:80, 3020m, n = 43.
B) BN 9756-14, 15: 4:78, 3688m, n = 172.
C) BN 50812- 1, 3: 8:80, 4090m, n = 83.


A
B
C
Frequency %
50
40
30
20
10
5
10
Length (1 mm size classes)

Family Caudinidae

Hedingia albicans (Theel, 1886)

BN 9753-7 (2), BN 51412-1 (1), BN 51708-2 (1),
BN 52019-1 (1), BN 52211-1 (3).

Bathymetric range in PSB : 1430 to 2790m.

Distribution : North Atlantic from off northwest Africa (3200m), Rockall Trough (1501 to 1706m), southwest of Iceland (1590 to 1628m) and the eastern seaboard of North America (1600 to 2423m). Also known in the Mediterranean, off southern India, and in the Bay of Bengal (484 to 814m). A variety *H. albicans* var. *glabra* is known from off New Zealand (1280m).

Ecological remarks : This species is a rare holothurian in the PSB found at mid-slope depths in keeping with its distribution elsewhere in the Atlantic. A maximum abundance of 21 individuals occured at St. 52211-1 but the abundance of this infaunal species is likely to be underestimated by the conventional towed gear used in this study.

Order APODIDA

Family Synaptidae

Labidoplax southwardorum Gage, 1985

BN 10112-1 (5), BN 10112-2 (1), BN 10113-1 (1),
BN 50913-1 (1).

Bathymetric range in PSB : 2640 to 3040m.

Distribution : Known only from the Rockall Trough and the PSB, 1000 to 3040m (Gage, 1985; Gage *et al*., 1985a; Harvey *et al*., in press; present records). The geographic distribution of this species may be greater since few deep-sea samples have been examined down to such a fine degree for small macrofauna. The time series sampling programme by the Scottish Marine Biological Association is an exception (Gage *et al*.,1980) and *L. southwardorum* has been found in many samples from the Rockall Trough.

Ecological remarks : A few remarks that are pertinent to the biology of all apodid holothurians are made in the section on *Myriotrochus bathybius*.

Protankyra brychia (Verrill, 1885)

BN 9756-14 (1), BN 10112-1 (1), BN 50604-1 (1),
BN 51412-1 (3), BN 51415-1 (9), BN 52216-8 (2).

Bathymetric range in PSB : 2640 to 4832m.

Distribution : Atlantic Ocean, 1464 to 1829m in the northwest Atlantic (Miller and Pawson, 1984) although Madsen (1953) proposed a deeper bathymetric limit of 2549m since Deichmann (1940) considered Theel's (1886b) *Synapta sp*. to be synonymous with *P. brychia*. In the eastern

Atlantic the species is reported as deep as 4990m (Ludwig and Heding, 1935). The eastern Atlantic material was originally considered to be a separate species, *P. abyssicola* (Theel, 1886a) but it was synonymised with *P. brychia* by Deichmann (1940).

Taxonomic remarks : The shallowest sample contains a fragment of *P. brychia* only 2.6mm long which possesses only wheel-shaped ossicles. The specimens might originally have been referred to the family Myriotrochidae which have wheel ossicles but recent evidence has shown that such ossicles may also be found in juvenile specimens of *P. brychia* (Gage *et al*., 1985a) and that these ossicles are similar to those reported from giant pelagic auricularia larvae (Chun, 1896; Pawson, 1971).

The specimen is in a good state of preservation and a number of features can be described. There are 12 tentacles which are all retracted. In this state two digits can be seen at the end of each tentacle but the number of lateral digits is unknown.

There are 10 calcareous ring plates. The two dorso-lateral radial plates are enlarged and are modified to accommodate the two extra tentacles (Fig. 42A). The interradial plates have a single tooth-like process which is about the same height as the basal part of the plate at the point where it articulates with the neighbouring radial plate (Fig. 42B). The posterior edges of both the radial and interradial plates are concave. In radial plates two small spurs or anterior processes are formed. These spurs may arch towards each other (Fig. 42A) forming a groove for the passage of the radial water vessel, but the spurs never appear to join up. The ventro-lateral radial plates are twice as wide, and the dorso-lateral plates about three times as wide, as the height of those

Figure 42. Protankyra brychia.

A) Dorso-lateral radial plate of the calcareous ring.

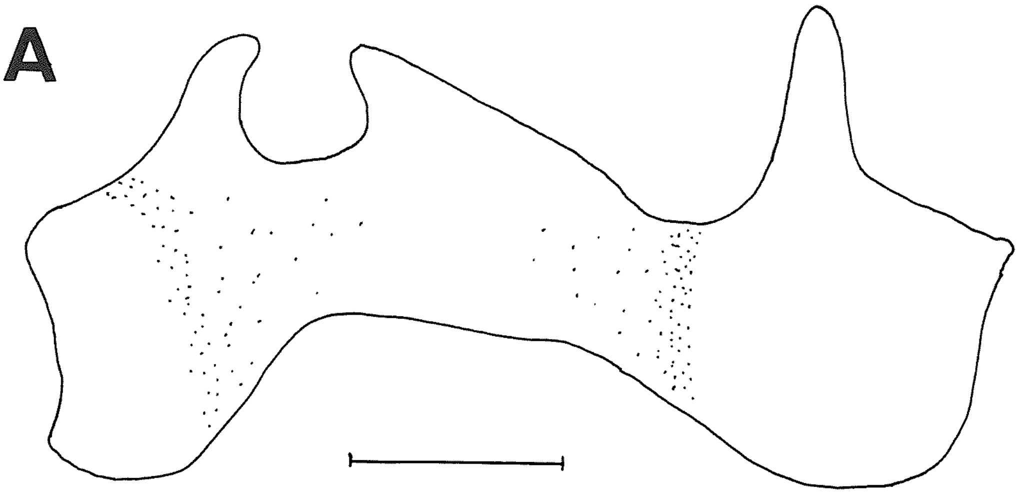
B) Ventro-lateral radial and ventral interradial plate of the calcareous ring.

C) Body wall ossicle.

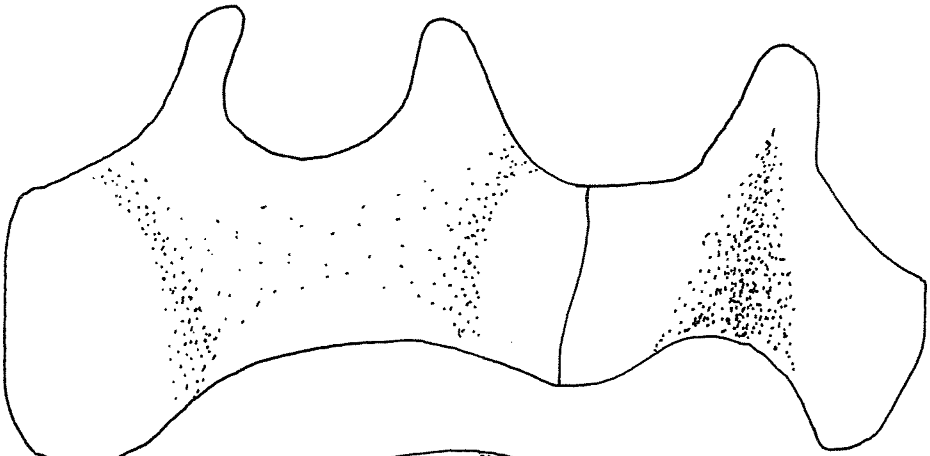
All from the anterior end of a specimen ca. 2.6mm long.

Scale bars : 100um.

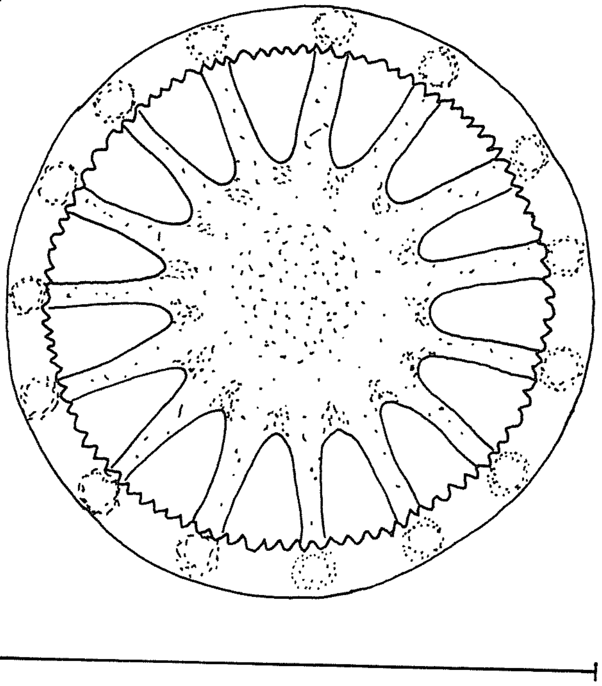
A



B



C



plates at their articulating edges (Figs 42A,B).

The ossicles of the body wall are only basket-shaped wheels (Fig. 42C). Seventeen wheels were examined in detail but only on 9 of these could the number of teeth be counted. The wheels range in diameter from 77 to 113µm and have a wide hub from which radiate 13 to 16 spokes. The rim thickness is about 5% of the wheel diameter and bears numerous, small, inward-pointing teeth. The teeth are only about 2µm long and vary in number from 73 to 104. Full details of the wheel parameters are given in Table 39.

Table 39. The parameters of the wheel ossicles from a juvenile specimen of <u>Protankyra brychia</u>. Mean values and the total range of each parameter are given. Abbreviations as in Table 1 (page 116).

Parameter	Mean	Range
D, µm	90	77 - 133
dh%	42.6	38.8 - 45.5
ns	14.6	13 - 16
nit	87.1	73 - 104
s/t%	16.8	15.1 - 19.0

Family Myriotrochidae

<u>Myriotrochus bathybius</u> H.L. Clark, 1920

OT 9638-2 (2), BN 9756-14 (2), BN 50812-1 (1), OT 50910-1 (1).

<u>Bathymetric range in PSB/PAP</u> : 3680 to 4341m.

<u>Distribution</u> : Cosmopolitan, from the tropical eastern Pacific (Clark, 1920), off Oregon (Carney and Carey, 1976), South Atlantic and Indian Oceans (Dr. B. Hansen,

personal communication) and northeast Atlantic, 1800 to 2946m (Gage and Billett, 1986; Harvey *et al*., in press).

Ecological remarks : The following ecological features that appertain to *M. bathybius* are also relevant for the other deep-sea apodid holothurians.

The discovery of *M. bathybius* in the northeast Atlantic in addition to another myriotrochid, *M. giganteus* Clark, 1920 (Gage and Billett, 1986), previously reported only from the eastern Pacific, demonstrates that infaunal apodid holothurians can have cosmopolitan distributions. The wide separation of localities in some species may simply be a sampling artefact since so few samples of small macrofauna have been taken in the deep sea. In the Rockall Trough, box corer samples show that the abundance of apodid holothurians is much higher than their expected abundance based on the number of specimens sampled by an epibenthic sledge (Gage and Billett, 1986). Apodid holothurians, therefore, are possibly more common in the deep sea than hitherto recognised.

Many of the apodid specimens came up in fragments. The ability of myriotrochid holothurians to autotomise is very marked in these deep-sea species.

Myriotrochus giganteus H.L. Clark, 1920

BN 51416-1 (1).

Bathymetric range in PSB : 2780 to 2790m.

Distribution : *M. giganteus* was originally known only from the Pacific Ocean (Clark, 1920; Carney and Carey, 1976), 3300 to 3900m. In addition, Gage and Billett (1986) have described material from the Rockall Trough and synonymised *Myriotrochus sp.* ex. gr. *maquariensis-giganteus* Belyaev and Mironov, 1982, from the equatorial eastern Pacific, with *M. giganteus*.

Taxonomic remarks : The specimen is only 8.7mm long but has wheel ossicles of the typical *M. giganteus* form. The wheels are most common at the posterior end.

Siniotrochus myriodontus Gage and Billett, 1986.

BN 9756-14 (4), BN 50603-1 (1), BN 50604-1 (1),
BN 51415-1 (1).

Bathymetric range in PSB/PAP : 3470 to 4000m.

Distribution : Known only from the PSB. This species is similar to *S. phoxus* Pawson, 1971 known only from the western Atlantic, 3985 to 4000m.

Taxonomic remarks : see Section 3.3 (page 111).

Ecological remarks : *S. myriodontus* appears to occur only around the base of the continental slope. For other remarks see *M. bathybius*.

Prototrochus zenkevitchi rockallensis Gage and Billett, 1986

BN 51403-3 (2), BN 51403-4 (1), BN 51420-1 (1),
BN 51420-4 (1), BN 51420-4 (1).

Bathymetric range in PSB : 1279 to 1333m.

Distribution : *P. zenkevitchi rockallensis* is only known from the northeast Atlantic, 1000 to 2946m (Gage *et al*., 1985a; Gage and Billett, 1986; Harvey *et al*., in press). Other subspecies of *P. zenkevitchi* come from considerably greater depths in the South Atlantic and Pacific Oceans (Belyaev, 1970; Belyaev and Mironov, 1978). The essentially bathyal distribution of the northeast Atlantic form may mean that it will be eventually recognised as a distinct species (Harvey *et al*., in press).

Ecological remarks : *P. zenkevitchi rockallensis* is known in the PSB only from the area where suspension-feeders are common (see Section 5.2). It is known from a similar depth (1330m) in the Whittard Canyon to the south of the PSB, but in the Rockall Trough it has been found over a considerably greater bathymetric range, 1000 to 2946m. For other remarks see *M. bathybius*.

Parvotrochus belyaevi Gage and Billett, 1986.

BN 52216-8 (2).

Bathymetric range on PAP : 4803 to 4832m.

Distribution : Previously known only from the Rockall Trough at shallower depths, 1160 to 2921m (Gage *et al*., 1985a; Gage and Billett, 1986; Harvey *et al*., in press), although most of the samples came from around the 2900 isobath. Total bathymetric range is now 1160 to 4832m.

Ecological remarks : An extremely small apodid holothurian, the largest known specimen is 2.3mm long (Gage and Billett, 1986). The PAP specimens are 2.5 and 2.7 mm long and show that the species is found on the abyssal plain as well as on the continental slope. For other remarks see *M. bathybius*.

5. Ecological Discussion

5.1 Holothurian biomass and abundance in relation to depth.

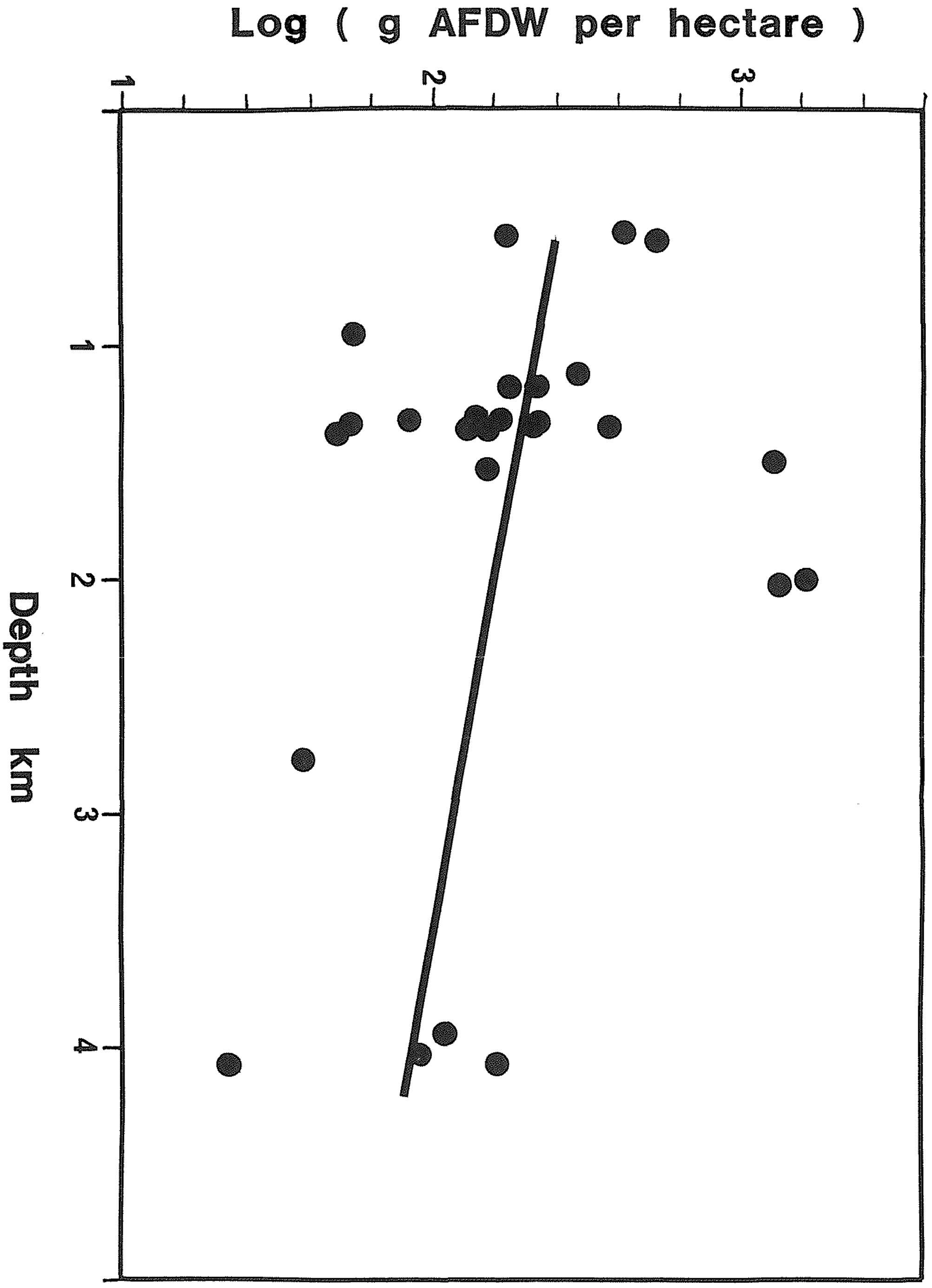
Although the total biomass of the epibenthic invertebrate megafauna decreases by a factor of 30 between 500 and 4100m in the PSB (Lampitt *et al*., 1986), a similar decrease in holothurian biomass is not evident (Fig. 43). This results, in part, from a change in the composition of the megafaunal taxa with increasing depth. At the top of the slope crustaceans and suspension-feeding sponges and coelenterates are dominant, but they are replaced on the middle and lower slope by echinoderms, in particular deposit-feeding holothurians. This is a general trend that is evident in many areas of the deep sea (see Section 1). Although there is no significant decrease in the biomass of holothurians between 500 and 4100m in the PSB, the biomass of deep-sea species is about 3 orders of magnitude less than that reported for some species from coral reef flats (Lawrence, 1980).

The greatest holothurian biomass in the PSB, about 1500g AFDW per hectare, is found at 1500 to 2000m. Using the calorific data presented by Walker *et al*. (1987a,b) this produces a calorific biomass of 36900 KJ per hectare at about 2000m, as opposed to 4900 and 2500 KJ per hectare at 1000 and 4000m respectively. These values are greater than those reported by Sibuet and Lawrence (1981) for depths of

Figure 43. Semilog plot showing holothurian AFDW biomass in relation to depth (km).

Regression : $y = 2.469 - 0.130\ x$,

standard error of y estimate = 0.440, $r^2 = 0.10$, $n = 27$.


Log (g AFDW per hectare)
1
2
3
Depth km
1
2
3
4

2100 to 2200m and for 4100m in the Bay of Biscay. Part of the discrepancy will have resulted from the sampling gear used in estimating the abundance of the holothurians. Sibuet and Lawrence (1981) noted that their trawl probably underestimated the true biomass by one-half, based on photographic observations made at the same sites. In addition, at 4100m, the data are not strictly comparable, since Sibuet and Lawrence (1981) provide data only for Psychropotes longicauda, one of several holothurians at this depth in the area (Sibuet, 1977). At about 2000m, however, the data are strictly comparable since, although the data in Sibuet and Lawrence (1981) are restricted to Benthogone rosea and Paelopatides grisea, few other species are found at this depth in either the Bay of Biscay or the PSB. Even doubling the data of Sibuet and Lawrence (1981) to allow for the inefficiency of the trawl, giving a total holothurian biomass of 8160 KJ per hectare at 2100m in the north and 16190 KJ per hectare at 2200m in the south of the Bay of Biscay, the PSB sustains a biomass that is some 2 to 5 times greater.

These discrepancies may simply reflect differences in community structure. However, at 2100m in the Bay of Biscay, holothurians account for about 62% of the total megafaunal biomass (97.27 cals / m^2, Sibuet and Lawrence (1981), as opposed to a total of 156 cals / m^2, Khripounoff, Desbruyeres and Chardy (1980)). In the PSB the holothurian biomass is about 4 times greater and accounts also for about 62% of the total megafaunal AFDW biomass. It is apparent, therefore, that the centre of the PSB (2000m) sustains not only a higher holothurian biomass but also a higher total megafaunal biomass than the Bay of Biscay stations. This could be the result of topography since the horseshoe shape of the PSB may lead to a concentration of organic material in the centre (i.e. at mid- slope depths).

Further comparisons may be made with another study that has estimated holothurian biomass in the northeast Atlantic. Rutgers van der Loeff and Lavaleye (1986) calculated a mean WW biomass for holothurians of 513g per hectare at a depth of 4750m south of the PAP which compares with a WW biomass of 36000g per hectare (mean of 4 samples) at 4000m on the PAP. Part of the discrepancy will again result from the different sampling gear used, but it will also reflect differences in the depth of the two samples and the location of the samples relative to the base of the continental slope. The trawl used by Rutgers van der Loeff and Lavaleye (1986) probably under-estimated epibenthic invertebrate abundance, since holothurian abundance, calculated from the IOS epibenthic sledge, is some 25 times greater at 4800m in the middle of the PAP than in their samples.

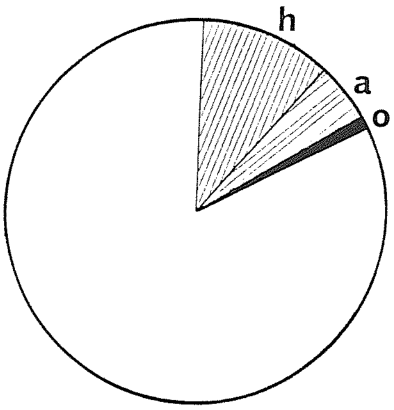
The increasing importance of holothurians and other echinoderms with increasing depth in the PSB can be seen by examining the proportion contributed by the various taxa to the total megafaunal AFDW biomass (Fig. 44). Generally, holothurians account for less than 10% of the total biomass on the upper slope. However, at depths greater than 1500m echinoderms become the dominant group and in some areas account for as much as 97% of the total megafaunal AFDW biomass. The proportion of the biomass provided by the various classes of the Echinodermata varies so that at some depths (e.g. 2000m) holothurians are dominant, but at others (e.g. 2500m) they are absent and asteroids are the principal faunal group. The reasons for the sharp fluctuations in holothurian biomass in this area of the PSB are discussed in relation to holothurian zonation in the next section.

The apparent importance of various faunal groups in the benthic community is dependent to some extent on the

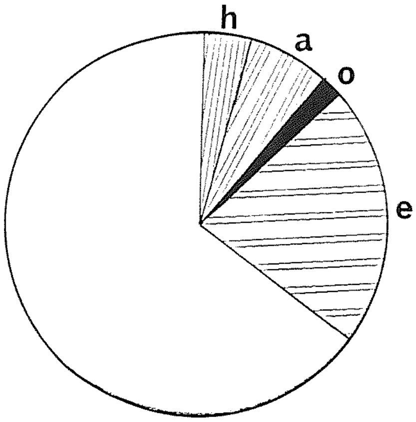
Figure 44. Pie charts showing the relative contribution made by holothurians (h), asteroids (a), ophiuroids (o) and echinoids (e) to the total invertebrate megafaunal AFDW biomass at various depths.

A) 500m,
B) 1000m,
C) 1500m,
D) 2000m,
E) 2500m,
F) 3500m,
G) 4000m.

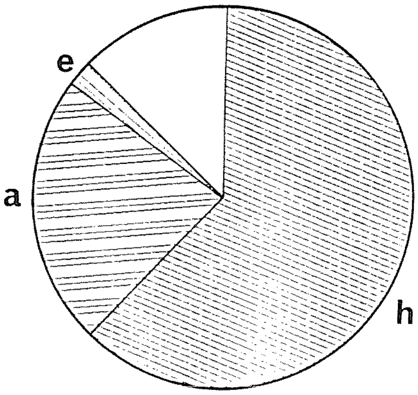
A



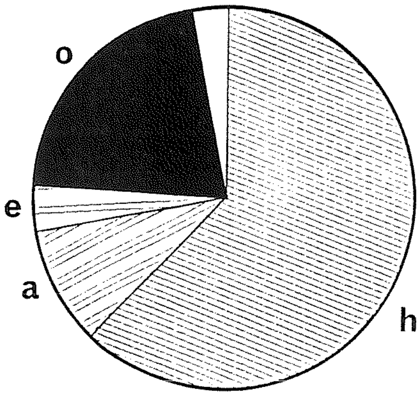
B



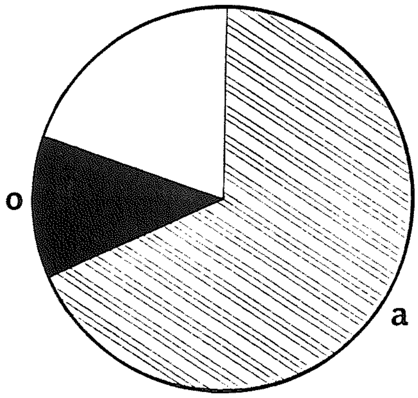
C



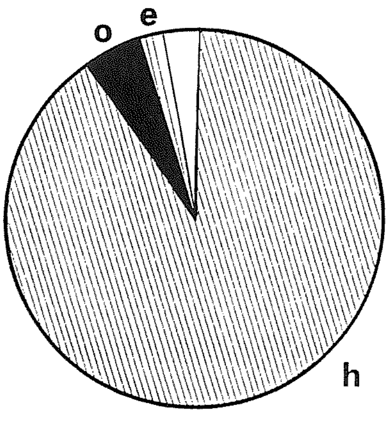
D



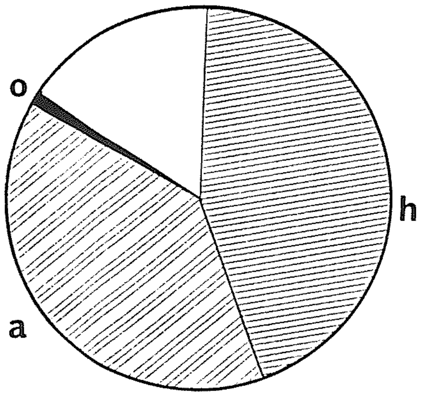
E



F



G

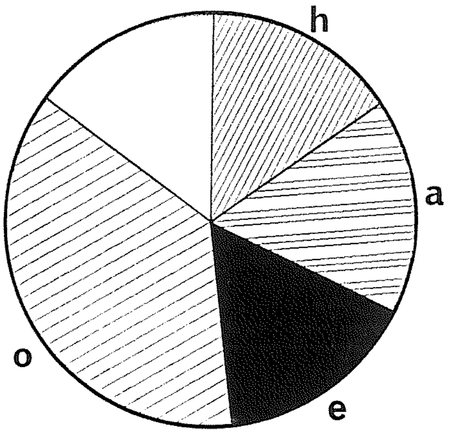


biomass unit used for comparison. AFDW or calorific value are the most meaningful units of biomass for ecological research, but they are often time-consuming to measure. For this reason most researchers have used other units to compare benthic populations, such as abundance (Sibuet, 1985), wet weight (Haedrich *et al*., 1980), or dry weight (Sibuet *et al*., 1984). All of these units have their drawbacks and, as shown in Fig. 45, they give quite different impressions of the relative importance of faunal groups.

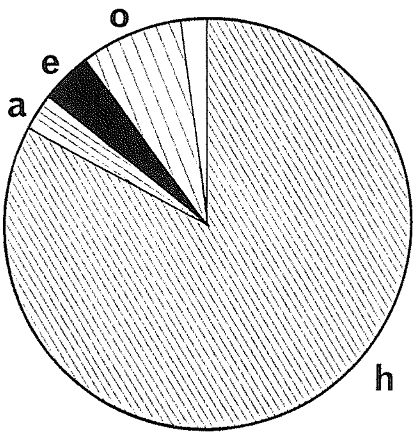
Numerical abundance may be a reasonable estimate of macrofaunal biomass (Rowe and Menzel, 1971), but data on the abundance of many holothurian species (Section 4.2) shows that holothurian abundance can vary greatly at any one depth. For instance, at 4000m holothurian abundance can vary by 5 orders of magnitude depending on whether the opportunistic species *Kolga hyalina* is present. Likewise, at shallower depths, the presence or absence of *Elpidia* can lead to similar fluctuations. However, owing to the small size of these holothurians their impact on AFDW biomass variability would be far less.

It is not surprising that WW biomass overestimates the importance of large animals with a high water content, such as holothurians (Fig. 45B), nor that dry weight biomass overestimates the importance of large animals with a well developed skeleton, such as the ophiuroids (Fig. 45C). Therefore, comparisons between different areas using WW or DW must take into account the faunal composition of those samples. However, in the PSB where the biomass of the megafauna has been estimated from 22 stations between 500 and 4100m, a similar relationship between biomass and depth is evident for WW, DW and AFDW despite the differences in faunal composition at each depth (Lampitt *et al*., 1986).

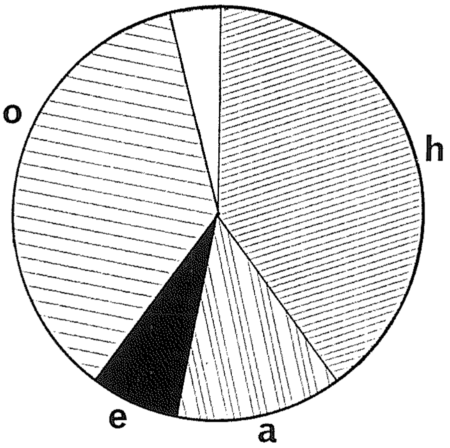
Figure 45. Pie charts showing the relative contribution made by holothurians (h), aasteroids (a), ophiuroids (o) and echinoids (e) to the total invertebrate megafaunal biomass at 2000m as measured by Abundance, Wet weight, Dry weight and Ash-free dry weight.



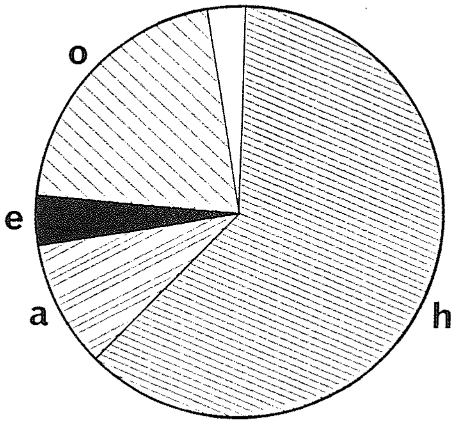
Abundance



Wet weight



Dry weight



Ash-free dry weight

5.2 Holothurian bathymetric zonation, scale and relationship to environmental characters.

The study of zonation in the deep sea is complex owing to the many variables that play a role in regulating the distribution of a species. Many of these variables are related to depth and therefore act in concert to control the bathymetric range of an organism. Section 1.11 (page 26) reviews current knowledge of holothurian bathymetric zonation and identifies three types of study that might extend our understanding of the relative importance of processes controlling zonation. In this section it is intended to tackle the third option, namely to give a detailed analysis of the zonation of the dominant holothurian species and where possible to compare their bathymetric ranges in the PSB with other regions in the northeast Atlantic, e.g. the Rockall Trough (Gage *et al*., 1985a,b; Gage, 1986; Harvey *et al*., in press). This detailed analysis can then be used for similar comparisons over a wider geographic range, and for comparison in the future with the zonation of other faunal groups in the PSB, such as fish, crustaceans and asteroids. The zonation of the PSB fauna can then be compared as a whole with zonation patterns found in other oceanic regions.

Comparisons with historical data from other areas must be tempered, however, by the recognition that some of the total bathymetric ranges quoted in Section 4.2 are subject to various sources of error. Apart from taxonomic difficulties where several species may be lumped together (e.g. ?*Pseudostichopus villosus*), or where a single species is separated into two or more forms, two other factors may be recognised. First, there can be contamination of samples from specimens captured in previous hauls. The PSB records have been carefully screened for all possible sources of contamination; it is apparent that other studies have failed to detect this source of error and, as a consequence, the global bathymetric ranges of some species have been exaggerated. Second, it is only in recent times that accurate monitoring of sample depth has been possible. Some old data have come from areas of steep terrain and it is obvious that when a sounding line was used at the end of a haul, the ship was at a completely different depth to that where the sample was taken. Several cases of this sort of error are highlighted in Section 4.2.

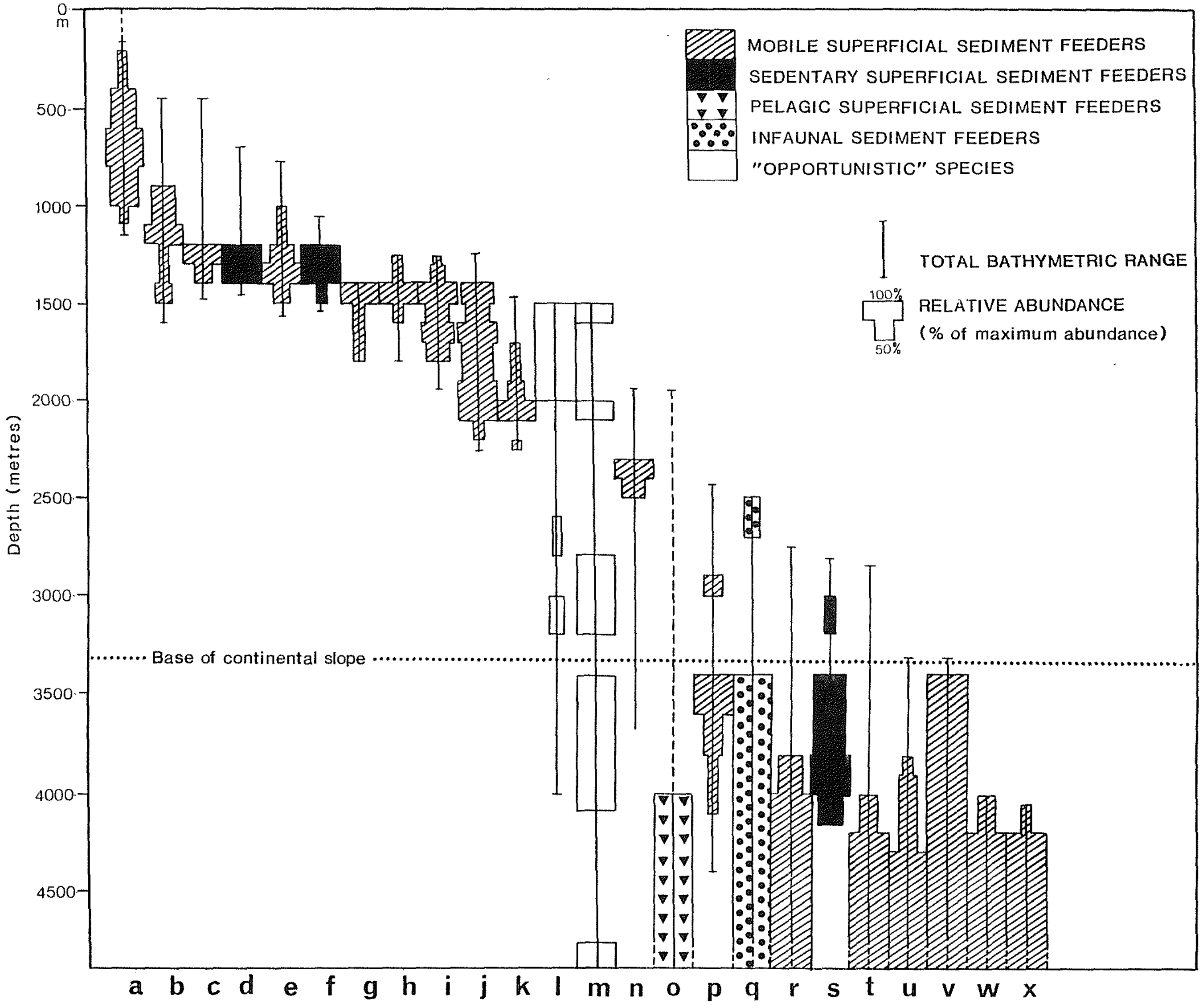
Carney *et al*. (1983) reviewed the patterns and causes of zonation found un the deep sea. Many studies have stressed the role of physical factors (Rowe and Menzies, 1969; Haedrich *et al*., 1980) but others have promoted the importance of biological interactions for some taxa (Rex, 1977). It is apparent that the rate of faunal change with depth is dependent on faunal group and to some extent on trophic level. It has been argued that competition in lower trophic groups will be alleviated by predation allowing broad, overlapping bathymetric ranges, whereas competition in higher trophic levels with little predation pressure would be greater, leading to resource partitioning and narrower bathymetric ranges with little overlapping (Rex, 1977). Haedrich *et al*. (1980), however, showed that some higher trophic levels, such as fish and decapod crustaceans, become less selective in feeding in the deep sea and have wide bathymetric ranges. Similarly, holothurians in the northeast Pacific show larger rates of faunal change than some macrofaunal groups (Carney and Carey, 1982).

With the exception of the ypsilothuriids, the population size distributions of deep-sea holothurians (Section 4.2) are skewed to large specimens suggesting that predation pressure is low and that the effect of predators on holothurian zonation will be minimal. Similarly lower trophic levels will have little effect on holothurian distribution since holothurians ingest detrital particles and have a negative selection even for meiofauna (Khripounoff and Sibuet, 1980; Sibuet *et al*., 1982). However, if factors influencing the deposition and concentration of organic detritus are the dominant factors influencing holothurian zonation, the effect other organisms have on the topography of the seabed and hence on the deposition of organic matter, may play some role in controlling holothurian distributions.

Most deep-sea samples are not quantitative and so the bathymetric ranges of species have been recognised from the shallowest and deepest records. Using these data, species recruitment curves have been plotted and have shown depths at which rapid faunal change occurs (e.g. Gage *et al*., 1985b). The total bathymetric range for the dominant 24 holothurian species on the main transect through the PSB (Fig. 6, Section 2.2) are plotted in Fig. 46. By viewing the figure with the Y-axis (Depth) at the bottom of the page (i.e as the X-axis) a species recruitment curve for the PSB holothurians can be seen. The data show a gradual replacement of species down the slope with one zone of rapid change at 1400 to 1500m, in contrast to a similar faunal change at 1000m for holothurians in the Rockall Trough (Gage *et al*., 1985b). While studies like these on the "coincidence of range" of species identify areas of importance for zonation, they give little other information. As Carney *et al*. (1983) conclude : "Our basic level of enquiry should be that of the individual species' range and the individual species' adaptations". They also suggested that "Rather than focusing on the upper and lower boundaries ..... population levels along the range should be examined ....".

Figure 46. Bathymetric distributions of the 24 most common holothurians in the Porcupine Seabight showing the total range and relative abundance of each species at various depths (see text). Feeding types denoted by pattern key. Species denoted by letter key at the bottom.

a. *Stichopus tremulus*.
b. *Laetmogone violacea*.
c. *Mesothuria intestinalis*.
d. *Echinocucumis hispida*.
e. *Bathyplotes natans*.
f. *Ypsilothuria talismani*.
g. *Paroriza pallens*.
h. *Mesothuria verrilli*.
i. *Mesothuria lactea*.
j. *Benthogone rosea*.
k. *Paelopatides grisea*.
l. *Elpidia sp*.
m. *Kolga hyalina*.
n. *Psychropotes depressa*.
o. *Peniagone diaphana*.
p. *Benthothuria funebris*.
q. *Molpadia blakei*.
r. *Deima validum*.
s. *Cherbonniera utriculus*.
t. *Oneirophanta mutabilis*.
u. *Psychropotes longicauda*.
v. *Benthodytes sordida*.
w. *Pseudostichopus villosus*.
x. *Paroriza prouhoi*.


0
m
500
1000
1500
2000
2500
3000
3500
4000
4500
Depth (metres)
MOBILE SUPERFICIAL SEDIMENT FEEDERS
SEDENTARY SUPERFICIAL SEDIMENT FEEDERS
PELAGIC SUPERFICIAL SEDIMENT FEEDERS
INFAUNAL SEDIMENT FEEDERS
"OPPORTUNISTIC" SPECIES
TOTAL BATHYMETRIC RANGE
100%
50%
RELATIVE ABUNDANCE
(% of maximum abundance)
Base of continental slope
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
x

With these particular recommendations in mind the zonation of holothurians in the PSB has been examined in more detail by comparing the relative abundance of each species in 100m depth bands. Data from the main transect and the Goban Spur data have been combined since the bathymetric ranges of most species is the same in these two areas. The abundance data from the epibenthic sledge samples (Tables in Section 4.2) have been pooled in 100m depth bands using the median depth of each sample to assign it to a particular band. The mean abundance for each species in a depth band has been calculated and expressed as a proportion (%) of the band in which that species was most common (100%) (Fig. 46). Where data from the epibenthic sledge were scanty, as is the case for most abyssal and a few slope species, abundance estimates from the otter trawl have been used also, supplemented by data on the proportion of samples in which species were recorded in each 100m band. Most PSB holothurians are epibenthic superficial deposit feeders but where the biology of a certain holothurian is different, e.g. an infaunal or a pelagic species, this is noted on Fig. 46. Each species is identified in the figure legend.

Three broad areas can be recognised. One on the upper and mid- slope where there is distinct zonation and most species are common only in a narrow depth band, the second on the mid- and lower slope where holothurians are scarce, and the third at abyssal depths beyond the base of the continental slope. The following discussion looks at each of these zones and attempts to recognise the features that regulate the distributions of the various species. Much of the discussion is conjectural since although the distributions of many species appear to be regulated by physical factors, there are very few of these data available for the PSB.

Little zonation is evident in the top 1000m of the PSB where *Stichopus tremulus* and, at deeper depths, *Laetmogone violacea* are the only common holothurians. However, distinct zonation is found at these depths for other taxa, such as decapod crustaceans and coelenterates (Dr. A.L. Rice, personal communication). As shown in Section 5.1, holothurians make only a minor contribution to the total biomass at these shallow depths and as a result are poor indicators of zonation. In contrast, below 1000m the holothurians become the dominant megafaunal invertebrates (Section 5.1). *L. violacea* is the most common holothurian between 1000 and 1200m and although abundant patches of this species occur also between 1400 and 1500m it is apparent that its abundance is low between 1200 and 1400m. This coincides with the same depths at which four other species, *Echinocucumis hispida*, *Ypsilothuria talismani*, *Bathyplotes natans* and *Mesothuria intestinalis* show their greatest abundance.

Depths between 1000 and 1300m are notable for the high abundance and biomass of the sponge *Pheronema grayi* (Lampitt *et al*., 1986). This sponge has a very restricted distribution on the Porcupine Bank and although it occurs over a total bathymetric range of 300m in the PSB, it is confined to a 100m depth band in any one area. In one phototransect the *Pheronema* were observed between 1050 and 1150m while in another phototransect, sampled just 35 km distant, the sponge occurred between 1150 and 1250m (Dr. A.L. Rice personal communication). It is inferred that the distribution of *Pheronema* is related to hydrographic features such as current regime and suspended particle load, but sadly there are few data on these features in the PSB. The upper slope surrounding the PSB is obviously a dynamic area since corals are common on the eastern side, and shallow depths on the Porcupine Bank support large populations of suspension feeders other then

Pheronema, such as the pennatulid *Kophobelemnon stelliferum*. Erosion of the Bank gives rise to nepheloid layers (Dickson and McCave, 1986) and complex bottom nepheloid layers are known to occur in the PSB at depths above the *Pheronema* community (Fig. 5, page 48).

Although hydrographic features appear to promote a suspension-feeding community between 1000 and 1400m on the Porcupine Bank, none of the four holothurian species common in this area are themselves suspension-feeders. Two are epibenthic deposit-feeders and the other two, the ypsilothuriids, are sedentary superficial sediment feeders (Section 4.2). These holothurians, therefore, are dependent upon a regular deposition of organic matter in their immediate vicinity. The ypsilothuriids might thrive around the sponges themselves, where the baffle effect of the *Pheronema* will lead to localised deposition, or gather at depths where a reduction in current speed leads to greater sedimentation. Intensive sampling at depths around the 1300m isobath straddled the lower boundary of the *Pheronema* community. Abundance data (Section 4.2) show that in this area the holothurians are most common at depths immediately below the sponges. Obviously the hydrographic features that promote the development of the suspension-feeding zone will have an effect over a wider depth range than that marked by the sponge. It is inferred that mean current speed will decrease to either side of the suspension-feeding area leading to greater deposition of particles and hence to the observed increase in the biomass of deposit-feeding holothurians.

However, the sharp boundaries that occur between holothurian species at about 1400m, and the way in which some species are restricted to narrow depth ranges, suggests that the situation is rather more complex. It is possible that a gradation in mean current velocity leads to a gradient in the size and type of particles deposited. Although gross microscopical and biochemical analyses have failed to show differences between the gut contents of different epibenthic species (Khripounoff and Sibuet, 1980), data presented in Section 5.3 suggest that some partitioning of particles between species may occur. This, coupled with a gradient in the types of particles deposited, could influence holothurian zonation.

Alternatively, the combined effect of temperature and pressure on cell membrane structure and enzymatic activity may influence zonation. Work on mesopelagic fish (Somero *et al.*, 1983) suggests that they are adapted to living optimally at specific depths where they out-compete other species that are more successful in shallower (warmer) and deeper (colder) water. It is unlikely, however, that these factors act over a small enough depth range in order to be able to account for the narrow holothurian zonation on the Porcupine Bank.

The four species that occur within or just below the *Pheronema* community are all found shallower in more northerly waters. Off Norway, *M. intestinalis* may be found at 20m, *E. hispida* at 50m, *Y. talismani* at about 500m and *B. natans* at 200m (Section 4.2). It is evident that all the species can survive over a wide range of pressure, although the fact that they occur in shallow water only in cold northerly latitudes, indicates that temperature does play a role in regulating their distribution. In the PSB these species occur at temperatures of 4 to 6 °C (Fig. 4, page 46). The effect of pressure on the biochemical activity of a species appears to set broad limits within which other features, such as temperature and food availability, fine-tune its zonation.

In Antarctic waters adaptation of metabolic activities to the cold environment is bought at the price of being sensitive to changes in temperature (Clarke, 1983). Deep-sea species too, and their larvae, might be particularly sensitive to increases in temperature. Many holothurians in the PSB have an upward bathymetric limit of 1400 to 1500m, including the "opportunistic" species *Kolga hyalina* which has a particularly wide depth range. These depths coincide with the bottom of the permenant thermocline and the lower limit of the Mediterranean Water mass (Figs 3 to 5). The thermocline, changes in water mass and the hydrographic regime may act as effective barriers to the upward extension of mid slope species, as proposed by Gage (1986) for a similar zonation boundary in the Rockall Trough, either through their physiological effects or by controlling the transport of lecithotrophic eggs and larvae (Section 5.5).

It is clear that while the data on holothurians have identified areas of importance in faunal zonation, more data on the physical environment, the feeding strategies of holothurians and their biochemical adaptations are needed. However, the proximity of an area of narrow holothurian zonation to the suspension-feeding community indicates that hydrographic features are important in controlling the zonation of deposit-feeders too on the upper slopes of the PSB.

The factors controlling the lower bathymetric limits of *Benthogone rosea* and *Paelopatides grisea* are unknown. Both species are part of a large echinoderm community at about 2000m which accounts for about 97% of the total invertebrate megabenthos AFDW biomass (Fig. 45). Some other echinoderms share a common lower boundary with the holothurians, e.g. the echinoid *Echinus affinis* and the asteroid *Plutonaster bifrons*, but others extend into deeper water, e.g. the asteroids *Pectinaster filholi*, *Benthopecten simplex* and *Bathybiaster vexillifer* (DSMB unpublished data). The apparent faunal discontinuity at about 2300m coincides with a trough in sampling effort (Fig. 7, page 56) making it look like a sharper boundary than perhaps it really is.

Apart from a small pocket of *Psychropotes depressa* at about 2400m epibenthic deposit-feeding holothurians are notable by their absence at depths between 2200 and 3400m in the PSB. Yet large populations of holothurians are found at these depths in the Bay of Biscay (Sibuet, 1977) and in the Rockall Trough (Gage *et al*., 1985a). In terms of topography there is no apparent reason for the paucity of deposit-feeding holothurians since gentle slopes of soft sediments are found down to depths of at least 3000m (Fig. 1, page 37). The deposit-feeding holothurian *Peniagone azorica* is ubiquitous between 2500 and 3000m in the Rockall Trough, but in the PSB only a few specimens have been collected (Section 4.2) and the only large invertebrate to occur in abundance is the omnivorous asteroid *Hymenaster membranaceus* (70% of the total invertebrate megabenthos AFDW biomass at 2500m, Fig. 44). Total megafaunal biomass is low between 2500 and 3000m in the PSB (Lampitt *et al*., 1986) which, together with the absence of epibenthic superficial deposit-feeders, suggests that the supply of organic matter is low. Even though the grain size of sediments at these depths is similar to that at 2000m, organic input could be different and lead to zonation, as proposed by Rowe and Menzies (1969). Once again, hydrographic processes and their effect on the deposition of organic particles are implicated. However, little is known of the physical oceanographic processes in the area, or of the effect the Gollum Channel System (Fig. 1) has on areas lying around it.

The base of the continental slope acts as an effective barrier to many abyssal species. Some abyssal species are found as shallow as 2700m, but the specimens at these depths are generally small. Two species, *Benthothuria funebris* and *Cherbonniera utriculus*, are particularly abundant close to the base of the slope, but the majority of the abyssal species show a reduction in abundance with proximity to the slope (Fig. 46). This is surprising because the presence of the sedentary *C. utriculus* in this area would indicate a depositional environment and hence an attraction for other holothurians. Perhaps the key lies in the presence of *B. funebris* which, it is argued in Section 4.2, is associated with areas of steep terrain and unstable sedimentary conditions. If the mouth of the PSB is subjected to intermittent downslope processes this could explain the decrease in abundance of abyssal species close to the base of the slope. Again, hydrographic process are implicated but there are no observations with which to match the biological data.

Many PSB holothurians have a similar bathymetric distribution in the Rockall Trough (Gage *et al*., 1985a; Harvey *et al*., in press). *C. utriculus* is an exception and occurs as shallow as 2500m in the Rockall Trough, but still close to the base of the slope which occurs at a shallower depth in this region. In contrast, the recorded bathymetric distributions of a number of species in the Bay of Biscay are quite different (Sibuet, 1977). Some of the discrepancies will result from differences in taxonomic interpretation, but it is still apparent that bathyal and abyssal species either mix or are closely zoned at about 3100m in the Bay of Biscay whereas they are widely separated in the PSB.

The data from the Seabight support Hansen's (1975) proposal of a separate bathyal and abyssal holothurian fauna with a boundary between the two groups at about 2500m although there is some degree of overlap. Those species that have a wide bathymetric range encompassing the two zones generally have opportunistic life histories. The reasons for a separate bathyal and abyssal fauna are not immediately obvious, for some abyssal species may occur as shallow as 1000m in other regions, e.g. *Deima validum* (page 198). Again, the effect of pressure appears to act over wide limits, and since temperature is almost constant below the permenant thermocline other factors must be considered. It is possible that the contrasting environments of the slope and the abyssal plain require different larval strategies for successful recruitment (Section 5.5), making it impossible for many abyssal species to occur on the continental slope.

5.3 Holothurian feeding and selectivity.

Studies on shallow-water and deep-sea deposit-feeding holothurians have indicated that some species select organically rich particles from the seabed (see Section 1.1). This has been shown by comparing the organic content of sediment from a holothurian's oesophagus with that of sediment sampled from the holothurian's locality. Generally the former is greater than the latter by a factor of 2 to 8, the "selection coefficient" (Kozyar, Sokolova and Zezina, 1974; Akhmet'yeva *et al*., 1982; Sibuet *et al*., 1982; Sibuet, 1984; in addition to references cited in Massin, 1982).

Not all increases in organic content have been attributed to selective feeding. Yingst (1974) detected only a small increase in organic matter between the gut contents of Parastichopus parvimensis and its surrounding sediment, an increase thought to arise from the holothurian's own digestive secretions. This contribution by the holothurian to the organic matter in its own gut may be an important source of error when comparing gut contents with sediment samples, particularly in environments such as the deep sea, where the organic content of the sediment is low.

To test this conclusion it is necessary to analyse a marker compound which, while it is associated with the holothurian's detrital food, could not be synthesised by the holothurian itself. The marker compound should exhibit a similar selection coefficient to the organic constituents (e.g. proteins or total organic matter) if the holothurian's own contribution to the organic matter in its gut is small. Chlorophyll and its breakdown products, referred to collectively here-in as the chloropigments, may be used as detrital markers since they are associated with many of the detrital particles that are deposited on the seafloor (Billett et al., 1983; Section 2.1, page 50). These particles, such as faecal pellets and amorphous aggregates ("marine snow"), account for the majority of the downward vertical detrital flux in the oceans (McCave, 1975; Honjo, 1980; Angel, 1984; Fowler and Knauer, 1986). Data on radionuclides in the marine environment indicate that holothurians feed readily on freshly deposited detritus (Feldt et al., 1985). It is clear, therefore, that chloropigments provide a valuable marker for examining holothurian feeding behaviour.

A second source of error in previous deep-sea studies comparing gut contents and sediment lies in the probity of the sediment sampling technique. Sediment has usually been sampled remotely by large, cumbersome box-corers, the best technology available to date. Such corers produce a bow wave which disturbs the superficial sediment layer as the corer penetrates the seafloor and there is often some erosion of the sediment surface within the box corer during its retrieval. Good samples can be obtained from box corers with hydraulically damped penetration (Soutar, Johnson, Fischer and Dymond, 1981), but sediment from this type of corer has not been used to date for comparison with holothurian gut contents.There is some doubt, therefore, about the ability of many box corers to sample the superficial sediment layer on which holothurians feed. It is possible that the published comparisons made between sediments and gut contents have merely reflected the relative skill with which scientists and holothurians sample the superficial sediment. In this study a new design of corer has been used which overcomes this problem.

Table 40: Station data for multiple corer (MC) and epibenthic sledge (BN) samples from the Porcupine Seabight.

Station	Depth	Date	Position Deg. N	 Deg. W	Gear
52218-1	1443 - 1447	26:6:85	49 25.4	12 49.8	BN
52218-3	1447	26:6:85	49 25.8	12 50.2	MC
11265-1	1440	19:4:86	49 26.8	12 51.3	MC
11265-3	1450 - 1470	19:4:86	49 24.7	12 52.3	BN
11267-1	1240	22:4:86	51 35.6	12 57.1	MC
11267-2	1240 - 1270	22:4:86	51 38.3	13 04.5	BN

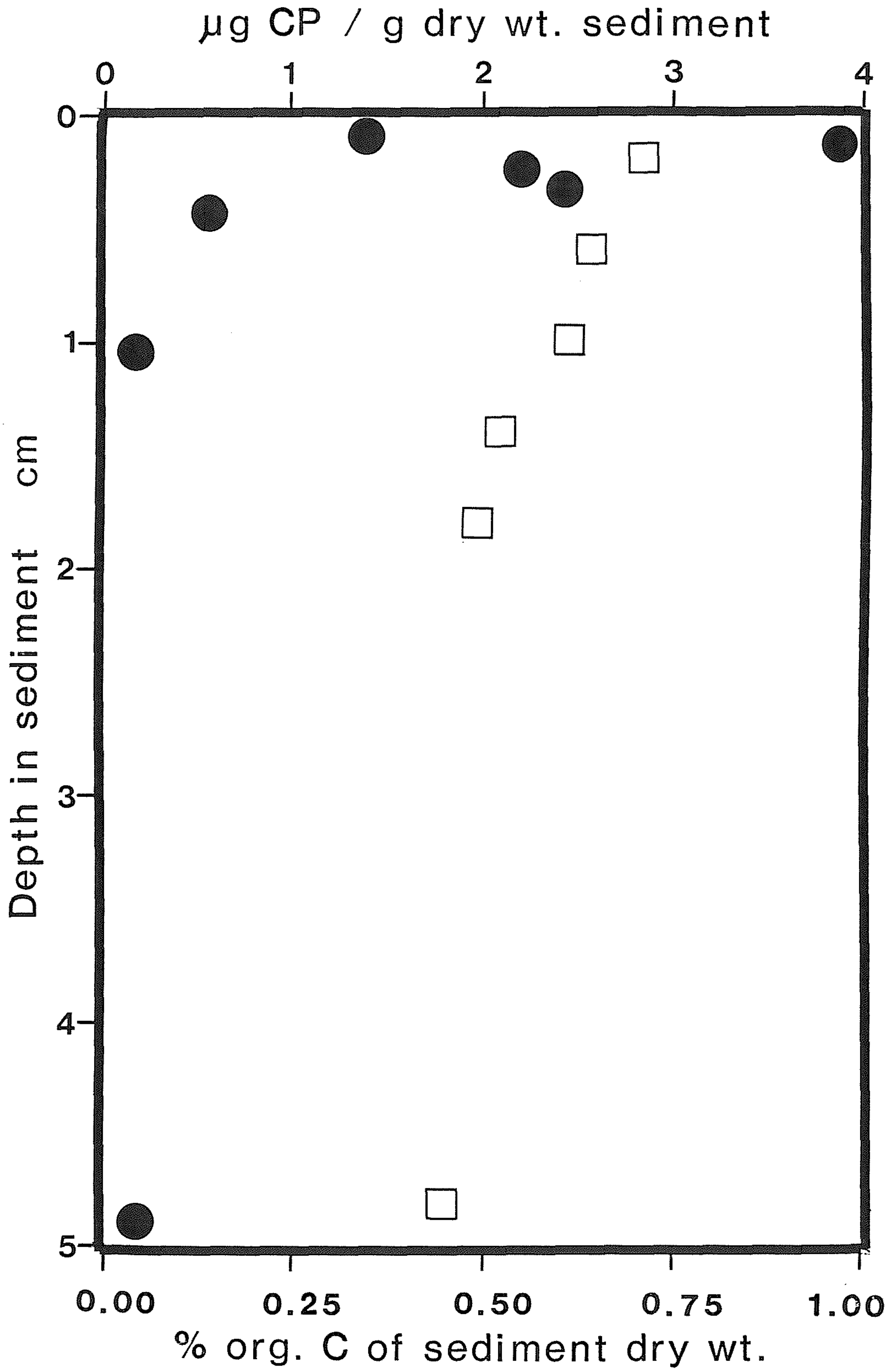
Samples for this study were taken at two sites in the Porcupine Seabight. One site, on the Goban Spur to the south of the Seabight, was sampled in June 1985 and April 1986, while the other site, in the north of the Seabight, was sampled in April 1986 only. For station details see Table 40. Sediment samples were taken with a multiple corer (Barnett, Watson and Connelly, 1984). On board ship the cores were frozen complete and then cut into layers, in some cases only 1mm thick, or the superficial layer was pipetted from the top of the core and frozen on pre-washed, ashed and weighed glass fibre filters (GFFs). Holothurians were collected using an IOS epibenthic sledge (see Section 2.2). Three species were studied, Paroriza pallens (St. 52218), Laetmogone violacea (St.11267) and Benthogone rosea (Stas 52218 and 11265). Five specimens of each holothurian were examined at each station, although quantitative data for B. rosea and P. pallens from St. 52218 are available only from 3 specimens of each species. The gut of each specimen was dissected and sediment from the oesophagus and the cloaca was frozen on GFFs.

The chloropigments in the sediment and gut content samples were analyzed as detailed in Section 2.2. Only the total quantity of chloropigments is used to determine feeding selectivity although the chromatograms from the gut contents and sediment samples are compared qualitatively. The dry weights of the samples were measured after the pigments had been extracted in acetone by drying at 40 °C for 24 hours. Values are expressed as μg total chloropigment per g sediment dry weight (salt included). Organic carbon in sediment samples was determined as detailed in Section 2.2. The samples of gut contents were too small for the accurate determination of organic carbon using the analytical methods available at IOS.

5.3.1 Distribution of chloropigments and organic carbon within the sediment.

Two cores from St. 11265 were subdivided into layers down to a depth of 5cm. One core was cut into 1mm layers from which seven selected layers were analysed for their total chloropigment content (Fig. 47). The chloropigments

Figure 47. Depth distribution of total chloropigments (CP) and organic carbon down to 5cm in cores from St. 11265. Chloropigments plotted as filled circles with salt included in dry weight. Organic carbon plotted as open squares with salt excluded from dry weight.


µg CP / g dry wt. sediment
0
1
2
3
4
0
1
2
3
4
5
Depth in sediment cm
0.00
0.25
0.50
0.75
1.00
% org. C of sediment dry wt.

are most abundant in the upper 5mm of the sediment and below this depth there is little change in the chloropigment concentration. The greatest concentration occurred between 1 and 4mm in the sediment and the concentration of chloropigments in the top 1mm was similar to that found in the superficial sediment of 6 other cores taken on the same deployment (Table 41). The second core was cut into 4mm layers and six layers were selected for total organic carbon analysis (Fig. 47). Higher levels of organic carbon are evident closer to the sediment surface.

Data from cores taken in June 1985 when a freshly deposited layer of detritus was found lying on top of the sediment also show sharp changes in the chloropigment concentration between the detrital layer, the superficial sediment lying immediately below the detrital layer, and the sediment at a depth of 1cm (Table 41).

5.3.2 Qualitative comparison of chloropigments in the sediment and holothurian gut contents.

The fluorescence chromatograms of the chloropigment separations for the detrital layer, the surface sediment and the oesophagus and cloaca contents of B. rosea and P. pallens, all from St. 52218, are presented in Figs 48 to 50. The five major peaks are associated primarily with the early degradation of chlorophyll a. Phaeophorbide pigments are the major chloropigments in all the chromatograms.

The chloropigment distribution in the surface sediment (Fig. 48B) is similar to that of the detrital layer lying over the sediment (Fig. 48A) although the total chloropigment concentration is much lower in the former (Table 41). Some admixture of the detrital layer will have

Figure 48. Fluorescence chromatograms of chloropigments in A) the detrital layer and B) the sediment lying underneath the detrital layer from St. 52218. The 5 major peaks are 1) an unknown polar degradation product of chlorophyll, 2) phaeophorbide pigments, 3) chlorophyll a, 4) phaeophytin a, and 5) ?pyrophaeophytin a. Relative fluorescence as for Figure 4. Sample dry wt. A) 0.050g, B) 0.176g.

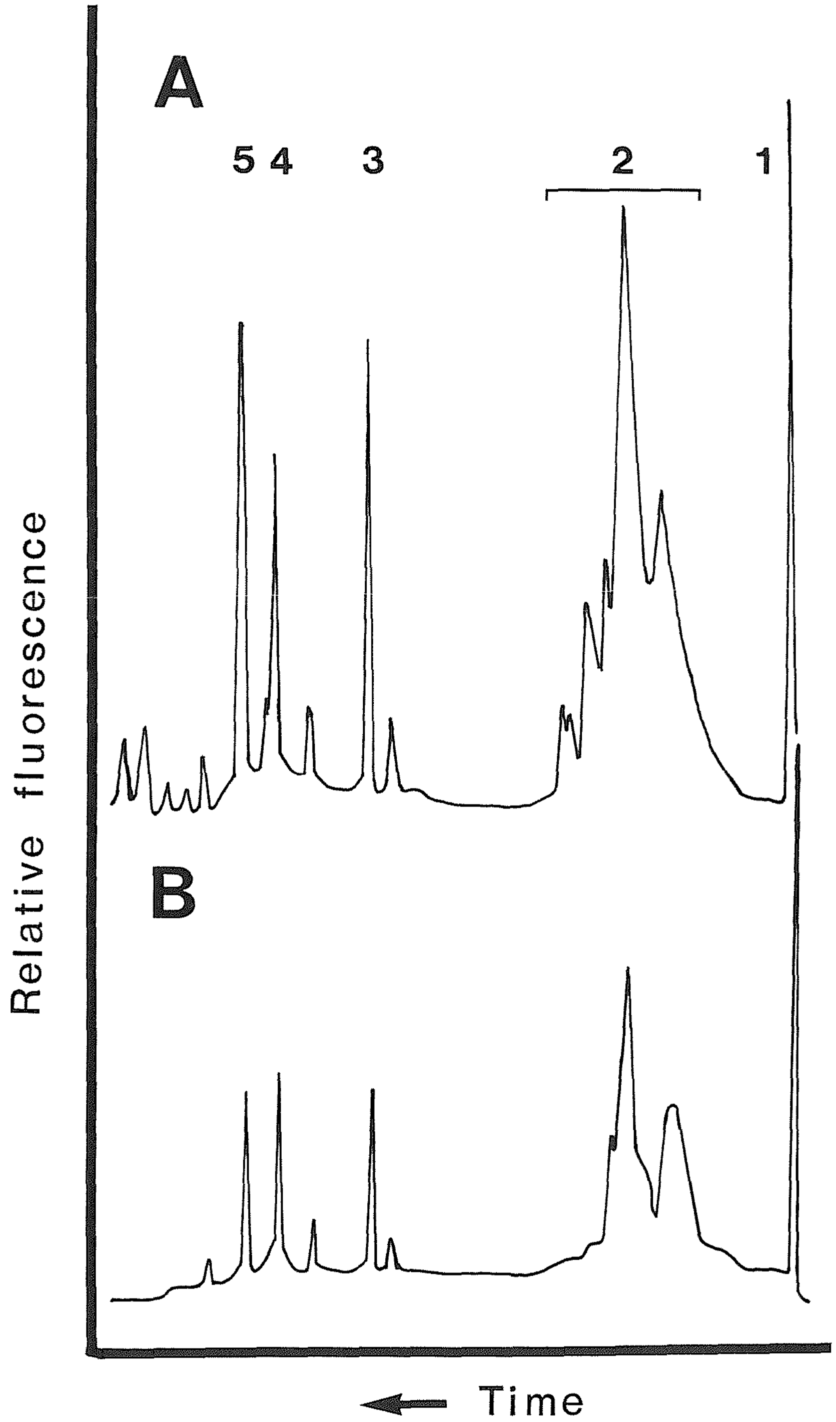

A
5
4
3
2
1
B
Relative fluorescence
Time

Figure 49. Fluorescence chromatograms of chloropigments in A) the oesophagus of B. rosea and B) the cloaca of the same specimen of B. rosea from St. 52218. The 5 major peaks identified are as for Figure 3. Relative fluorescence shows the relative concentration of each chloropigment. The height of each peak is dependent on the abundance of the pigment and the sample size. Sample dry wt. A) 0.049g B) 0.043g.

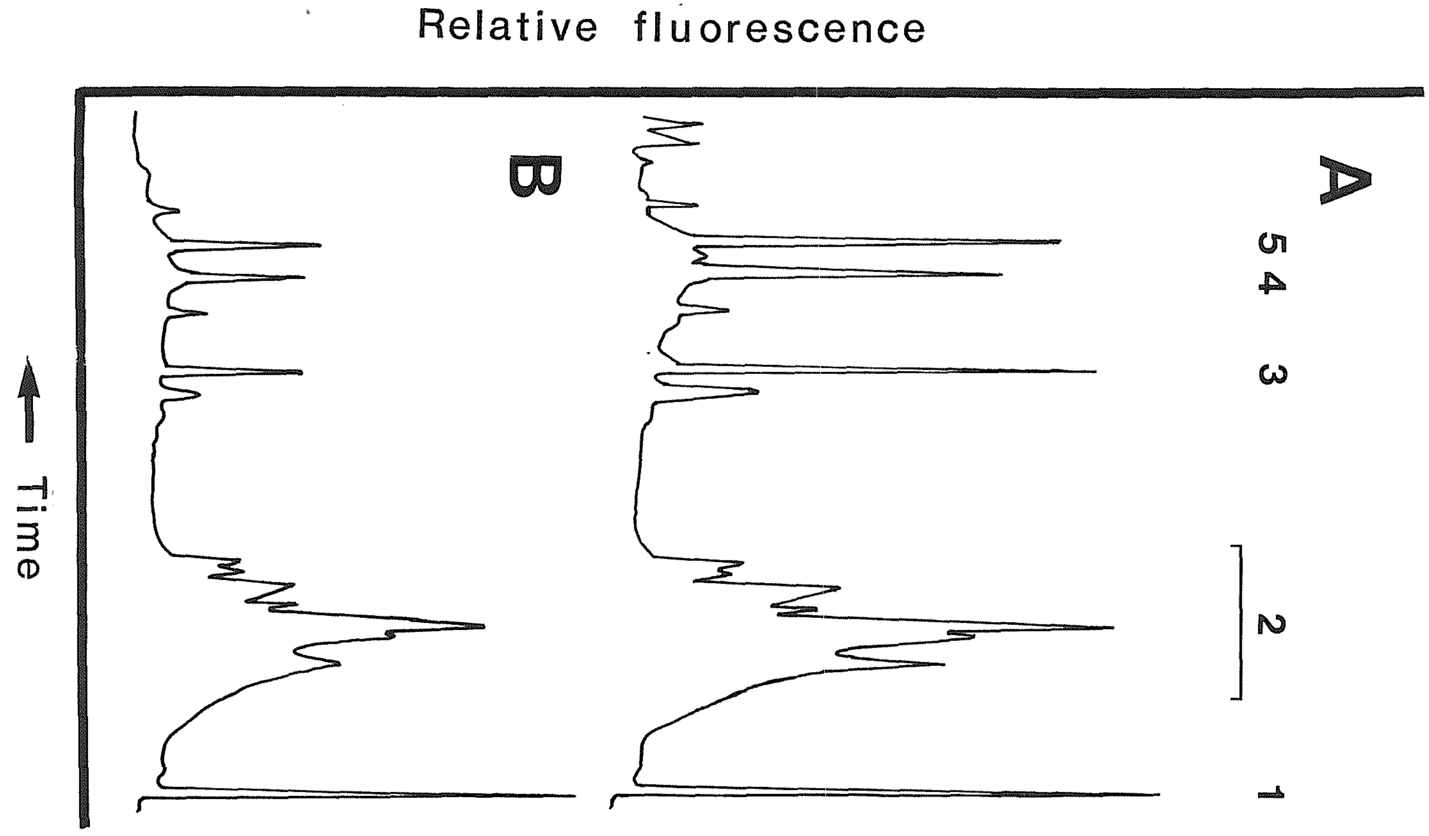
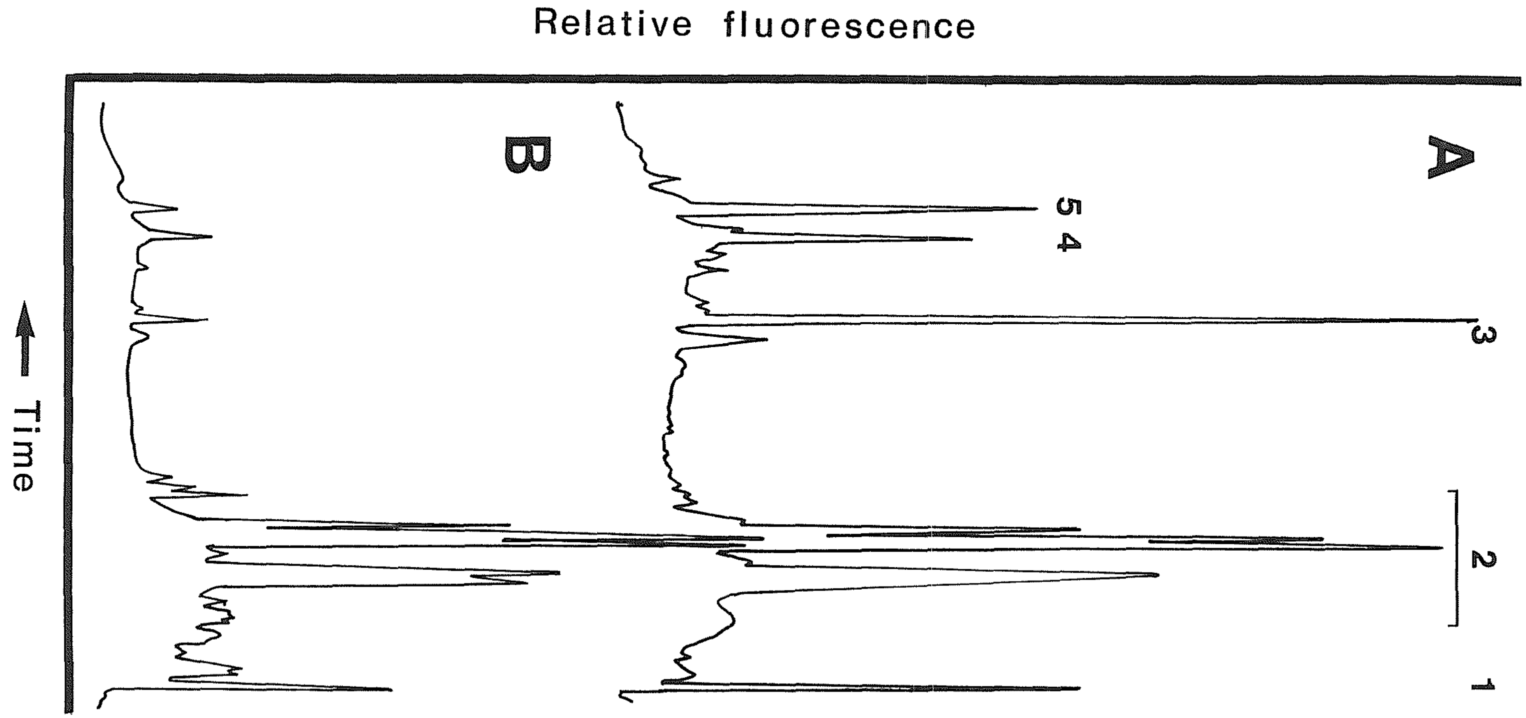

Relative fluorescence
A
B
5
4
3
2
1
Time

Figure 50. Fluorescence chromatograms of chloropigments in A) the oesophagus of *P. pallens* and B) the cloaca of the same specimen of *P. pallens* from St. 52218. The five major peaks identified are as for Figure 3. Relative fluorescence as for Figure 4. Sample dry wt. A) 0.154g B) 0.232g.


Relative fluorescence
Time
A
B
1
2
3
4
5

occurred with the underlying sediment resulting in these similar chromatograms. There are differences in the relative proportions of the phaeophorbide pigments which may signal the influence of detritus deposited in previous years and its subsequent degradation by the benthic fauna.

The fluorescence chromatogram for the oesophagus contents of *B. rosea* (Fig. 49A) is identical with that from the detrital layer (Fig. 48A). This, together with the similar total concentration of chloropigments (Table 41), indicates that *B. rosea* feeds directly on the detrital layer. The chromatogram for the cloaca contents of *B. rosea* (Fig. 49B) shows a reduction in the relatively less polar chloropigments (chlorophyll *a*, phaeophytin *a* and ?pyrophaeophytin *a*) suggesting that they are less stable in the gut than the phaeophorbide pigments.

The chromatograms for the gut contents of *P. pallens* (Figs 50A,B) differ from those for *B. rosea* (Figs 49A,B) in the relative proportions of the phaeophorbide pigments and in the relatively small amounts of phaeophytin and ?pyrophaeophytin in the former species. A selective degradation of chlorophyll *a*, phaeophytin *a* and ?pyrophaeophytin *a* appears to occur from one end of the gut to the other in *P. pallens*.

The chromatograms for the superficial sediment samples taken in April 1986 (Stas 11265 and 11267) are similar to the sediment layer chromatogram from St. 52218 (Fig. 48B) with lower levels of chlorophyll *a*, phaeophytin *a* and ?pyrophaeophytin *a*, relative to the phaeophorbide pigments. This is not surprising since the samples from April 1986 were taken before the onset of the spring bloom and hence before the deposition of fresh detritus in that year. The chromatograms for the gut contents of *L. violacea* and *B. rosea* from Stas 11267 and 11265 respectively are almost identical to those of the superficial sediment from their respective stations.

5.3.3 Quantitative comparison of sediment and holothurian gut contents.

The total concentration of chloropigments in the sediment and gut contents of L. violacea, B. rosea and P. pallens are given in Table 41. There is a significant increase in the chloropigment concentration in the oesophagus contents of L. violacea and B. rosea in the samples from April 1986 ($p < 0.05$) as shown by a non-parametric significance test. Using the mean values for chloropigment concentration from these stations, selection coefficients of 4 and 20 are indicated for B. rosea and L. violacea respectively.

Table 41: The range, mean and standard deviation of the total chloropigment concentration in sediment samples and the oesophagus and cloaca contents of holothurians, expressed as µg chloropigment per g dry weight of sediment (including salt). n = number of samples.

Sample	n	min	max	mean	SD
St. 11265					
Sediment - top 1mm	7	0.53	1.69	1.32	0.35
B. rosea oesoph.	5	2.28	8.70	5.84	2.86
cloaca	5	2.73	6.08	4.54	1.27
St. 11267					
Sediment - top 1mm	3	0.45	1.11	0.73	0.28
L. violacea oesoph.	5	6.11	26.58	14.69	6.79
cloaca	5	4.93	15.59	9.83	4.21
St. 52218					
Detrital layer	3	26.75	67.69	44.65	17.16
Superficial sediment	3	3.80	6.82	4.84	1.40
Sediment - at 1cm	1	0.63	0.63	0.63	
B. rosea oesoph.	3	20.06	45.53	32.15	9.49
cloaca	3	15.99	44.06	26.70	12.38
P. pallens oesoph.	3	5.51	15.71	11.45	4.33
cloaca	3	4.06	7.42	5.18	1.58

In contrast, no selectivity is evident for either B. rosea or P. pallens in June 1985, and in both cases the chloropigment concentration in the oesophagus is equal to, or less than, the concentration in the detrital layer. There is no significant difference between the concentration in the gut contents of either species and the detrital layer ($p > 0.05$, t-test). This results, in part, from the small sample sizes and the high variability in the chloropigment concentration of the detrital samples, for the concentration of chloropigments in the gut contents of P. pallens is consistently lower than that of the detrital layer. In contrast, a t-test comparison of the oesophagus contents of B. rosea and P. pallens shows that their chloropigment concentrations are significantly different ($p < 0.05$).

A comparison of the oesophagus contents with the cloaca contents on an individual basis for L. violacea, B. rosea and P. pallens, shows that for most specimens the chloropigment content in their cloaca is less than that in the oesophagus. However, in some cases the reverse is true. The simplest explanation for this is that the holothurians are feeding on a patchy food resource and that the organic content of the oesophagus of an individual is not necessarily comparable with that of the cloaca. When mean values from a number of specimens are examined (Table 41), the mean concentration of chloropigments is less in the cloaca than in the oesophagus in all 3 species, substantiating the qualitative evidence (section 5.3.2) that the chloropigments are transformed during passage through the gut. However, no significant difference is apparent between the two compartments of the gut for the species examined ($p > 0.05$, t-test), possibly an artefact resulting from the limited sample sizes.

5.3.4 Discussion.

Where selectivity during holothurian feeding has been indicated in the present samples by the chloropigment content, the selection coefficient has been similar to, or has even exceeded, values previously reported for other organic compounds (see above). If a holothurian makes a substantial contribution to the organic matter in its gut then the opposite result would have been expected. This implies that the holothurian's contribution is not significant. A note of caution is necessary though, for the selection coefficient may vary with season, geographic location, and the sediment sampling technique.

Detailed analysis of the vertical distribution of chloropigments and organic carbon within the sediment samples (Fig. 47) shows an exponential decrease in their total concentration with increasing depth. In studies using hydraulically damped box corers, which sample the sediment surface intact, similar exponential decreases in particulate organic carbon have been found (Soutar et al., 1981; Emerson, Fischer, Reimers and Heggie, 1985; Jahnke, Emerson, Cochran and Hirschberg, 1986). It is clear that the top few millimetres of the sediment are radically different from the underlying sediment and therefore great care must be taken in sampling the sediment-water interface if valid comparisons are to be made between the superficial sediment and holothurian gut contents.

The data from the Porcupine Seabight indicate that the selection coefficient for B. rosea, and probably other epibenthic deposit-feeding holothurians, changes on a seasonal basis and is related to the annual cycle in the deposition of detritus. Photographs taken in June 1985 from a camera mounted on the epibenthic sledge show that the recently deposited detritus covered about 80% of the sediment surface in a fine, even layer providing holothurians like *B. rosea* with an almost homogeneous food source. The observed quantitative and qualitative similarities in the chloropigments of the detritus and the oesophagus contents of *B. rosea* (Table 41; Figs 48,49) implies that it feeds readily and indiscriminately on the detritus, a conclusion substantiated by photographic evidence from time-lapse photography (Fig. 27H, page 159, Dr. R.S. Lampitt, personal communication). The detrital material is known to contain nutritious organic compounds such as polyunsaturated fatty acids (Rice *et al*., 1986).

Photographic observations from the Seabight over the past 8 years show that the detritus seldom remains for very long as a blanket on the seabed. Nearbed currents move the detritus over the seabed and, when critical current velocities are reached, the detrital particles are resuspended (Lampitt, 1985). The combination of bottom topography and nearbed currents eventually produces a mosaic of detrital patches (Billett & Hansen, 1982; Billett *et al*., 1983; Sibuet, 1984), presenting the holothurian with a heterogeneous distribution of its food. Holothurians may then seek out nutritious material by some sorting mechanism which suspends the smaller, less-dense particles (Sibuet *et al*., 1982) or resort to detecting patches of sediment with higher levels of organic matter. The strategy adopted may vary according to the scale of the patches.

It is not possible to resolve which method of selection is operating from the data presented in this study. Although several sediment samples were analysed at each station, all the samples came from the same deployment of the multiple corer. Therefore, at each station all the cores were taken in close proximity to eachother and as a consequence the variability of chloropigments over a wide area is not known. However, the high variability in the chloropigment concentration in the oesophagus of the holothurians, and the fact that in some specimens the concentration of chloropigments was greater in the cloaca than in the oesophagus, indicate that the holothurians are feeding on a patchy food resource.

A note of caution is necessary here concerning the selection coefficients calculated in Section 5.3.3, for the concentrations of chloropigments in the gut contents of _L. violacea_ and _B. rosea_ were compared with sediment samples taken from a single small area of the seabed. Different selection coefficients may have been found if the variability of chloropigment concentration had been known from a wide area at each locality.

Spatial variability in the food supply for holothurians is also indicated by other studies. Samples from hydraulically damped box corers show that the organic content of the superficial sediment layer can be highly variable (Emerson _et al_., 1985; Jahnke _et al_., 1986). Indirect evidence for the patchy distribution of food for deposit-feeding holothurians is also indicated by studies on the spatial distribution of holothurians on the seabed (Section 5.4; Pawson, 1982a). More data are needed on the distribution and temporal variability of organic matter in the superficial sediment layer, and on chemosensitivity in holothurians, as originally suggested by Sibuet (1984).

Sokolova (1958) and Hansen (1975) noted the diversity of tentacle structure in deep-sea holothurians, but neither author was able to detect any correlation between tentacle structure and the gut contents of the holothurians when analysed under the light microscope. However, chemical analyses may eventually be able to show different feeding strategies in sympatric species. For example, the differences in the fluorescence chromatograms between the gut contents of P. pallens and B. rosea from St. 52218 (Figs 49,50) may result from differences in their feeding strategy. There is a measure of doubt in accepting this interpretation because the larger sample size used for the analysis of P. pallens gut contents may have lead to the incomplete extraction of the chloropigments in this species (Ms. C. Llewellyn, personal communication). However, if this was the case then greater differences would be expected between, say, chlorophyll a and the phaeophorbide pigments, rather than between the phaeophorbide pigments themselves. The differences between B. rosea and P. pallens are therefore considered to be real, especially in view of the differences in the structure of the tentacles of the two species. P. pallens has a digitate tentacle with about twelve marginal processes surrounding the tentacle disc, while B. rosea has a peltate tentacle lacking any marginal processes. Thus, P. pallens may be able to pick up individual large particles which the tentacles of B. rosea would find difficult to manipulate.

Many of the detrital particles that reach the seabed are several millimetres in diameter (Billett et al., 1983; Lampitt, 1985). Detrital particles of different sizes could well have a different chloropigment composition since they will be transported and degraded by different pathways. The difference in the fluorescence chromatograms for the two species may therefore indicate that P. pallens selects slightly different (larger?) particles than B. rosea. A subjective analysis of the particles in the guts of the two species by Khripounoff and Sibuet (1980) has shown that there are indeed qualitative differences between the particles that they ingest. However, it is not clear if the specimens used in this analysis came from the same station. In contrast, a comparison of the granulometry of the sediment and of the the stomach contents of

B. rosea and *P. pallens*, all from the same area, did not show any significant differences in the size of particles ingested by the two species (Khripounoff and Sibuet, 1980).

Holothurians often dominate the invertebrate megabenthic communities at bathyal and abyssal depths. Whatever feeding selection processes are operating it is clear that holothurians play a major role in the early degradation of organic matter reaching the seabed. Therefore the elucidation of feeding strategies of epibenthic holothurians is vital if biogeochemical fluxes at the sediment-water interface are to be understood.

5.4 Small scale spatial distributions of holothurians.

The spatial distributions of holothurians on the seabed can be studied by analysing photographs taken during epibenthic sledge hauls (see Section 2.2). However, the abundances of most species in the PSB are too low to allow their spatial distributions to be studied using this technique. Patchiness in the distribution of many species is evident from the large variability in the abundance of any one species at a chosen depth (Section 4.2), but such patchiness is on a scale that cannot be resolved from the photographs. Photographs are taken every 15 seconds while the sledge is on the seabed which at a towing speed of about 1.5 knots leads to a distance of about 12m between consecutive photographs. Some species, such as *Benthogone rosea*, can be found in 3 or 4 consecutive frames which may indicate the presence of large patches. The holothurians may occur in aggregations some 30 to 50m in diameter, as found for the echinoid *Phormosoma placenta* (Grassle *et* *al*., 1975), but the data are too scanty for any statistically significant results to be drawn. In contrast to the low abundance of most PSB holothurians, the profusion of small *Kolga hyalina* in the PSB has allowed the distribution of this species to be studied in detail. Dense aggregations have been observed on a scale smaller than the area covered by a photograph and temporal changes in its dispersion pattern have been demonstrated.

Aggregations of small holothurians have been reported before in the vicinity of canyon systems in the northwest Atlantic. Stanley and Kelling (1968), while carrying out a geological survey of the Wilmington Canyon, noted aggregations of "large elongate granules" in their photographs from a depth of 1500m, which were later identified as *Peniagone*-like holothurians (Rowe, 1971, 1972). Similar aggregations were found at 2000 to 2400m in the Hatteras Canyon (Rowe, 1971), along the lower continental slope near the Hydrographer Canyon (Rowe, 1972), and at 1615m within a gully north of Cape Hatteras (Ross, 1970; Heezen and Hollister, 1971 in Rowe, 1971). In addition, Ohta (1983) has noted aggregations of *Peniagone japonica* in canyon-like settings at depths of 500 to 1700m off Japan.

The abundance of *K. hyalina* was estimated in each frame by superimposing the photographs on a perspective grid constructed by photographing a test grid, subdivided into 5 by 5 cm sub-units, in a water tank at IOS. Modifications to the structure of the epibenthic sledge during the period of this study led to a change in the position of the camera on the sledge and hence to the area of seabed photographed. Initially (in 1978) the camera was placed at a shallow angle (Rice *et al*., 1979) but small variations in the elevation of the sledge relative to the bottom, caused by uneven topography, led to large differences in the area covered by each photograph. The camera was therefore mounted (from 1979) at a greater height and at a steeper angle which not only reduced the total surface area covered by each photograph but also reduced the variability in the area photographed. A trapezoid-shaped area of 1 m^2 with parallel sides 73 and 127 cm long has been used for analysing the photographs taken since 1979. A similar shaped area covering 0.95 m^2 was used for photographs taken in 1978. In both cases only the front portion of the photographs was used for analysis since outside this area it was not possible to identify the small *K. hyalina* with any confidence.

The numbers of *K. hyalina* visible in each photograph are plotted in Figs 51 and 52. Treating the analysed area in each photograph as a trapezoid-shaped quadrat, the degree of aggregation at each station was determined using Lloyd's measure of patchiness $\overset{*}{x}/\bar{x}$, where $\overset{*}{x}$ is the index of mean crowding (the mean number, per individual, of other individuals in the same sampling unit) and $\bar{x}$ is the sample mean (for formulae see Lloyd, 1967). For an aggregated pattern $\overset{*}{x}/\bar{x} > 1$ with no specific value for maximum aggregation, and $\overset{*}{x}/\bar{x} = 1$ for a random pattern. The index of patchiness measures the range in abundance of a spatial pattern and as it is independent of mean density it is useful when comparing populations with different abundances (Pielou, 1974). However, at low abundance, in this case about 2 individuals per square metre, the detection of a patchy distribution may be dependent on the number of sampling units since the probability of encountering an aggregation will be low (e.g. St. 52403-14, see below).

Dense aggregations of *K. hyalina* were encountered at Stas 9756-9 (4050m) and 9756-14 (3690m) sampled in April 1978 (Fig.51). Although the largest aggregation, of about 700 individuals (Fig 53A), was gathered around a

Figure 51. The number of *Kolga hyalina* within the analysed area of each photograph arranged in sequence. The spaces in between the observations represent either a photograph in the series that was unusable or, if marked by a continuous line at the bottom, a photograph devoid of *K. hyalina*. In order that all the histograms could be drawn to the same scale and that small fluctuations could be seen, the peaks in the histograms were truncated at 100 individuals and the total number of *K. hyalina* entered at the top of the corresponding column. The patchiness for each station is expressed by Lloyd's index of patchiness and its standard error (see text).

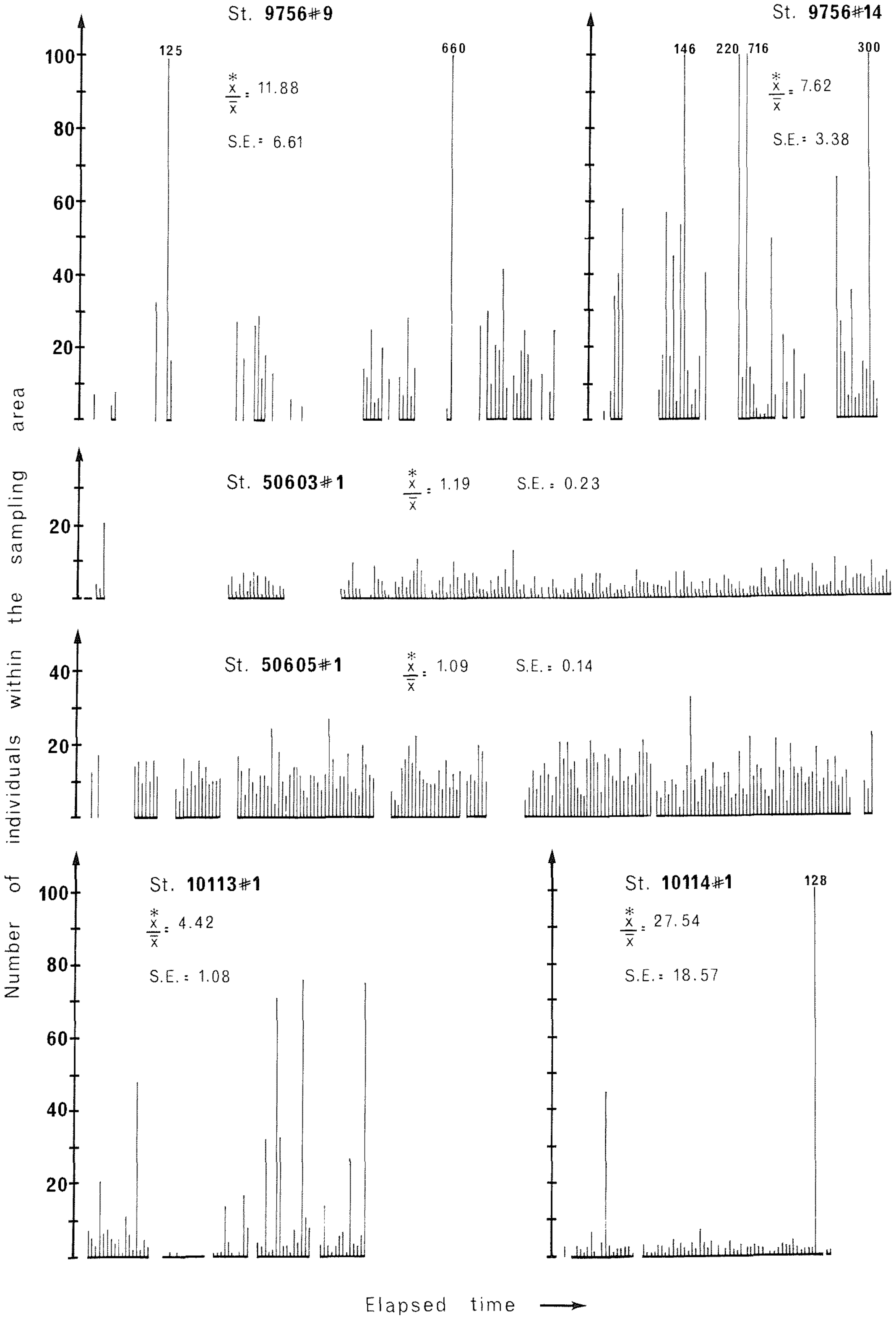
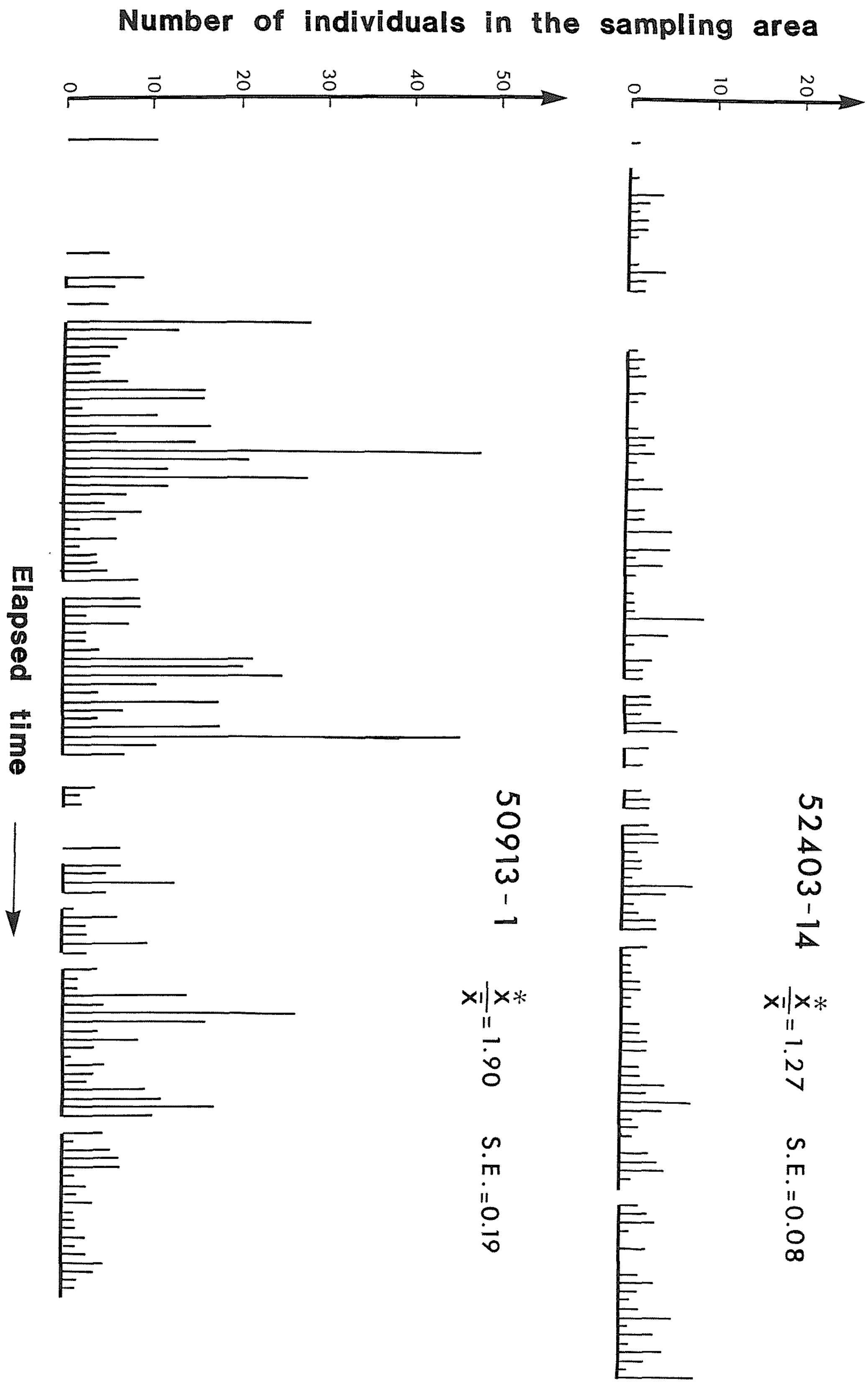

St. 9756#9
$\frac{\overset{*}{x}}{\bar{x}}$ = 11.88
S.E. = 6.61
125
660
St. 9756#14
146
220
716
300
$\frac{\overset{*}{x}}{\bar{x}}$ = 7.62
S.E. = 3.38
St. 50603#1
$\frac{\overset{*}{x}}{\bar{x}}$ = 1.19
S.E. = 0.23
St. 50605#1
$\frac{\overset{*}{x}}{\bar{x}}$ = 1.09
S.E. = 0.14
St. 10113#1
$\frac{\overset{*}{x}}{\bar{x}}$ = 4.42
S.E. = 1.08
St. 10114#1
128
$\frac{\overset{*}{x}}{\bar{x}}$ = 27.54
S.E. = 18.57
100
80
60
40
20
Number of individuals within the sampling area
Elapsed time

Figure 52. The number of K. hyalina within the analysed area of each photograph arranged in sequence for samples taken in November 1980 (St. 50913-1) and December 1986 (St. 52403-14). Details as for Figure 51.


Number of individuals in the sampling area
0
10
20
0
10
20
30
40
50
52403-14
$\frac{\overset{*}{x}}{\bar{x}}=1.27$
S.E.=0.08
50913-1
$\frac{\overset{*}{x}}{\bar{x}}=1.90$
S.E.=0.19
Elapsed time

sedimentary ring structure, there was no obvious relationship between K. hyalina aggregations and sediment topography. At both stations, particularly St. 9756-9, the erratic behaviour of the sledge led to mud clouds obscuring many photographs. Where possible, the patchiness index was calculated using these partly obscured photographs in addition to those covering the standard sampling area. At St. 9756-9 only three dense aggregations were seen, two occurred on photographs partly obscured by mud (Fig. 53B), while the third lay totally outside the area of the photograph used for the analysis of patchiness. This illustrates to some extent the dependence of the patchiness index on the number of sampling units.

A large number of photographs were available from Stas 50603-1 (4000m) and 50605-1 (2900m) sampled in July 1979 (Fig. 51). Despite the intensity of sampling no aggregations were found, suggesting that the holothurians were more evenly distributed than in April 1978. It seems improbable that dense aggregations were missed by chance at either station owing to the large number of photographs taken. Patchiness values at both stations approached unity (random distribution), but tests for randomness using the "index of dispersion" (Andrew and Mapstone, 1987) failed to show agreement with the expected Poisson distribution ($P < 0.01$). Both stations were sampled during the summer when detrital material collects on the seabed in the PSB (see Sections 2.1 and 5.3), although detrital patches around mounds and other sedimentary structures were obvious only at St. 50603-1 (Fig. 54A).

Dense clumps of holothurians were also absent at St. 10113-1 (2760m) sampled in September 1979 (Fig. 51), although some degree of aggregation is indicated by the patchiness index. Several photographs had 70 to 80 individuals in patches that were on a scale greater than that

Figure 53. A) St. 9756-14. Dense aggregations of *Kolga hyalina* gathered around a sedimentary ring structure. B) St, 9756-9. Aggregation of *K. hyalina*.

covered by a single photograph but smaller than could be detected by consecutive photographs. Two dense aggregations of several hundred individuals were seen at St. 10114-1 (4040m), also sampled in September 1979, but owing to poor focussing of the camera it was difficult to detect single K. hyalina with any confidence. Both peaks in abundance evident in Fig. 51 correspond to clumps of K. hyalina that are lying only partly in the area of the photographs that was analysed. The index of patchiness is particularly sensitive to the quality of the data at this station and all that can be concluded is that the degree of aggregation is as great as, if not greater than, the samples taken in April 1978.

More K. hyalina were photographed in November 1980 and December 1986 at Stas 50913-1 (3000m) and 52403-14 (4800m) respectively. Although there was a tendency towards aggregation at the former station, with a maximum abundance of 48 individuals in one photograph, no such distribution was evident at the latter station (max. abundance - 9 individuals per frame) (Fig. 52). In both cases dense clumps were not detected. For the latter station it is possible that clumps were present but were very rare. However, this seems improbable as over 200 photographs, covering some 500 square metres, were taken at this station.

A dispersed pattern was evident at St. 51619-1 (1500m) sampled by the photosledge in July 1982. Unfortunately the camera angle was set incorrectly for this haul and no quantitative data are available. As detailed in Section 4.2 subsequent sampling in this same area in 1983 failed to show any trace of K. hyalina suggesting that either the entire population had been predated upon or that the holothurians had moved to another area.

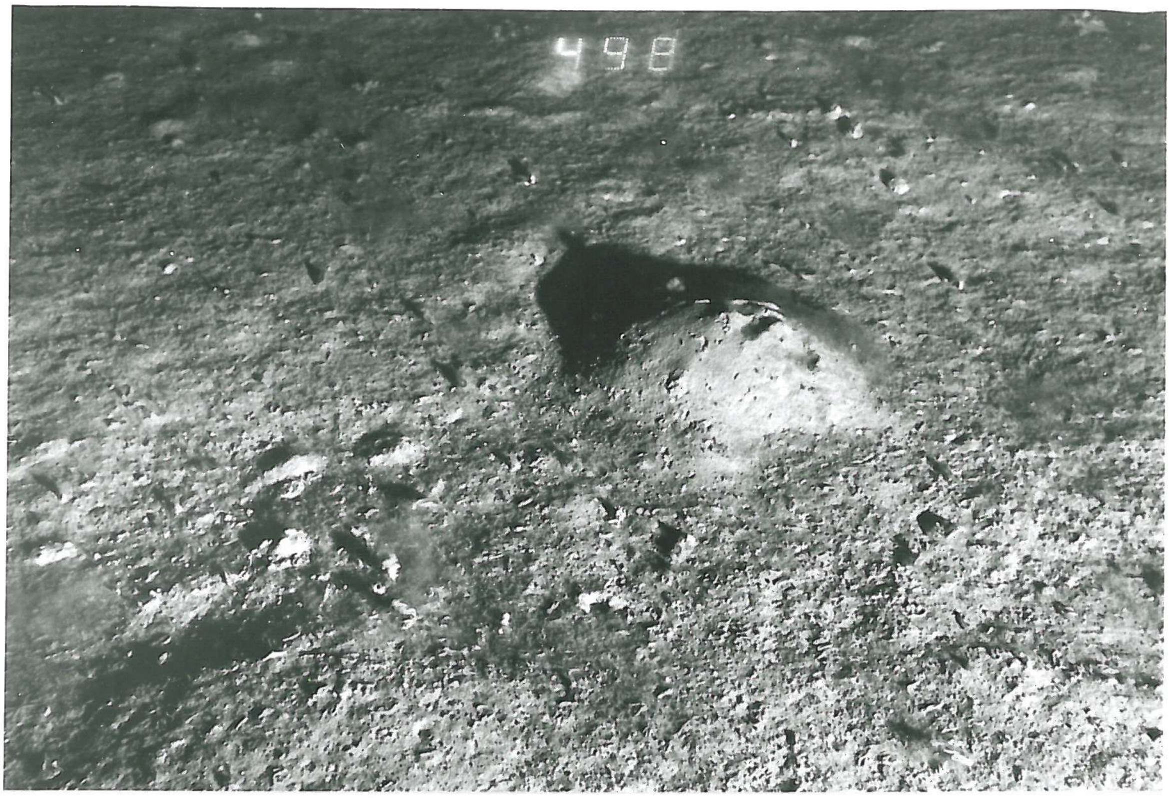
Support for the latter scenario comes from time-lapse photographic observations using Bathysnap (Lampitt and Burnham, 1983) and detailed in Section 4.2. Two Kolga aggregations passed through the field of view of the camera within a 16 hour period with all the holothurians travelling in the same direction. This uniformity in orientation was also evident in photographs from St. 9756-14 where 90% of the individuals were facing into the prevailing current, as determined from the angle of sea-anemone tentacles and the way in which mud, stirred up by the towing warp, was swept away in front of the sledge. No preference in orientation was noted at any other station. Preferred orientation of other holothurians in aggregations, such as Paelopatides gigantea (Heezen and Hollister, 1971), Ellipinion delagei (Pawson, 1982a), Scotoplanes sp. (Barham et al., 1967; Pawson, 1976), and Peniagone japonica (Ohta, 1983), have been noted also, and in a few cases it is evident that these holothurians also face into the prevailing current.

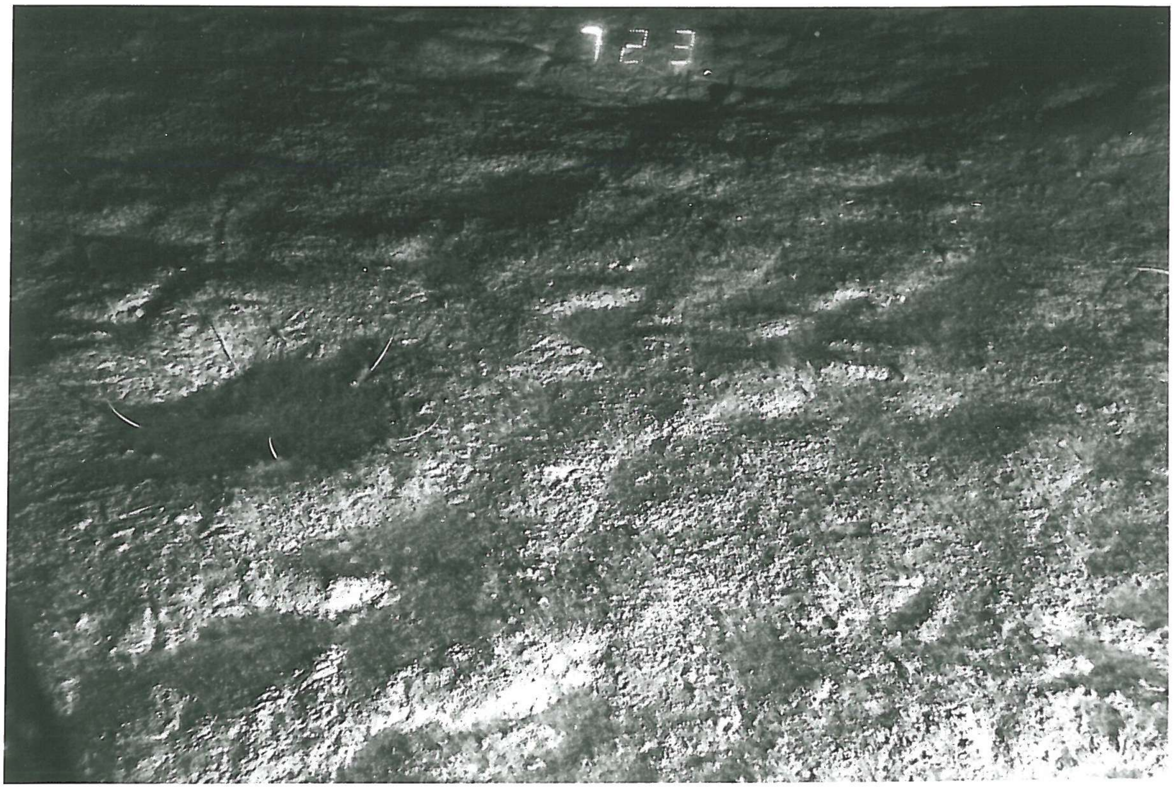
It is apparent that dense clumps of Kolga (Fig. 53A) are not merely point aggregations centred, for instance, on a localised food source, which then disperse once the organic matter has been consumed, but that there is some social interaction between the holothurians that maintains the aggregation as it passes over the seabed.

Another important feature is the variability of the distribution pattern of K. hyalina with time. Temporal changes are indicated by the similarity of the distribution patterns at Stas 50603-1 and 50605-1, both sampled in summer, despite being sampled in two contrasting areas, and by the transformation in the distribution patterns in both areas when they were sampled again just 2 months later (Stas 10113-1 and 10114-1) (Fig. 51). This change in distribution pattern coincides with the period when the detrital layer changes from an even to a patchy layer. During summer months when detrital material is deposited as an even layer on the seabed (Billett et al., 1983; Lampitt, 1985), at least for a few weeks, the holothurians are able to feed on an evenly distributed food source (see Section 5.3). In this case a distribution pattern tending towards randomness would be expected and is observed. However, detrital material seldom remains on the sediment surface as an even layer for very long, but is resuspended and moved about so that it collects around mounds and within hollows (Fig. 54A,B). A patchy food resource is formed, the scale of which is determined by the microtopography of the seafloor (see Section 5.3) and which could lead therefore to the observed K. hyalina aggregations.

However, the simple cause and effect of patchy detrital layers does not explain adequately the observations of herding. It is clear that the causes of aggregation formation and maintainance are far mor complex. Resource limitation has been invoked by Jumars and Gallagher (1982) as a possible explanation for the herding behaviour of the echinoid Phormosoma placenta (Grassle et al., 1975). These echinoids occur in rare clumps, about 40 to 50m in diameter, that occupy only a small proportion of the sediment surface. The aggregations were observed to be in slow but continuous motion across the seabed, presumably in search of pastures new, since food would soon be used up within the aggregation. The herds may form as an adaption to reduce the probability of an echinoid recrossing an area that has been fed upon before the food resource has been replenished. However, this type of feeding strategy seems unlikely for K. hyalina since clumps are found even at low population densities (e.g. the Bathysnap observations).

Figure 54. A) St. 50603-1. Several *K. hyalina* with patches of detritus. B) St. 50602-2. The ophiuroid *Ophiomusium lymani* in a hollow covered by detrital material. Other flocculent patches can be seen also.


498


723

Other factors, therefore, must be sought to explain the maintainance of *Kolga* patches. The most plausible is that aggregations aid reproductive success. There is little doubt that *K. hyalina* has a highly synchronous and periodic reproductive cycle (Section 4.2). Although no correlation between gonad maturation and spatial pattern could be found, maintainance of an aggregation would ensure that all the individuals develop concurrently and would experience the same environmental clues that might initiate periodic gametogenesis and spawning. In addition, aggregation would increase fertilisation success by ensuring that all the gametes are released at the same time and in the same place.

Reproduction may be the root cause of aggregation but food resources will undoubtedly play a role in controlling the dimensions of the aggregations. In areas at the base of the slope (Stas 9756-9, 9756-14, 10114-1) where there are numerous biogenic sedimentary structures, detrital material will be distributed more heterogeneously than at depths of about 2900m (Stas 10113-1, 50913-1) where few biogenic structures are found. The influence of micro-topography on the distribution of organic matter in surface sediments could account for the observed greater degree of aggregation at the base of the continental slope than at either 2900m or 4800m on the abyssal plain (St. 52403-14).

5.5 Holothurian reproduction and life-history strategies.

Little is known of the mode of development of deep-sea holothurians even though this feature is of crucial importance in understanding life-history strategies. Data from shallow-water benthic invertebrates has allowed a general relationship to be formed between egg size and the type of development adopted (Thorson, 1950, see Section 1.4, page 13). Using this relationship the development of deep-sea species may be inferred from the maximum egg diameter found. However, the organic content of eggs is not necessarily related to egg size (Strathmenn and Vedder, 1977; Turner and Lawrence, 1979; Emlet *et al*., 1987) and as a result eggs of a similar diameter can lead to different forms of development. For deep-sea holothurians, knowledge of their geographic and bathymetric distributions may help in elucidating their mode of development. In particular, the larval development of species living on the slope should differ from that of species living on the abyssal plain, for in the one environment the holothurians must maintain their populations in a narrow, often discontinuous band around the margins of the ocean, while in the other they occupy a vast and, in many ways, continuous environment.

The holothurian species in the PSB can be split into 5 groups based on their bathymetric zonation detailed in Section 5.2. The maximum egg sizes known for each species within these groups are summarised in Table 42. Three groups lie on the continental slope, the fourth includes species which occur on the abyssal plain but which are also common on the lower slope, while the fifth group includes the species that live primarily on the abyssal plain.

Table 42. The maximium egg diameter (µm) of holothurians from the Porcupine Seabight, arranged according to their bathymetric zonation. Species that occur in more than one group, e.g. *Kolga hyalina*, are placed in the group in which their abundance was the greatest.

A. Upper slope.		
	Stichopus tremulus	120
	Bathyplotes natans	280
	Echinocucumis hispida	320
	Ypsilothuria talismani	340
	Thyone gadeana	400
	Laetmogone violacea	400
	Psolus squamatus	450
	Mesothuria intestinalis	650
B. Middle slope.		
	Mesothuria maroccana	200
	Paroriza pallens	250
	Mesothuria verrilli	400
	Mesothuria lactea	400
	Benthogone rosea	750
	Paelopatides grisea	1600
	Psychropotes depressa	1900
C. Lower slope.		
	Cherbonniera utriculus	200
	Peniagone azorica	300
	Ypsilothuria bitentaculata	350
	Benthothuria funebris	1500
D. Lower slope / Abyssal plain.		
	Myriotrochus bathybius	160
	Myriotrochus giganteus	200
	Protankyra brychia	200
	Molpadia blakei	200
	Kolga hyalina	240
	Peniagone diaphana	300
	Enypniastes diaphana	3500
E. Abyssal plain.		
	Pseudostichopus sp.	300
	Paroriza prouhoi	400
	Pseudostichopus villosus	400
	Mesothuria candelabri	500
	Deima validum	800
	Oneirophanta mutabilis	950
	Benthodytes sordida	2000
	Psychropotes semperiana	3500
	Psychropotes longicauda	4000

As noted for other taxa (Thorson, 1950; Ocklemann, 1965; Knudsen, 1967, 1970) there is a reduction in the number of holothurian species in the deep sea that develop via a planktotrophic (feeding) larval stage. Only the shallowest species in the PSB, S. tremulus, has an egg size (120µm) that can be interpreted unequivocally as leading to planktotrophic development. This type of development is consistent with the wide distribution of S. tremulus at shallower depths on the continental shelf and over a wide bathymetric range at the top of the slope (ca. 1000m). It is probably not necessary for the deep-sea populations of S. tremulus to maintain themselves, since larvae from the continental shelf populations will be carried into deeper water. In contrast, other slope-dwelling holothurians must ensure that their larvae do return to the adult habitat.

Many echinoderm planktotrophic larvae have a long pelagic development. Strathmann (1978) found that for 12 shallow-water echinoderms with planktotrophic development the minimum time from fertilisation to settlement was 6 to 8 weeks. If larvae from slope-dwelling holothurians developed in surface waters for this length of time it is probable that only a few would return to a habitat suitable for adult development. Slope-dwelling echinoderms that possess small eggs indicative of planktotrophic development, such as he ophiuroid Ophiura ljungmani (Schoener, 1972; Tyler and Gage, 1979, 1980) and the asteroid Plutonaster bifrons (Tyler and Pain, 1982), have wide bathymetric ranges (Gage et al., 1983), in contrast to most holothurian species which have restricted bathymetric ranges. This is one indication that development for many holothurians occurs by some other pathway.

With the possible exception of the hermaphrodite M. intestinalis, most species on the upper slope produce eggs 200 to 450µm in diameter, indicative of lecithotrophic (non-feeding) larval development (Table 42). The duration of lecithotrophic development can be short (abbreviated development) and is known to take only a matter of days in both ophiuroid species with egg diameters of 130 to 350µm (Hendler, 1975) and the molpadiid holothurian Molpadia intermedia (270µm egg diameter) (McEuen and Chia, 1985). However, in the absence of a suitable settling substrate it is known that development of lecithotrophic larvae can be extended greatly (Yamaguchi, 1974). This type of rapid lecithotrophic development would be a distinct advantage for a species living on the slope.

Development rates in the deep sea are not known and could be longer than in shallow water owing to the low temperatures typical of bathyal and abyssal depths. However, low metabolic rates in the deep sea are regarded as an adaptation to low food availability rather than the effect of low temperature and high pressure (Somero et al., 1983). In some cases metabolic rates in the deep sea, as shown for example by barophilic bacteria (Yayanos et al., 1979; Tabor et al., 1982), can be as high as those measured in shallow water. Therefore where food is non-limiting, such as in a lecithotrophic egg, metabolic rates and hence development could be as fast in the deep sea as in shallow water. However, Emlet et al. (1987) conclude from reviewing the developmental rates of shallow-water echinoderms, including those from Antarctica, that neither acclimitization nor adaptation (to low temperatures) provide complete temperature compensation, and that for some unknown reason development is necessarily slower at lower temperatures. Indeed, some deep-sea species might benefit from prolonged larval development at low temperatures.

Many mid and lower slope holothurians also produce eggs of an intermediate size (Table 42) and probably develop in a similar fashion to the upper slope species. Abbreviated larval development of the opportunistic holothurian K. hyalina indicated by its intermediate egg size (240µm), is substantiated by the appearance of large numbers of juveniles from the same reproductive event in circumscribed areas on the seabed. It is clear that the juveniles are dispersed from the adult population, but at the same time the dispersal phase must be short or the juveniles would be spread over a much wider area. Surprisingly, the geographic distributions of slope species that produce eggs of an intermediate size are quite variable. For instance, B. natans (280µm) is reported to have an almost cosmopolitan distribution, while P. pallens (250µm) appears to be restricted to mid-slope depths in the northeast Atlantic. The organic composition of shallow-water echinoderm eggs has been shown to be quite variable (Turner and Lawrence, 1979). It is possible that the composition of deep-sea echinoderm eggs could influence the type of development adopted, in particular the buoyancy of the egg and the duration of the larval phase.

Not all the species living on the slope have lecithotrophic larval development. Some species have eggs over 1mm in diameter indicative of direct development without a larval stage. Direct development is often equated with limited dispersal because very often it occurs on the seabed. However, there is growing evidence that in the deep sea direct development occurs in the pelagic environment for many species.

Details are given in Section 4.2 of juvenile psychropotid holothurians that have been sampled by pelagic nets. Adults produce eggs 2 to 4mm in diameter (Table 42). Most of the juveniles have been found within a few hundred metres above the seabed, although a few have occurred a few thousands of metres above the seafloor. None have been reported from surface waters, suggesting that development occurs in the abyssopelagic and bathypelagic zones. This type of development has several advantages. First, it allows the wide dispersal of the juvenile. Mortality resulting from juveniles drifting into areas unsuitable for adult development would be minimal since the abyssal environment is so vast. Second, biomass of midwater animals, and hence, it is presumed, potential predators of juvenile holothurians, decreases exponentially through the water column (Angel and Baker, 1982), although there is also an increase in biomass close to the seabed (Wishner, 1980). Predation of juveniles, therefore, would be expected to be lower in the abyssopelagic zone than in either surface waters or on the seabed. Hansen (1975) suggested that the large egg size of psychropotid holothurians could be an adaptation to prolonged pelagic development, but equally, as suggested by Strathmann (1977) for development in other invertebrates, a large egg will produce a large larva or juvenile at metamorphosis thereby reducing predation of both the pelagic phase and the juvenile when it settles on the seabed.

Slope-dwelling holothurians that produce large eggs, such as _Paelopatides grisea_, _Benthothuria funebris_ and _Psychropotes depressa_ (Table 42), might be expected to have direct, pelagic development like the species on the abyssal plain, and indeed a pelagic juvenile of _P. depressa_ has been collected in a pelagic trawl (see Section 4.2). However, the slope holothurians have restricted bathymetric ranges and therefore short development possibly close to the seabed would be expected. Certainly the eggs of slope-dwelling psychropotids are smaller than those of related abyssal species (Hansen, 1975), possibly indicating shorter development for the former group.

Further evidence for the pelagic development of large echinoderm eggs comes from studies on echinothuriid sea urchins. The eggs of deep-sea echinothuriids, 1100 to 1250µm in diameter (Tyler and Gage, 1984), are considered to undergo direct development, as shown for the shallow-water species Asthenosoma ijimai (Amemiya and Tschiya, 1979). However, contrary to the the notion that development of these eggs will occur close to the seabed, in situ studies using a submersible have shown that the eggs of the deep-sea echinothuriid Phormosoma placenta are positively buoyant with the potential of reaching the surface waters in about 3 days from a depth of about 1000m (Young and Cameron, 1987). However, the advantages of direct development in surface waters are difficult to perceive unless the genetic advantages of being dispersed widely by surface currents outweigh the disadvantages of mortality arising from, 1) eggs being swept away from areas suitable for adult development, and 2) greater predation in surface waters. Young and Cameron (1987) suggest that development should be faster in warm surface waters but, as detailed above, development could be as rapid at bathyal depths. Alternatively, the low temperature of the deep sea could be a boon to a species that needs long pelagic development as part of its life-history strategy.

In the northeast Atlantic, and other oceanic areas, near-bed currents on the continental slope run parallel to the contours (see Section 2.1, page 50). Lecithotrophic larval development or direct pelagic development in the nearbed currents, which in some respects might be classified as demersal development, would be an advantage since it provides dispersal, possibly for many kilometres

(Scheltema, 1972), but at the same time it increases the probability that a larva or juvenile would return to a site suitable for adult development. Both temperature and pressure exert an influence on metabolic processes (Somero *et al*., 1983) and therefore could play a critical role in maintaining eggs and larvae within the benthopelagic zone.

The egg size of several abyssal species indicates that they too undergo lecithotrophic larval development (Table 42). The molpadiids, *Molpadia blakei* and *Cherbonniera utriculus*, probably have abbreviated development, as shown for *M. intermedia* (McEuen and Chia, 1985). This type of development would be suitable for *C. utriculus* which occurs in a narrow band close to the base of the continental slope in the northeast Atlantic. In contrast, *M. blakei* occurs throughout the north Atlantic at abyssal depths, but significantly it does not appear to extend into other oceans unlike abyssal species with large eggs.

The small egg size of some abyssal species does not necessarily curtail their geographic distributions. Several apodid species, such as *Protankyra brychia*, *Myriotrochus bathybius* and *M. giganteus*, have wide geographic ranges (Gage *et al*., 1985a; Gage and Billett, 1986). As indicated in Section 4.2, *P. brychia* may produce a large auricularia larva that develops near the sea surface (Pawson, 1971; Gage *et al*., 1985a). The myriotrochid holothurians may develop in the same way as *P. brychia* and appear to have a similar (?opportunistic) life-history strategy to *Ophiura ljungmani* (an ophiuroid which produces small eggs indicative of planktotrophic development), as indicated by macrofaunal recolonization experiments in the deep sea (Grassle and Morse-Porteous, 1987). Planktotrophic development of abyssal invertebrates is not without precedent, for many deep-sea gastropod and bivalve species are known to produce planktotrophic larvae

(Bouchet and Waren, 1979; Lutz *et al*., 1980; Rex and Waren, 1982). Although the fecundity of these molluscs is low, as in apodid holothurians, Rex and Waren (1982) suggested that the supposed longevity of deep-sea organisms, coupled with iteroparity, should overcome the high mortality experienced by surface-dwelling planktotrophic larvae.

Seasonal reproduction is not apparent in any of the truly deep-sea holothurians studied in the PSB. However, the opportunistic species *K. hyalina* breeds periodically while the reproductive effort of some species, such as *C. utriculus* and *Bathyplotes natans*, may change seasonally (Tyler and Muirhead, 1986; Tyler *et al*., 1987). Despite the fact that most deep-sea holothurians breed continuously, the population size distributions for many species are heterogeneous, although in most cases they are dominated by large specimens (see Section 4.2). Similar size distributions were noted by Rex *et al*. (1979) for the deep-sea gastropod *Benthonella tenella* and were interpreted as representing, to a large degree, recruitment success. Recruitment of macrofauna has been shown to be spatially and temporally variable by both disturbance (Smith, 1986; Smith *et al*., 1986) and recolonization experiments (Desbruyeres *et al*., 1980; Desbruyeres *et al*., 1985; Grassle and Morse-Porteous, 1987).

Similar variability is evident in the recruitment of megafaunal holothurians in the PSB and PAP. Most populations were dominated by large specimens but in some samples numerous juveniles were found. One sample from the centre of the PAP, St. 50515-1, was particularly notable for numerous juveniles of a number of species, *Deima validum*, *Oneriophanta mutabilis*, *Psychropotes longicauda*, and *Pseudostichopus villosus*). Very few juveniles of these species were found in other samples. Local organic enrichment of the sediment inducing recruitment to the area may have led to the observed pattern, since recruitment of larvae and post-larvae (Gage, 1982; Desbruyeres *et al.*, 1985) is influenced by the temporal and spatial variability of organic detritus on the seabed.

In summary, development of deep-sea holothurians occurs by a number of different pathways. Most holothurians on the continental slope produce eggs indicative of lecithotrophic larval development which, it is postulated, will take place in the nearbed currents. These currents generally run parallel to the contours thereby keeping the larvae/juveniles close to areas suitable for adult development. Large eggs produced by abyssal species appear to undergo direct development in the pelagic environment. Although in situ studies have shown that large echinoderm eggs are positively bouyant with the potential to rise to surface waters, it is likely that buoyancy is regulated to maintain the eggs/larvae in the comparitively safer waters of the deep sea. Developmental rates in the deep sea could be comparable to those in shallow water, but equally, prolonged development in cold water by teleplanic larvae or juveniles could benefit some species. Although most species breed continuously, recruitment is variable both spatially and temporally.

6. Bibliography

Akhmet'yeva, Ye.A., B.A. Smirnov and O.K. Bordovskiy, 1982. On some characteristic features of organic matter composition in the intestine contents of the bottom detritus-feeders - holothurians. *Oceanology* *22*, 755-757.

Alberic, P., J-P. Feral and M. Sibuet, 1987. Les acides amines libres, reflet de l'activite bacterienne dans les contenus digestifs des holothuries : difference entre zones abyssale et littorale. *C. R. Acad. Sci. Paris* *305*, Serie III, 203-206.

Aldred, R.G., K. Riemann-Zurneck, H. Thiel and A.L. Rice, 1979. Ecological observations on the deep-sea anenome *Actinoscyphia aurelia*. *Oceanol. Acta* *2*, 389-395.

Aldred, R.G., M.H. Thurston, A.L. Rice and D.R. Morley, 1976. An acoustically monitored opening and closing epibenthic sledge. *Deep-Sea Res*. *23*, 167-174.

Amemiya, S. and T. Tsuchiya, 1979. Development of the echinothurid sea urchin *Asthenosoma ijimai*. *Mar. Biol.* *52*, 93-96.

Andrew, N.L. and B.D. Mapstone, 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanogr. Mar. Biol. Ann. Rev.* *25*, 39-90.

Angel, M.V., 1984. Detrital organic fluxes through pelagic ecosystems. In M.J.R. Fasham (ed.), *Flows of energy and materials in marine ecosystems. Theory and practice*. p. 475-516. New York, Plenum Press.

Angel, M.V. and A. de C. Baker, 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the northeast Atlantic. *Biol. Oceanogr*. *2*, 1-30.

Baird, B.H. and D. Thistle, 1986. Uptake of bacterial extracellular polymer by a deposit-feeding holothurian (*Isostichopus badionotus*). *Mar. Biol*. *92*, 183-187.

Baker, A. de C., M.R. Clarke and M.J. Harris, 1973. The N.I.O. combination net (RMT1+8) and further developments of rectangular mid-water trawls. *J. mar. biol. Ass. U.K.* *53*, 167-184.

Barham, E.G., N.J. Ayer and R.E. Boyce, 1967. Macrobenthos of the San Diego Trough : photographic census and observations from bathyscaphe, "Trieste". *Deep-Sea Res.* *14*, 773-784.

Barnes, A.T., L.B. Quetin, J.J. Childress and D.L. Pawson, 1976. Deep-sea macroplanktonic sea cucumbers : suspended sediment feeders captured from deep submergence vehicle. *Science* *194*, 1083-1085.

Barnett, P.R.O., J. Watson and D. Connelly, 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanol. Acta* *7*, 399-408.

Belyaev, G.M., 1970. Ultra-abyssal holothurians of the genus *Myriotrochus* (order Apoda, fam. Myriotrochidae). In V.G. Bogorov (ed.), *Fauna of the Kurile-Kamchatka Trench and its environment. Trudy Inst. Okeanol. 86, 458-488. (English transalation, 1972, Proceedings of the Shirshov Institute of Oceanology, 86, 482-515. Israel Program for Scientific Transalations*, Jerusalem.

Belyaev, G.M., 1971. Deep water holothurians of the genus *Elpidia*. *Trudy Inst. Okeanol.* *92*, 326-367.

Belyaev, G.M. and A.N. Mironov, 1978. Holothurians of the genus *Myriotrochus* from the southern part of the Atlantic Ocean. *Trudy Inst. Okeanol.* *113*, 198-207.

Belyaev, G.M. and A.N. Mironov, 1981. Some new deep-sea species of Myriotrochidae (Holothurioidea) from the northern and southwestern parts of the Pacific Ocean. *Trudy Inst. Okeanol.* *115*, 165-173.

Belyaev, G.M. and A.N. Mironov, 1982. The holothurians of the family Myriotrochidae (Apoda) : composition , distribution and origin. *Trudy Inst. Okeanol.* *117*, 81-120.

Belyaev, G.M. and M.E. Vinogradov, 1969. A new pelagic holothurian (Elasipoda, Psychropotidae) from the abyssal of the Kurile-Kamchatka Trench. *Zool. Zh.* *48*, 709-716.

Bertelsen, E., 1980. Notes on Linophrynidae V: A revision of the deep-sea anglerfishes of the *Linophryne arborifera*-group (Pisces, Ceratioidei). *Steenstrupia* *6*, *29-70*.

Billett, D.S.M., 1986. The rise and rise of the sea cucumber. *New Scientist* No. 1500, 48-51.

Billett, D.S.M., 1987. Echinodermata. Section 28. In H.S.J.Roe *et al.*, Great Meteor East : A biological characterisation. p. 163-180. *Institute of Oceanographic Sciences Report* No. 248.

Billett, D.S.M. and B. Hansen, 1982. Abyssal aggregations of *Kolga hyalina* D and K (Echinodermata, Holothurioidea) in *the northeast* Atlantic Ocean, a preliminary report. *Deep-Sea Res.* *29*, 799-818.

Billett, D.S.M., R.S. Lampitt, A.L. Rice and R.F.C. Mantoura, 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* *302*, 520-522.

Billett, D.S.M., B. Hansen and Q.J. Huggett, 1985. Pelagic Holothurioidea of the northeast Atlantic. In B.F. Keegan and B.D.S. O'Connor (eds.), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway*. p. 399-411. Rotterdam, Balkema.

Bisol, P.M., R. Costa and M. Sibuet, 1984. Ecological and genetical survey on two deep-sea holothurians : *Benthogone rosea* and *Benthodytes typica*. *Mar. Ecol. Prog. Ser.* *15*, 275-281.

Bordovskiy, O.K., M.N. Sokolova, B.A. Smirnov, Ye.A. Akhmet'yeva and O.N. Zezina, 1974. Evaluation of the role of bottom fauna in the transformation of organic matter in sediments (with specific reference to the deep-sea detritus-feeders in the Kurile-Kamchatka Trench). *Oceanology* *14*, 128-132.

Bouchet, P., 1976. Mise en evidence d'une migration de larves veligeres entre l'etage abyssal et la surface. *C. r. hebd. Seanc. Acad. Sci. Paris* (D) *283*, 821-824.

Bouchet, P. and J. Lutzen, 1976. *Pisolamia*, nouveau genre de Gasteropode, parasite de *l'holothurie* abyssale *Oneirophanta mutabilis*. *C. r. hebd. Seanc. Acad. Sci. Paris* *282*, 1013-1016.

Bouchet, P. and J. Lutzen, 1980. Deux Gasteropodes parasites d'une Holothurie Elasipode. *Bull. Mus. natn. Hist. nat., Paris* (4) *2*, 59-75.

Bouchet, P. and A. Waren, 1979. Planktotrophic larval development in deep-water gasteropods. *Sarsia* *64*, 37-40.

Bouland, C., C. Massin and M. Jangoux, 1982. The fine structure of the buccal tentacles of *Holothuria forskali* (Echinodermata, Holothuroidea). *Zoomorph.* *101*, 133-149.

Boxshall, G.A. and H.S.J. Roe, 1980. The life history and ecology of the aberrant bathypelagic genus *Benthomisophria* Sars, 1909 (Copepoda : Misphrioida). *Bull. Br. Mus. nat. Hist. (Zool.)* *38*, 9-41.

Briggs, K.B., 1985. Deposit feeding by some deep-sea megabenthos from the Venezuela Basin : selective or non-selective. *Mar. Ecol. Prog. Ser.* *21*, 127-134.

Bruun, A.F., 1957. Deep sea and abyssal depths. In J.W. Hedgepeth (ed.), *Treatise on marine ecology and paleoecology* Vol. 1. *Ecology*. *Mem. geol. Soc. Am.*, No. 67, 641-672.

Cameron, J.L. and P.V. Fankboner, 1984. Tentacle structure and feeding processes in life stages of the commercial sea cucumber *Parastichopus californicus* (Stimpson). *J. exp. mar. Biol. Ecol.* *81*, 193-209.

Carey, A.G., 1972. Food sources of the sublittoral, bathyal and abyssal asteroids in the northeast Pacific Ocean. *Ophelia* *10*, 35-47.

Carney, R.S. and A.G. Carey, 1976. Distribution pattern of holothurians on the northeastern Pacific (Oregon, U.S.A.) continental shelf slope, and abyssal plain. *Thalassia jugosl*. *12*, 67-74.

Carney, R.S. and A.G. Carey, 1982. Distribution and diversity of holothuroids (Echinodermata) on Cascadia Basin and Tufts Abyssal Plain. *Deep-Sea Res*. *29*, 597-607.

Carney, R.S., R.L. Haedrich and G.T. Rowe, 1983. Zonation of fauna in the deep sea. In G.T. Rowe (ed.), *The Sea*. Vol. 8 *Deep-Sea Biology*. p. 371-398. New York, Wiley-Interscience.

Cherbonnier, G., 1941. Etude anatomique et biogeographique sur deux *Cucumaria* abyssaux : *C. abyssorum* Theel et *C. albatrossi* n.sp. *Bull. Mus. natn. Hist. nat., Paris* (2) *13*, 93-103.

Cherbonnier, G., 1969. Echinodermes recoltes par le "Thalassa" au large des cotes ouest de Bretagne et du Golfe de Gascogne (3-12 Aout 1967). *Bull. Mus. natn. Hist. nat., Paris* (2) *41*, 343-361.

Cherbonnier, G., 1970. Echinodermes recoltes par la "Thalassa" au large des cotes d'Espagne et du Golfe de Gascogne. (18-25 Octobre 1968). *Bull. Mus. natn. Hist. nat., Paris* (2) *41*, 1266-1277.

Chun, C., 1896. Atlantis. Biologische studien uber pelagische organismen *Auricularia nudibranchiata*. *Biblthca. zool*. II. *19*, 55-75.

Chun, C., 1900. *Aus den Tiefen des Weltmeeres*. Jena : Gustav Fischer Verlag, 549p.

Clark, H.L., 1907. The apodous holothurians. *Smithson. Contr. Knowl*. *35*, No. 1723, 231pp.

Clark, H.L., 1920. Tropical Pacific Holothurioidea. *Mem. Mus. comp. Zool. Harv*. *39*, 115-154.

Clarke, A., 1983. Life in cold water : The physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Ann. Rev.* *21*, 341-453.

Cooper, L.H.N. and D. Vaux, 1949. Cascading over the continental slope of water from the Celtic Sea. *J. mar. biol. Ass. U.K.* *28*, 719-750.

Dahl, E., L. Laubier, M. Sibuet and J-O. Stromberg, 1976. Some quantitative results on benthic communities of the deep Norwegian Sea. *Astarte* *9*, 61-79.

Danielssen, D.C. and J. Koren, 1882. Holothurioidea. *The Norwegian Deep-Sea Expedition 1876-1878. Zoology* *4*,1-95.

Deichmann, E., 1930. The holothurians of the western part of the Atlantic Ocean. *Bull. Mus. comp. Zool. Harv.* *71*, 43-226.

Deichmann, E., 1940. Report on the holothurians, collected by the Harvard-Havana Expeditions 1938 and 1939, with a revision of the Molpadonia of the Atlantic Ocean. *Mem. Soc. Cubana Hist. Nat.* *14*, 183-240.

Deichmann, E., 1954. The holothurians of the Gulf of Mexico. *Fishery Bull. Fish Wildl. Serv. U.S.* *55*,381-410.

Deming, J.W. and R.R. Colwell, 1982. Barophilic bacteria associated with digestive tracts of abyssal holothurians. *App. Environ. Microbiol.* *44*, 1222-1230.

Desbruyeres, D., J.Y. Bervas and A. Khripounoff, 1980. Un cas de colonisation rapide d'un sediment profond. *Oceanol. Acta* *3*, 285-291.

Desbruyeres, D., J.W. Deming, A. Dinet and A. Khripounoff, 1986. Reactions de l'ecosysteme benthique profond aux perturbations : Nouveaux resultats experimentaux. In L. Laubier and C. Monniot (eds.), *Peuplements profonds du Golfe de Gascogne. Campagnes Biogas.* p. 193-208. Brest, IFREMER.

Dickson, R.R. and I.N. McCave, 1986. Nepheloid layers on the continental slope west of Porcupine Bank. *Deep-Sea Res.* *33*, 791-818.

Dickson, R.R., W.J. Gould, T.J. Muller and C. Maillard, 1985. Estimates of the mean circulation in the deep (>2000m) layer of the eastern North Atlantic. *Prog. Oceanog.* *14*, 103-127.

Dickson, R.R., W.J. Gould, C. Griffiths, K.J. Medler and E.M. Gmitrowicz, 1986. Seasonality in currents of the Rockall Channel. *Proc. Roy. Soc. Edinb.* *88B*, 103-125.

Ekman, S. 1927. Holothurien der Deutschen Sudpolar-Expedition 1901-193 aus der Ostantarktis und von den Kerguelen. Dt. Sudpol.-Exped. 19 (Zool. 11), 359-419.

Ellett, D.J. and J.H.A. Martin, 1973. The physical and chemical oceanography of the Rockall Channel. Deep-Sea Res. 20, 585-625.

Ellett, D.J., A. Edwards and R. Bowers, 1986. The hydrography of the Rockall Channel - an overview. Proc. Roy. Soc. Edinb. 88B, 61-81.

Emerson, S., K. Fischer, C. Reimers and D. Heggie, 1985. Organic carbon dynamics and preservation in deep-sea sediments. Deep-Sea Res. 32, 1-21.

Emlet, R.B., L.R. McEdward and R.R. Strathmann, 1986. Echinoderm larval ecology viewed from the egg. Echinoderm Studies 2, 55-136.

Fankboner, P.V., 1978. Suspension-feeding mechanisms of the armoured sea cucumber Psolus chitinoides Clark. J. exp. mar. Biol. Ecol. 31, 11-25.

Feldt, W., G. Kanisch, M. Kanisch and M. Vobach, 1985. Radio-ecological studies of sites in the northeast Atlantic used for dumping of low-level radioactive wastes - Results of the research cruises of the FRV "Walther Herwig" 1980-1984. Arch. FischWiss. 35, 91-195.

Feral, J.-P., 1985. Changes in analyzed organic matter and energetic content of two thin-skinned holothuroids Leptosynapta galliennei and Eumolpadia violacea at critical stages of their life cycle. In B.F. Keegan and B.D.S. O'Connor (eds.), Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway. p. 421-429. Rotterdam, Balkema.

Fowler S.W. and G.A. Knauer, 1986. Role of the large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanog. 16, 147-194.

Fujioka, K., A. Taira, K. Kobayashi, K. Nakamura, T. Ilyama, J.-P. Cadet, S. Lallemand and D. Girard (eds.), 1987. 6000 meters deep : a trip to the japanese trenches. Tokyo, University of Tokyo Press. 106pp.

Gage, J.D., 1985. New Synapitidae (Holothuroidea : Apoda) from the Rockall Trough. J. mar. biol. Ass. U.K. 65, 255-261.

Gage, J.D., 1986. The benthic fauna of the Rockall Trough : regional distribution and bathymetric zonation. Proc. Roy. Soc. Edinb. 88B, 159-174.

Gage, J.D. and D.S.M. Billett, 1986. The family Myriotrochidae Theel (Echinodermata : Holothurioidea) in the deep northeast Atlantic Ocean. Zool. J. Linn. Soc. 88, 229-276.

Gage, J.D. and P.A. Tyler, 1982. Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson. Oceanol. Acta 5, 73-83.

Gage, J.D. and P.A. Tyler, 1985. Growth and recruitment of the deep-sea urchin *Echinus affinis*. Mar. Biol. 90, 41-53.

Gage, J.D., R.H. Lightfoot, M. Pearson and P.A. Tyler, 1980. An introduction to a sample time-series of abyssal macrobenthos : methods and principle sources of variability. Oceanol. Acta 3, 169-176.

Gage, J.D., M. Pearson, A.M. Clark, G.L.J. Paterson and P.A. Tyler, 1983. Echinoderms of the Rockall Trough and adjacent areas. 1. Crinoidea, Asteroidea and Ophiuroidea. Bull. Br. Mus. nat. Hist. (Zool.) 45, 263-308.

Gage, J.D., D.S.M. Billett, M. Jensen and P.A.Tyler, 1985a. Echinoderms of the Rockall Trough and adjacent areas. 2. Echinoidea and Holothurioidea. Bull. Br. Mus. nat. Hist. (Zool.) 48, 173-213.

Gage, J.D., M. Pearson, D.S.M. Billett, A.M. Clark, M. Jensen, G.L.J. Paterson and P.A.Tyler, 1985b. Echinoderm zonation in the Rockall Trough (NE Atlantic). In B.F. Keegan and B.D.S. O'Connor (eds.), Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway. p. 31-36. Rotterdam, Balkema.

Giese, A.C., 1966. On the biochemical constitution of some echinoderms. In R.A. Boolootian (ed.), Physiology of Echinodermata. p. 757-796. New York, Interscience.

Gilchrist, J.D.F., 1920. *Planktothuria diaphana* gen. et sp. n. Q. Jl. microsc. Sci. 64, 373-382.

Gordon, J.D.M. and J.A.R. Duncan, 1985. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. Prog. Oceanog. 15, 37-69.

Grassle, J.F., 1977. Slow recolonisation of deep-sea sediment. Nature 265, 618-619.

Grassle, J.F. and L.S. Morse-Porteous, 1987. Macrofaunal colonisation of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Res. 34, 1911-1950.

Grassle, J.F., H.L. Sanders, R.R. Hessler, G.T. Rowe and T. McLellan, 1975. Pattern and zonation : a study of the bathyal megafauna using the research submersible "Alvin". *Deep-Sea Res.* *22*, 457-481.

Grieg, J.A., 1921. Echinodermata. *Rep. scient. Results "Michael Sars" N. Atlantic deep sea Exped.* *3*, (2), 1-47.

Haedrich, R.L. and J.E. Maunder, 1985. The echinoderm fauna of the Newfoundland continental slope. In B.F. Keegan and B.D.S. O'Connor (eds.), *Echinodermata : Proceedeings of the Fifth International Echinoderm Conference, Galway*. p. 37-46. Rotterdam, Balkema.

Haedrich, R.L., G.T. Rowe and P.T. Polloni, 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J. mar. Res.* *33*, 191-212.

Haedrich, R.L., G.T. Rowe and P.T. Polloni, 1980. The megabenthic fauna of the deep sea south of New England, USA. *Mar. Biol.* *57*, 165-179.

Hammond, L.S., 1982. Analysis of grain-size selection by deposit-feeding holothurians and echinoids (Echinodermata) from a shallow reef lagoon, Discovery Bay, Jamaica. *Mar. Ecol. Prog. Ser.* *8*, 25-36.

Handley, R.L., 1971. *A geophysical study of the Porcupine Seabight*. Ph. D. thesis, University of Birmingham.

Hansen, B., 1956. Holothurioidea from depths exceeding 6000 meters. *Galathea Rep.* *2*. 33-54.

Hansen, B., 1968. Brood protection in a deep-sea holothurian, *Oneirophanta mutabilis* Theel. *Nature* *217*, 1062-1063.

Hansen, B., 1972. Photographic evidence of a unique type of walking in deep-sea holothurians. *Deep-Sea Res.* *19*, 461-462.

Hansen, B., 1975. Systematics and biology of the deep-sea holothurians. Part 1. Elasipoda. *Galathea Rep.* *13*, 1-262.

Hansen, B., 1978. *Scotothuria herringi*, a new genus and species of bathypelagic holothurians (Holothurioidea, Aspidochirota, Synallactidae). *Steenstrupia* *5*, 33-39.

Hansen, B., in press. The genus *Staurocucumis* Ekman and its possible affinity with *Echinocucumis* Sars (Holothuroidea, Dendrochirota). *Proceedings of the Sixth International Echinoderm Conference, Victoria*.

Hansen, B. and F.J. Madsen, 1956. On two bathypelagic holothurians from the South China Sea. Galathea Rep. 2, 55-59.

Hargreaves, P.M., 1984. The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern north-east Atlantic Ocean during autumn 1979. J. mar. biol. Ass. U.K. 64, 829-857.

Harvey, J., 1982. θ-S relationships and water masses in the eastern North Atlantic. Deep-Sea Res. 29, 1021-1033.

Harvey, R., J.D. Gage, D.S.M. Billett, A.M. Clark and G.L.J. Paterson, in press. Echinoderms of the Rockall Trough and adjacent areas. 3. Additional records. Bull. Br. Mus. nat. Hist. (Zool.).

Hauksson, E., 1979. Feeding biology of Stichopus tremulus, a deposit-feeding holothurian. Sarsia 64, 155-160.

Hedgepeth, J.W., 1957. Classification in marine environments. In J.W. Hedgepeth (ed.), Treatise on marine ecology and paleoecology. Vol. 1, Ecology. Mem. geol. Soc. Am. No. 67, p.17-27.

Hedges, J.I. and J.H. Stern, 1984. Carbon and nitrogen determinations of carbonate-containing solids. Limnol. Oceanog. 29, 657-663.

Heding, S., 1931. On the classification of the molpadids (preliminary notice). Vidensk Meddr. dansk. naturh. Foren. 92, 275-284.

Heding, S., 1935. Holothurioidea. Part 1. Apoda, Molpadioidea, Gephyrothurioidea. Dan. Ingolf-Exped. 4 (9), 1-84.

Heding, S., 1940. Die holothurien der deutschen Tiefsee-Expedition. II. Aspidochirote und Elasipode formen. Wiss. Ergebn. dt. Tiefsee-Exped. Valdivia. 24, 317-375.

Heding, S., 1942. Holothurioidea. Part 2. Aspidochirota, Elasipoda, Dendrochirota. Dan. Ingolf-Exped. 4 (13), 1-39.

Heezen, B.C. and C.D. Hollister, 1971. The face of the deep. London, Oxford University Press.

Heezen, B.C., M. Ewing and R.J. Menzies, 1955. The influence of submarine turbidity currents on abyssal productivity. Oikos 6, 170-182.

Heezen, B.C., E.T. Bruce, J.B. Hersey and M. Tharp, 1964. Chain and Romanche fracture zones. Deep-Sea Res. 11, 11-33.

Hendler, G., 1975. Adaptational significance of the patterns of ophiuroid development. Amer. Zool. 15, 691-715.

Herouard, E., 1902. Holothuries provenant des campagnes de la "Princess-Alice" (1892-1897). Result. Camp. scient. Prince Albert I, 21, 1-61.

Herouard, E., 1906. Holothuries. Expedition Antarctique Belge. Result. Voyage S.Y. "Belgica". Zoologie. 16pp.

Herouard, E., 1923. Holothuries provenant des campagnes des yachts "Princess-Alice" et "Hirondelle II" (1898-1915). Result. Camp. scient. Prince Albert I, 66, 1-163.

Hines, A.H., 1986. Larval problems and perspectives in life histories of marine invertebrates. Bull. Mar. Sci. 39, 506-525.

Holligan, P.M. and S.B. Groom, 1986. Phytoplankton distributions along the shelf break. Proc. Roy. Soc. Edinb. 88B, 239-263.

Holligan, P.M., M. Viollier, D.S. Harbour, P. Camus and M. Champagne-Philippe, 1983. Satellite and ship studies of coccolithophore production along a continental shelf. Nature 304, 339-342.

Holligan, P.M., R.D. Pingree and G.T. Mardell, 1985. Oceanic solitons, nutrient pulses and phytoplankton growth. Nature 314, 348-350.

Honjo, S., 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. mar. Res. 38, 53-97.

Honjo, S., 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science 218, 883-884.

Horikoshi, M., 1976. Benthos. In S. Motoda (ed.), Seeweeds and benthos. (Kaiyo Kagagu Kiso Koza, Vol. 5), p. 149-451. Tokyo, University of Tokyo Press.

Huggett, Q.J., 1987. Mapping of hemipelagic versus turbiditic muds by feeding traces observed in deep-sea photographs. In P.P.E. Weaver and J. Thomson (eds), Geology and geochemistry of abyssal plains. Geological Society Special Publication No. 31, 105-112.

Humes, A.G., 1974. New cyclopoid copepods associated with an abyssal holothurian in the eastern North Atlantic. J. nat. Hist. 8, 101-117.

Hunter-Rowe, C.K.A., F. Jeal and A.B. West, 1976. Observations on the feeding behaviour of Thyone fusus (O.F. Muller). Scient. Proc. R. Dubl. Soc. 5, 459-468.

Huthnance, J.M., 1986. The Rockall slope current and shelf-edge processes. Proc. Roy. Soc. Edinb. 88B,83-101.

Hyman, L.H., 1955. The Invertebrates : Echinodermata. New York, McGraw-Hill. 763 pp.

Jahnke, R.A., S.R. Emerson, J.K. Cochran and D.J. Hirschberg, 1986. Fine scale distributions of porosity and particulate excess 210Pb, organic carbon and CaCO in the surface sediments of the deep equatorial Pacific. Earth planet. Sci. Lett. 77, 59-69.

Jannasch, H.W. and C.O. Wirsen, 1977. Microbial life in the deep sea. Scient. Am. 236, 42-52.

Jespersen, A. and J. Lutzen, 1971. On the ecology of the aspidochirote sea cucumber Stichopus tremulus (Gunnerus). Norw. J. Zool. 19, 117-132.

Jumars, P.A., 1978. Spatial autocorrelation with RUM (Remote Underwater Manipulator) : vertical and horizontal structure of a bathyal benthic community. Deep-Sea Res. 25, 589-604.

Jumars, P.A. and E.D. Gallagher, 1982. Deep-sea community structure : three plays on the benthic proscenium. In W.G. Ernst and J. Morin (eds), Ecological processes in the deep sea. p.217-255. Englewood Cliffs, N.J., Prentice-Hall.

Kenyon, N.H., R.H. Belderson and A.H. Stride, 1978. Channels, canyons and slump folds on the continental slope between south-west Ireland and Spain. Oceanol. Acta 1, 369-380.

Khripounoff, A., 1979. Relations trophiques dans l'ecosysteme benthique abyssal atlantique : descriptions et bilan energetique. These 3eme cycle, Universite Pierre et Marie Curie, Paris. 132pp.

Khripounoff, A. and M. Sibuet, 1980. La nutrition d'echinodermes abyssaux I. Alimentation des holothuries. Mar. Biol. 60, 17-26.

Khripounoff, A., D. Desbruyeres and P. Chardy, 1980. Les peuplements benthiques de la faille Vema: donnees quantitatives et bilan d'energie en milieu abyssal. Oceanol. Acta 3, 187-198.

Kidd, R.B. and Q.J. Huggett, 1981. Rock debris on abyssal plains in the North east Atlantic: a comparison of epibenthic sledge hauls and photographic surveys. *Oceanol. Acta* *4*, 99-104.

Kirkegaard, J.B. and D.S.M. Billett, 1980. *Eunoe laetmogonensis*, a new species of polynoid worm, commensal with the bathyal holothurian *Laetmogone violacea*, in the North-east Atlantic. *Steenstrupia* *6*, 101-109.

Knudsen, J., 1967. The deep-sea Bivalvia. *Scient. Rep. John Murray Exped.* *11*, 237-343.

Knudsen, J., 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Rep.* *11*, 3-236.

Koehler, R., 1896. Echinodermes. Resultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne Aout-Septembre 1895. *Annls Univ. Lyon* *26*, 33-127.

Koehler, R., 1927. *Les Echinodermes des mers d'Europe.* Tome 2, Paris, Gaston Doin et Cie, 339pp.

Koehler, R. and C. Vaney, 1903. *Entosiphon deimatis*, nouveau Mollusque parasite d'une holothurie abyssale. *Revue Suisse Zool.* *11*, 23-41.

Kozyar, L.A., M.N. Sokolova and O.N. Zezina, 1974. Spores and pollen from higher plants in the nutrition of marine invertebrates. *Okeanologiya* *14*, 431-434.

Lampitt, R.S., 1984. The use of time lapse photography in the deep sea. *Prog. underwat. Sci.* *9*, 115-120.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Res.* *32*, 885-897.

Lampitt, R.S. and D.S.M. Billett, 1985. Deep-sea echinoderms: a time and motion study. In B.F. Keegan and B.D.S. O'Connor (eds), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway.* p. 160 [Absract]. Rotterdam, Balkema.

Lampitt, R.S. and M.P. Burnham, 1983. A free fall time lapse camera and current meter system "Bathysnap" with notes on the foraging behaviour of a bathyal decapod shrimp. *Deep-Sea Res.* *30*, 1009-1017.

Lampitt, R.S., D.S.M. Billett and A.L. Rice 1986. Biomass of the invertebrate megabenthos from 500 to 4100m in the northeast Atlantic Ocean. *Mar. Biol.* *93*, 69-81.

Lawrence, J.M., 1980. Numbers and biomass of the common holothuroids on the windward reef flat at Enwetak Atoll, Marshall Islands. In M. Jangoux (ed.), Echinoderms : Present and past. p. 201-204. Rotterdam, Balkema.

Lawrence, J.M. and J. Kafri, 1979. Numbers, biomass, and caloric content of the echinoderm fauna of the rocky shores of Barbados. Mar. Biol. 52, 87-91.

Le Danois, E., 1948. Les profondeurs de la mer. Paris, Payot. 303pp.

Lee, A. and D. Ellett, 1965. On the contribution of overflow water from the Norwegian Sea to the hydrographic structure of the North Atlantic Ocean. Deep-Sea Res. 12, 129-142.

Lemche, H., B. Hansen, F.J. Madsen, O.S. Tendal and T. Wolff, 1976. Hadal life as analyzed from photograph. Vidensk. Meddr. dansk. naturh. Foren. 139, 263-336.

Li, W.Q., N.L. Guinasso, K.H. Cole, M.D. Richardson, J.W. Johnson and D.R. Schink, 1985. Radionuclides as indicators of sedimentary processes in abyssal Caribbean sediments. Mar. Geol. 68, 187-204.

Lloyd, M., 1967. Mean crowding. J. anim. Ecol. 36, 1-30.

Ludwig, H., 1894. The Holothurioidea. Reports of an expedition off the west coasts of Mexico, Central and South America, and off the Galapagos Islands ..... "Albatross" 1891. Mem. Mus. comp. Zool. Harv. 17, 1-183.

Ludwig, H. and S.G. Heding, 1935. Die Holothurien der deutschen Tiefsee-Expedition. I. Fusslose und Dendrochirote Formern. Wiss. Ergebn. dt. Tiefsee-Exped "Valdivia" 24, 121-214.

Lutz, R.A., D. Jablonski, D.C. Rhoads and R.D. Turner, 1980. Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galapagos Rift. Mar. Biol. 57, 127-133.

Lutzen, J., 1979. Studies on the life history of Enteroxenos Bonnevie, a gastropod endoparasitic in aspidochirote holothurians. Ophelia 18, 1-51.

Madsen, F.J., 1941. On Thyone wahrbergi n. sp., a new holothurian from the Skagerrak, with remarks on T. fusus (O.F.M.) and other related species. Goteborgs K. Vetensk.- o. VitterSamh. Handl. F.6, Ser. B. 1, 1-31.

Madsen, F.J., 1953. Holothurioidea. Rep. Swed. deep-sea Exped. 2 (Zool.) 12, 149-173.

Madsen, F.J., 1961. On the zoogeography and origin of the abyssal fauna, in view of the knowledge of the Porcellanasteridae. Galathea Rep. 4, 177-218.

Mantoura, R.F.C. and C.A. Llewellyn, 1983. The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural water by reverse-phase high performance liquid chromatography. Analytica chim. acta 151, 297-314.

Marenzeller, E. von, 1983. Contribution a l'etude des holothuries de l'Atlantique Nord. Result. Camp. scient. Prince Albert I, 6, 1-22.

Margolin, A.S., 1976. Swimming of the sea cucumber Parastichopus californicus (Stimpson) in response to sea stars. Ophelia 15, 105-114.

Massin, C., 1978. Etude de nutrition chez les holothuries aspidochirotes (Echinodermes). Comportement alimentaire, structure et fonctions de l'appareil digestif. These de Doctorat, Universite Libre de Bruxelles.

Massin, C., 1980. The sediment ingested by Holothuria tubulosa Gmel (Holothuroidea : Echinodermata). In M. Jangoux (ed.), Echinoderms, Past and present, p.205-208. Rotterdam, Balkema.

Massin, C., 1982. Food and feeding mechanisms, Holothuroidea. In M. Jangoux and J.M. Lawrence (eds.), Echinoderm nutrition, p.43-55. Rotterdam, Balkema.

Massin, C., 1984. Structures digestives d'holothuries Elasipoda (Echinodermata) : Benthogone rosea Koehler, 1896 et Oneirophanta mutabilis Theel, 1879. Arch. Biol. (Bruxelles) 95, 153-185.

Massin, C., M. Jangoux and M. Sibuet, 1978. Description d' Ixoreis psychropotae nov. gen. nov. sp. coccidie parasite du tube digetif de l'Holothurie abyssal Psychropotes longicauda Theel. Protistologica 14, 253-259.

Mauviel, A. and M. Sibuet, 1985. Repartition des traces animales et importance de la bioturbation. In L. Laubier and C. Monniot (eds), Peuplements profonds du Golfe de Gascogne. Campagnes Biogas. p. 157-173. Brest, IFREMER.

McCave, I.N., 1975. Vertical flux of particulates in the ocean. Deep-Sea Res. 22, 491-502.

McEuen, F.S., and F.-S. Chia 1985. Larval development of a molpadiid holothuroid, Molpadia intermedia (Ludwig, 1894) (Echinodermata). Can. J. Zool. 63, 2553-2559.

McKenzie, J.D., 1987. The ultrastructure of the tentacles of eleven species of dendrochirote holothurians studied with special reference to the surface coats and the papillae. *Cell. Tissue Res*. *248*, 187-199.

Menzies, R.J., R.Y. George and G.T. Rowe, 1973. *Abyssal environment and ecology of the world oceans*. New York, Wiley-Interscience. 488pp.

Merrett, N.R., 1978. On the identity and pelagic occurrence of larval and juvenile stages of rattail fishes (Family Macrouridae) from 60 N, 20 W and 53 N, 20 W. *Deep-Sea Res*. *25*, 147-160

Merrett, N.R. and N.B. Marshall, 1981. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08 -27 N). *Prog. Oceanog*. *9*, 185-244.

Mileikovsky, S.A. 1971. Types of larval develoment in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol*. *10*, 193-213.

Miller, J.E. and D.L. Pawson, 1984. Holothurians. (Echinodermata : Holothuroidea). *Mem. Hourglass Cruises* *7*, 1-79.

Miller, J.E. and R.L. Turner, 1986. *Psolus pawsoni* (Echinodermata: Holothuroidea), a new bathyal sea cucumber from the Florida East Coast. *Proc. Biol. Soc. Wash*. *99*, 478-485.

Monniot, C. and M. Segonzac, 1985. La campagne oceanographique abyssal Abyplaine. Caracteristiques des stations et des peuplements benthiques. *Oceanol. Acta* *8*, 67-76.

Mortensen, Th. 1927. *Handbook of the echinoderms of the British Isles*. 471pp. Oxford University Press, London.

Motokawa, T., 1984. Connective tissue catch in echinoderms. *Biol. Rev*. *59*, 255-270.

Murray, J., 1895. A summmary of the scientific results obtained at the sounding, dredging and trawling stations of the "H.M.S. Challenger". *Challenger Rep., Summary Res*. *2*, 797-1608.

Naylor, D. and S.N. Mounteney, 1975. *Geology of the north-west European continental shelf*. Vol 1. Graham Trotman Dudley, 162pp.

Naylor, D. and P. Shannon, 1982. *Geology of offshore Ireland and west Britain*. Graham and Trotman.

Ockelmann, K., 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proc. First. Eur. malac. Congr. London 1962*, 25-35.

Ohshima, H., 1915. Report on the holothurians collected by the "Albatross" in the northwestern Pacific. *Proc. U.S. natn. Mus*. *48*, 213-291.

Ohta, S., 1983. Photographic census of large-sized benthic organisms in the bathyal zone of Suruga Bay, Central Japan. *Bull. Ocean Res. Inst. Univ. Tokyo*, No. 15, 1-244.

Ohta, S., 1985. Photographic observations of the swimming behaviour of the deep-sea pelagothuriid holothurian *Enypniastes* (Elasipoda, Holothurioidea). *J. oceanogr. Soc. Japan* *41*, 121-133.

Osterberg, C., A.G. Carey and H. Curl, 1963. Acceleration of sinking rates of radionuclides in the ocean. *Nature* *200*, 1276-1277.

Ostergren, Hj., 1938. Studien uber die Seewalzen. *Goteborgs K. Vetensk.- o. VitterSamh. Handl*. 5B,*5*,1-151.

Panning, A., 1949. Versuch einer neuordnung der familie Cucumariidae (Holothurioidea, Dendrochirota). *Zool. Jb.* (*Syst*.) *78*, 403-470.

Pawson, D.L., 1965. The bathyal holothurians of the New Zealand region. *Zoology Publs. Vict. Univ. Wellington* *39*, 1-33.

Pawson, D.L., 1966. Ecology of holothurians. In R.A. Boolootian (ed.), *Physiology of Echinodermata*. p.63-71. New York, Interscience.

Pawson, D.L., 1969. Holothuroidea from Chile. Report No. 46 of the Lund University Chile expedition 1948-1949. *Sarsia* *38*, 121-145.

Pawson, D.L., 1970. The marine fauna of New Zealand : sea cucumbers (Echinodermata : Holothurioidea). *New Zealand Oceanographic Inst. Mem*. No. 52, 71pp.

Pawson, D.L., 1971. Second New Zealand record of the holothurian giant larva *Auricularia nudibranchiata* Chun. *N.Z. Jl. mar. freshw. Res*. *5*, 381-387.

Pawson, D.L., 1976. Some aspects of the biology of deep-sea echinoderms. *Thalassia jugosl*. *12*, 287-293.

Pawson, D.L., 1982a. Deep-sea echinoderms in the Tongue of the Ocean, Bahama Islands, a survey, using the research submersible "Alvin". *Mem. Aust. Mus*. No. 16, 129-145.

Pawson, D.L., 1982b. Holothuroidea. In S.P. Parker (ed.), *Synopsis and classification of living organisms*, Vol. 2. p. 813-818. New York, McGraw-Hill.

Pawson, D.L., 1986. *Psychropotes hyalinus*, new species, a swimming elasipod sea cucumber (Echinodermata: Holothuroidea) from the North Central Pacific Ocean. *Proc. Biol. Soc. Wash*. *98*, 523-525.

Pawson, D.L. and H.B. Fell, 1965. A revised classification of the dendrochirote holothurians. *Breviora* No. 214, 1-7.

Pawson, D.L. and E.J. Foell, 1986. *Peniagone leander*, new species, an abyssal benthopelagic sea cucumber (Echinodermata : Holothuroidea) from the eastern central Pacific Ocean. *Bull. Mar. Sci*. *38*, 293-299.

Pearse, J.S., 1965. Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common antarctic asteroid. *Antarctic Res. Ser*. *5*, 39-85.

Pequegnat, W.E., B.M. James, A.H. Bouma, W.R. Bryant and A.D. Fredericks, 1972. Photographic study of the deep-sea environment of the Gulf of Mexico. In *Texas A&M University: Oceanographic Studies* Vol. 3, pp. 67-128.

Perrier, R., 1896. Sur les Elasipodes recueillis par le "Travailleur" et le "Talisman". *C. r. hebd. Seanc. Acad. Sci., Paris* *123*, 900-903.

Perrier, R., 1902. Holothuries. *Exped. scient. Travailleur Talisman* *5*, 273-554.

Pielou, E.C., 1974. *Population and community ecology : principals and methods*. New York, Gordon and Breach. 424pp.

Prim, P., J.M. Lawrence and R.L. Turner, 1976. Protein, carbohydrate, and lipid levels of the adult body wall of *Actinopyga agassizi*, *Synaptula hydriformis* and *Pentacta pygmaea* (Echinodermata : Holothuroidea). *Comp. Biochem. Physiol*. *55B*, 307-309.

Rex, M.A., 1977. Zonation in deep-sea gastropods : the importance of biological interactions to rates of zonation. In B.F. Keegan, P. O'Ceidigh and P.J.S. Boaden (eds), *Biology in benthic organisms*. p. 521-530. Oxford, Pergamon Press.

Rex, M.A. and A. Waren, 1982. Planktotrophic development in deep-sea prosobranch snails from the western North Atlantic. Deep-Sea Res. 29, 171-184.

Rex, M.A., C.A. van Ummersen and R.D. Turner, 1979. Reproductive pattern in the abyssal snail Benthonella tenella (Jeffreys). In S.E. Stancyk (ed.), Reproductive ecology of marine invertebrates. p. 173-188. Columbia, University of South Carolina Press.

Reys, J.P., 1959. Thyone cherbonnieri nov. sp. et remarques sur le genre Thyone en Mediterranee. Recl. Trav. Stn. mar. Endoume 29, 173-175.

Rhoads, D.C. and D.K. Young, 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Mar. Biol. 11, 255-261.

Rice, A.L., 1986. British oceanographic vessels 1800-1950. London, The Ray Society.

Rice, A.L., R.G. Aldred, D.S.M. Billett and M.H. Thurston, 1979. The combined use of an epibenthic sledge and a deep-sea camera to give quantitative relevance to macrobenthos samples. Ambio Spec. Rep. 6, 59-72.

Rice, A.L., R.G. Aldred, E. Darlington and R.A. Wild, 1982. The quantitative estimation of the deep-sea megabenthos, a new approach to an old problem. Oceanol. Acta 5, 63-72.

Rice, A.L., D.S.M. Billett, J. Fry, A.W.G. John, R.S. Lampitt, R.F.C. Mantoura and R.J. Morris, 1986. Seasonal deposition of phytodetritus to the deep-sea floor. Proc. Roy. Soc. Edinb. 88B, 265-279.

Richardson, M.D., K.B. Briggs and D.K. Young, 1985. Effects of biological activity by abyssal benthic macroinvertebrates on a sedimentary structure in the Venezuela Basin. Mar. Geol. 68, 243-267.

Roberts, D., 1979. Deposit-feeding mechanisms and resource partitioning in tropical holothurians. J. exp. mar. Biol. Ecol. 37, 43-56.

Roberts, D. and C. Bryce, 1982. Further observations on tentacular feeding mechanisms in holothurians. J. exp. mar. Biol. Ecol. 59, 151-163.

Roberts, D.G., P.M. Hunter and A.S. Laughton, 1979. Bathymetry of the northeast Atlantic : continental margin around the British Isles. *Deep-Sea Res.* *26*, 417-428.

Robison, B.H. and T.M. Lancraft, 1984. An upward transport mechanism from the benthos. *Naturwissenschaften* *71*, 322.

Roe, H.S.J. and D.M. Shale, 1979. A new multiple rectangular midwater trawl (RMT 1+8M) and some modifications to the Institute of Oceanographic Sciences' RMT 1+8. *Mar. Biol.* *50*, 283-288.

Rokop, F.J., 1974. Reproductive patterns in the deep-sea benthos. *Science* *186*, 743-745.

Rokop, F.J., 1977. Seasonal reproduction of the brachiopod *Frieleia hallii* and the scaphopod *Cadulus californicus* at bathyal depths in the deep sea. *Mar. Biol.* *43*, 237-246.

Ross, D.A., 1970. *Introduction to oceanography*. New York, Meredith Corporation. 384pp.

Rowe, G.T., 1971. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. *Deep-Sea Res.* *18*, 569-581.

Rowe, G.T., 1972. The exploration of submarine canyons and their benthic faunal assemblages. *Proc. Roy. Soc. Edinb.* *B73*, 159-169.

Rowe, G.T., 1974. The effects of the benthic fauna on the physical properties of deep-sea sediments. In A.L. Inderbitzen (ed.), *Deep-Sea sediments*. p. 381-400. New York, Plenum.

Rowe, G.T. and D.W. Menzel, 1971. Quantitative benthic samples from the deep Gulf of Mexico with some comments on the measuremant of deep-sea biomass. *Bull. Mar. Sci.* *21*, 556-566.

Rowe, G.T. and R.J. Menzies, 1969. Zonation of large benthic invertebrates in the deep sea off the Carolinas. *Deep-Sea Res.* *16*, 531-537.

Rowe, G.T., P.T. Polloni and R.L. Haedrich, 1982. The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep-Sea Res.* *29*, 257-278.

Rutgers van der Loeff, M.M. and M.S.S. Lavaleye, 1986. Sediments, fauna and the dispersal of radionuclides at the N.E. Atlantic dumpsite for low-level radioactive waste. *Report of the Dutch DORA program*. Texel, Netherlands Institute for Sea Research. 134pp.

Sanders, H.L., 1979. Evolutionary ecology and life-history patterns in the deep sea. Sarsia 64, 1-7.

Sars, M., 1868. Om nogle Echinodermer og Coelenterater funde ved Lofoten. Forh. Vidensk Selsk. Krist. 1867, 19-23.

Scheltema, R.S., 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates : a speculative summary. In R.W. Brauer (ed.), Barobiology and experimental biology in the deep sea. p. 58-66. Chapel Hill, University of North Carolina Press.

Schoener, A., 1968. Evidence for reproductive periodicity in the deep sea. Ecology 49, 81-87.

Schoener, A., 1972. Fecundity and possible mode of development of some deep-sea ophiuroids. Limnol. Oceanogr. 17, 193-199.

Sibuet, M., 1974. Cherbonniera utriculus gen. nov., sp. nov., petite Holothurie (Molpadonia, Molpadiidae) des vases abyssales du Nord-Est Atlantique. C. r. hebd. Seanc. Acad. Sci., Paris (D) 279, 1443-1445.

Sibuet, M., 1977. Repartition et diversite des echinodermes (Holothurides-Asterides) en zone profonde dans le Golfe de Gascogne. Deep-Sea Res. 24, 549-563.

Sibuet, M., 1980. Adaptation des echinodermes a la vie abyssale. In M. Jangoux (ed.), Echinoderms : present and past. p. 233-240. Rotterdam, Balkema.

Sibuet, M., 1984. Les invertebres detritivores dans l'ecosysteme abyssal. Selection de la nourriture et regime alimentaire chez les holothuries. Oceanis 10, 623-639.

Sibuet, M., 1985. Quantitative distribution of echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, Echinoidea) in relation to organic matter in the sediment, in deep sea basins of the Atlantic Ocean. In B.F. Keegan and B.D.S. O'Connor (eds), Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway. p. 99-108. Rotterdam, Balkema.

Sibuet, M. and J.M. Lawrence, 1981. Organic content and biomass of abyssal holothuroids (Echinodermata) from the Bay of Biscay. Mar. Biol. 65, 143-147.

Sibuet, M. and M. Segonzac, 1985. Abondance et repartition de l'epifaune megabenthique. In L. Laubier and C. Monniot (eds), Peuplements profonds du Golfe de Gascogne. Campagnes Biogas. p.143-156. Brest, IFREMER.

Sibuet, M., A. Khripounoff, J. Deming, R. Colwell and A. Dinet, 1982. Modification of the gut contents in the digestive tract of abyssal holothurians. In J.M. Lawrence (ed.), Echinoderms, Proceedings of the International Conference, Tampa Bay, p.421-428. Rotterdam, Balkema.

Sibuet, M., C. Monniot, D. Desbruyeres, A. Dinet, A. Khripounoff, G.T. Rowe and M. Segonzac, 1984. Peuplements benthiques et caracteristiques trophiques du milieu dans la plaine abyssale de Demerara. Oceanol. Acta 7, 345-358.

Smith, C.R., 1986. Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea. J. mar. Res. 44, 567-600.

Smith, C.R. and S.C. Hamilton, 1983. Epibenthic megafauna of a bathyal basin off southern California : patterns of abundance, biomass and dispersion. Deep-Sea Res. 30, 907-928.

Smith, C.R., P.A. Jumars and D.J. DeMaster, 1986. In situ studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. Nature 323, 251-253.

Smith, K.L., 1978. Benthic community respiration in the N.W. Atlantic Ocean : in situ measurements from 40 to 5200m. Mar. Biol. 47, 337-347.

Smith, K.L., 1983. Metabolism of two dominant epibenthic echinoderms measured at bathyal depths in the Santa Catalina Basin. Mar. Biol. 72, 249-256.

Sokolova, M.N., 1958. The food of the deep-water benthic invertebrate detritophages. Trudy Inst. Okeanol. 27, 123-153.

Somero, G.N., J.F. Siebenaller and P.W. Hochachka, 1983. Biochemical and physiological adaptations of deep-sea animals. In G.T. Rowe (ed.), The Sea, Vol. 8. Deep-sea biology. p. 261-330. New York, Wiley-Interscience.

Soutar, A., S. Johnson, K. Fischer and J. Dymond, 1981. Sampling the sediment-water interface - evidence for an organic-rich surface layer. EOS 62, 905.

Stanley D.J. and G. Kelling, 1968. Photographic investigation of sediment texture, bottom current activity, and benthonic organisms in the Wilmington Submarine Canyon. U.S. Coast Guard Oceanogr. Rep. 22, 95pp.

Strathmann, R., 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. Am. Nat. 111, 373-376.

Strathmann, R., 1978. Length of pelagic period in echinoderms with feeding larvae from the northeast Pacific. J. exp. mar. Biol. Ecol. 34, 23-37.

Strathmann, R. and K. Vedder, 1977. Size and organic content of eggs of echinoderms and other invertebrates as related to developmental strategies and egg eating. Mar. Biol. 39, 305-309.

Suchanek, T.H., S.L. Williams, J.C. Ogden, D.K. Hubbard and I.P. Gill, 1985. Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna : Δ13 C evidence. Deep-Sea Res. 32, 201-214.

Suess, E., 1980. Particulate organic carbon flux in the oceans - surface productivity and oxygen utilization. Nature 288, 260-263.

Tabor, P.S., J.W. Deming, K. Ohwada and R.R. Colwell, 1982. Activity and growth of microbial populations in pressurized deep-sea sediment and animal gut samples. Appl. Environ. Microbiol. 44, 413-422.

Tanou, E. and N. Handa, 1980. Vertical transport of organic materials in the northern North Pacific as determined by sediment trap experiment. J. oceanogr. Soc. Japan 36, 231-245.

Theel, H., 1882. Report of the Holothurioidea dredged by "H.M.S. Challenger" during the years 1873-1876. Part 1. Rep. scient. Results Voy. Challenger (Zool.) 4 (13), 1-176.

Theel H., 1886a. Report on the Holothurioidea dredged by "H.M.S. Challenger" during the years 1873-1876. Part 2. Rep. scient. Results Voy. Challenger (Zool.) 14 (39), 1-290.

Theel, H., 1886b. Report on the Holothurioidea in the "Blake" expedition. Bull. Mus. comp. Zool. Harv. 13 (1), 1-21.

Thomson, C.W., 1873. The depths of the sea. London, Macmillan. 527pp.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol Rev. 25, 1-45.

Thurston, M.H., D.S.M. Billett and E. Hassack, 1987. An association between Exspina typica Lang (Tanaidacea) and deep-sea holothurians. J. mar. biol. Ass. U.K. 67,11-15.

Turekian, K.K., J.K.Cochran, D.P. Kharkar, R.M. Cerrato, J.M. Vaisnys, H.L. Sanders, J.F. Grassle and J.A. Allen, 1975. Slow growth rate of a deep-sea clam determined by 228Ra chronology. *Proc. Nat. Acad. Sci. USA*, *72*, 2829-2832.

Turner, R.L. and J.M. Lawrence, 1979. Volume and composition of echinoderm eggs : implications for the use of egg size in life-history models. In S.E. Stancyk (ed.), *Reproduction of marine invertebrates*. p. 25-40. Columbia *Unversity of South Carolina Press.*

Tyler P.A. and D.S.M. Billett, in press. The reproductive ecology of elasipodid holothurians from the N.E. Atlantic. *Biol. Oceanogr*.

Tyler, P.A. and J.D. Gage, 1979. Reproductive ecology of deep-sea ophiuroids from the Rockall Trough. In E.Naylor and R.G. Hartnoll (eds), *Cyclic phenomena in marine plants and animals*. p. 215-222. *Oxford, Pergamon Press.*

Tyler, P.A. and J.D. Gage, 1980. Reproduction and growth of the deep-sea brittlestar *Ophiura ljungmani* (Lyman). *Oceanol. Acta* *3*, 177-185.

Tyler, P.A. and J.D. Gage, 1983. The reproductive biology of *Ypsilothuria talismani* (Holothurioidea: *Dendrochirota) from the N.E.* Atlantic. *J. mar. biol. Ass. U.K*. *63*, 609-616.

Tyler, P.A. and J.D. Gage, 1984. The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, North-East Atlantic Ocean). *Mar. Biol*. *80*, 63-74.

Tyler, P.A. and J.D. Gage, 1984. Seasonal reproduction of *Echinus affinis* (Echinodermata : Echinoidea) in the *Rockall Trough,* northeast Atlantic Ocean. *Deep-Sea Res*. *31*, 387-402.

Tyler, P.A. and A. Muirhead, 1986. Studies of the reproductive biology of deep-sea megabenthos. VI. The Aspidochirota (Holothurioidea, Echinodermata). *DOE contract report* No. DOE/RW/8 065.

Tyler, P.A. and S.L. Pain, 1982. The reproductive biology of *Plutonaster bifrons*, *Dytaster insignis* and *Psilaster andromeda (Asteroidea : Astropectinidae) from the Rockall* Trough. *J. mar. biol. Ass. U.K*. *62*, 869-887.

Tyler, P.A., A. Grant, S.L. Pain and J.D. Gage, 1982. Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature* *300*, 747-750.

Tyler, P.A., A. Muirhead, D.S.M. Billett and J.D. Gage, 1985a. Reproductive ecology of deep-sea holothurians *Laetmogone violacea* and *Benthogone rosea* (Elasiopoda : *Holothurioidea*). *Mar. Ecol. Prog. Ser.* *23*, 269-273.

Tyler, P.A., J.D. Gage and D.S.M. Billett, 1985b. Life-history biology of *Peniagone azorica* and *P. diaphana* (Echinodermata : Holothurioidea) from the north-east Atlantic Ocean. *Mar. Biol.* *89*, 71-81.

Tyler, P.A., A. Muirhead, J.D. Gage and D.S.M. Billett, 1985c. Gametogenic strategies in deep-sea echinoids and holothurians from the N.E. Atlantic. In B.F. Keegan and B.D.S. O'Connor (eds), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway.* p. 135-140. Rotterdam, Balkema.

Tyler, P.A., D.S.M. Billett and J.D. Gage, 1987. The ecology and reproductive biology of *Cherbonniera utriculus* and *Molpadia blakei* from the N.E. Atlantic. *J. mar. biol. Ass. U.K.* *67*, 385-397.

Vangrieshem, A., 1985. Hydrologie et circulation profonde. In L. Laubier and C. Monniot (eds), *Peuplements profonds du Golfe de Gascogne. Campagnes Biogas*. p.43-70. Brest, IFREMER.

Verrill, A.E., 1884. Notice of a remarkable marine fauna occupying the outer banks off the southern coast of New England, No. 9. *Am. J. Sci.* *28*, 213-220.

Walker, M., P.A. Tyler and D.S.M. Billett, 1987a. Biochemical and calorific content of deep-sea aspidochirotid holothurians from the northeast Atlantic Ocean. *Comp. Biochem. Physiol.* *88A*, 549-551.

Walker, M., P.A. Tyler and D.S.M. Billett, 1987b. Organic and calorific content of the body tissues of deep-sea elasipodid holothurians in the northeast Atlantic Ocean. *Mar. Biol.* *96*, 277-282.

Weliky, K., E. Suess, C.A. Ungerer, P.J. Muller and K. Fischer, 1983. Problems with accurate carbon measurements in marine sediments and particulate matter in sea-water : A new approach. *Limnol. Oceanogr.* *28*, 1252-1259.

Wesenburg-Lund, E. 1941. Notes on Polychaeta. 1. *Vidensk. Meddr. dansk. naturh. Foren.* *105*, 31-48.

Weston, J.F., 1985. Comparison between Recent benthic foraminiferal faunas of the Porcupine Seabight and western approaches continental slope. *J. Micropal.* *4*, 165-183.

Wishner, K.F., 1980. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Res. 27, 203-216.

Yamaguchi, M., 1974. Larval life span of the coral reef asteroid Gomophia egyptyaca Gray. Micronesica j. Coll. Guam 10, 57-64.

Yamaguchi, M. and J.S. Lucas, 1984. Natural parthenogenesis, larval and juvenile development, and geographical distribution of the coral reef asteroid Ophidiaster granifer. Mar. Biol. 83, 33-42.

Yayanos, A.A., A.S. Dietz and R.V. Boxtel, 1979. Isolation of a deep-sea barophilic bacterium and some of its growth characteristics. Science 205, 808-810.

Yingst, J.Y., 1974. The utilization of organic detritus and associated microorganisms by Parastichopus parvimensis, a benthic deposit-feeding holothurian. Ph.D. thesis, University South California, Los Angeles, 154p.

Young, C.M. and J.L. Cameron, 1987. Laboratory and in situ floatation rates of lecithotrophic eggs from the bathyal echinoid Phormosoma placenta. Deep-Sea Res. 34, 1629-1639.

Young, D.K., W.H. Jahn, M.D. Richardson and A.W. Lohanick, 1985. Photographs of deep-sea Lebensspuren : A comparison of sedimentary provinces in the Venezuela Basin, Caribbean Sea. Mar. Geol. 68, 269-301.

Zenkevitch, L.A. and Ya. Birstein, 1960. On the problem of the antiquity of the deep-sea fauna. Deep-Sea Res. 7, 10-23.

Appendix 1. Station data for epibenthic sledge, bottom trawl and midwater trawl hauls in which holothurians were present in the Porcupine Seabight and Porcupine Abyssal Plain. Station numbers are preceeded by a gear code : BNF - fine mesh epibenthic sledge sample; BNC - coarse mesh epibenthic sledge sample; OT - Otter trawl; GT - Granton trawl; ST - single warp trawl; RMT8 - IOS Rectangular Midwater Trawl. For references to the types of gear used see page 62. For details of how the area sampled was calculated see page 63.

A. Benthic Samples.

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m² Area posn	*10,000m² Area Odo
OT 9638- 2	9:11:77	4043	4104	49 50	14 07	4.788	
OT 9640- 1	11:11:77	3749	3757	50 03	13 51	9.605	
OT 9752- 1	7: 4:78	1007	1042	51 16	11 43	3.352	
OT 9753- 4	7: 4:78	1942	1947	50 55	12 12	5.533	
BNF 9753- 7	8: 4:78	1942	1942	50 55	12 11	0.247	
OT 9753- 8	8: 4:78	1942	1942	50 55	12 11	3.352	
BNF 9754- 3	9: 4:78	1484	1484	51 08	12 02	0.484	
OT 9756- 3	11: 4:78	4080	4156	49 48	14 15	5.442	
OT 9756- 5	12: 4:78	4012	4020	49 49	14 06	7.661	
BNF 9756- 9	13: 4:78	4039	4069	49 47	14 02	0.631	0.125
BNF 9756-14	15: 4:78	3680	3697	50 04	13 56	1.026	0.144
OT 9774- 1	21: 4:78	1494	1572	51 04	11 59	4.448	
BNC 9775- 3	22: 4:78	2012	2019	50 57	12 22	1.003	0.064
OT 9776- 1	23: 4:78	800	808	49 29	11 38	3.671	
BNF 9776- 2	23: 4:78	770	785	49 23	11 36	0.537	0.184
OT 9777- 2	23: 4:78	205	280	49 15	11 15	6.709	
OT 9778- 1	24: 4:78	1016	1055	49 15	12 07	3.463	
BNF 9779- 1	24: 4:78	1398	1404	49 22	12 49	0.700	0.191
BNC 10106- 1	4: 9:79	2300	2315	50 42	12 51	1.020	
BNF 10108- 1	5: 9:79	1385	1390	49 21	12 49	0.474	
BNF 10109- 8	7: 9:79	1120	1130	49 12	12 19	0.816	
BNC 10110- 1	7: 9:79	920	930	49 19	11 43	0.552	
BNF 10111- 8	9: 9:79	1630	1640	49 33	13 07	0.637	0.152
BNF 10112- 1	9: 9:79	2645	2660	50 25	13 19	0.871	
BNF 10112- 2	9: 9:79	2640	2650	50 25	13 20	0.216	0.071
BNF 10112- 3	10: 9:79	2740	2750	50 19	13 26	0.577	0.131
BNF 10113- 1	10: 9:79	2755	2760	50 16	13 32	0.309	0.126
BNF 10114- 1	10: 9:79	4040	4060	49 46	14 08	0.268	0.111
BNF 10115- 1	11: 9:79	3900	3950	49 46	13 56	0.391	0.136
BNC 10120- 1	13: 9:79	400	400	49 28	11 21	0.272	0.101
OT 11116- 1	24: 5:84	4800	4800	47 45	15 25	10.518	
OT 11118- 1	25: 5:84	4450	4680	45 31	18 34	10.358	
OT 50503- 1	1: 6:79	992	1042	51 37	13 15	3.666	
GT 50504- 1	1: 6:79	970	975	51 55	12 53		
GT 50505- 1	1: 6:79	1270	1300	51 44	12 48		
GT 50506- 1	2: 6:79	490	490	51 57	13 35		
GT 50507- 1	2: 6:79	770	795	51 52	13 17		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m^2 Area posn	*10,000m^2 Area Odo
ST 50508- 1	3: 6:79	980	980	51 34	13 18		
OT 50509- 1	3: 6:79	1490	1523	51 14	13 17	3.666	
OT 50510- 1	3: 6:79	1925	1960	51 06	13 00	5.579	
OT 50511- 1	4: 6:79	2405	2435	50 32	12 59	6.535	
OT 50512- 1	4: 6:79	3022	3110	50 12	13 35	6.535	
OT 50513- 1	5: 6:79	3400	3600	50 06	14 00	6.693	
OT 50514- 1	5: 6:79	4017	4095	49 42	14 01	8.129	
OT 50515- 1	6: 6:79	4505	4515	49 45	15 06	6.854	
OT 50517- 1	7: 6:79	1785	1794	49 28	13 18	4.304	
OT 50518- 1	7: 6:79	2045	2110	49 27	13 21	6.535	
OT 50519- 1	8: 6:79	1431	1465	49 30	12 46	4.941	
GT 50520- 1	8: 6:79	1230	1245	49 35	12 07		
GT 50521- 1	8: 6:79	965	970	49 30	11 49		
OT 50522- 1	8: 6:79	965	1000	49 25	11 45	3.826	
OT 50523- 1	9: 6:79	455	490	49 30	11 25	3.347	
OT 50524- 1	9: 6:79	736	790	49 36	11 36	6.057	
OT 50601- 1	1: 7:79	770	927	51 20	11 42	5.100	
BNF 50602- 2	1: 7:79	1955	1980	51 01	13 07	0.602	
OT 50602- 3	2: 7:79	1817	1930	51 07	13 21	8.610	
BNF 50603- 1	2: 7:79	4000	4000	49 45	14 01	0.779	
BNF 50604- 1	4: 7:79	3490	3550	50 06	13 52	0.852	
BNF 50605- 1	5: 7:79	2820	2930	50 11	13 30	0.944	
BNC 50606- 1	6: 7:79	1110	1120	50 40	14 10	0.443	0.137
OT 50606- 2	6: 7:79	1080	1120	50 41	14 03	4.140	
BNC 50606- 5	6: 7:79	1120	1140	50 43	13 57	0.417	
OT 50607- 1	7: 7:79	700	712	51 02	14 10	4.460	
BNC 50607- 2	7: 7:79	700	700	51 01	14 07	0.467	0.146
BNC 50608- 2	7: 7:79	510	510	51 19	14 23	0.848	0.212
BNC 50609- 1	8: 7:79	400	400	51 40	14 16	0.085	0.068
OT 50609- 3	8: 7:79	405	410	51 38	14 21	3.826	
BNC 50610- 1	8: 7:79	980	980	51 26	13 24	0.306	0.075
OT 50611- 1	8: 7:79	1365	1410	51 18	13 18	6.217	
BNC 50613- 1	9: 7:79	2440	2440	50 30	13 03	0.474	
OT 50701- 1	11:10:79	2870	2890	54 34	11 54		
OT 50702- 1	13:10:79	755	815	51 17	11 38	2.550	
OT 50703- 1	13:10:79	1575	1625	49 33	12 34		
OT 50704- 1	13:10:79	1260	1265	49 40	12 07		
OT 50705- 1	14:10:79	740	745	49 24	11 32	3.347	
GT 50707- 1	15:10:79	770	790	49 54	11 16		
GT 50708- 1	16:10:79	1050	1065	49 23	12 01		
GT 50709- 1	16:10:79	1260	1260	49 24	12 22		
OT 50710- 1	17:10:79	1800	2000	49 34	13 28		
OT 50711- 1	18:10:79	4780	4795	49 53	15 36	9.177	
OT 50712- 1	19:10:79	2700	2775	50 11	13 21	4.655	
GT 50713- 1	20:10:79	1245	1275	51 22	13 18		
GT 50714- 1	20:10:79	925	960	51 45	13 15		
OT 50715- 1	21:10:79	1635	1720	51 20	12 57	3.990	
GT 50716- 1	21:10:79	745	750	51 53	13 26		
GT 50717- 1	21:10:79	500	510	52 00	13 33		

						*10,000m^2	*10,000m^2
Station	Date	min D	max D	Deg. N	Deg. W	Area posn	Area Odo
OT 50801- 1	30: 7:80	1245	1285	49 35	12 11	4.782	
OT 50802- 1	30: 7:80	1857	1910	49 40	12 37	3.826	
GT 50803- 1	31: 7:80	450	555	49 26	11 28		
GT 50804- 1	31: 7:80	690	690	49 25	11 33		
GT 50805- 1	31: 7:80	1000	1000	49 36	11 51		
OT 50806- 1	1: 8:80	510	515	49 27	11 27	4.460	
OT 50807- 1	1: 8:80	790	795	49 24	11 37	4.140	
OT 50808- 1	1: 8:80	955	965	49 35	11 49		
GT 50809- 1	1: 8:80	1250	1250	49 32	12 10		
OT 50810- 1	2: 8:80	1605	1694	49 34	12 42	4.460	
OT 50811- 1	2: 8:80	4350	4400	49 39	14 34	7.970	
BNF 50812- 1	3: 8:80	4080	4100	49 45	14 10		0.179
OT 50812- 2	3: 8:80	4035	4140	49 53	14 17	10.361	
OT 50813- 1	4: 8:80	3640	3715	50 14	14 08	8.129	
OT 50814- 1	4: 8:80	2715	3000	50 20	13 32	22.344	
OT 50815- 1	5: 8:80	1280	1344	51 36	13 04		
GT 50816- 1	5: 8:80	1000	1000	51 46	13 05		
GT 50817- 1	6: 8:80	750	750	51 55	13 15		
GT 50818- 1	6: 8:80	515	520	52 00	13 31		
OT 50819- 1	6: 8:80	500	512	52 05	13 29	3.188	
OT 50820- 1	6: 8:80	714	725	51 55	13 19	5.420	
OT 50821- 1	6: 8:80	982	990	51 48	13 05	5.260	
OT 50822- 1	7: 8:80	2095	2150	50 57	13 12	10.773	
BNC 50823- 1	8: 8:80	2830	2830	50 12	13 32		0.208
OT 50902- 1	7:11:80	1825	1865	51 16	12 47	4.941	
OT 50903- 1	7:11:80	1250	1265	51 16	13 24	4.620	
OT 50904- 1	8:11:80	1020	1035	51 20	13 28	5.100	
OT 50905- 1	8:11:80	755	820	51 42	13 24	5.100	
OT 50906- 1	9:11:80	2585	2705	50 25	13 27	8.290	
OT 50907- 1	10:11:80	2820	3120	49 53	13 32	8.610	
OT 50910- 1	10:11:80	4265	4320	49 50	14 45	9.245	
BNF 50913- 1	12:11:80	3000	3040	50 12	13 40		0.373
BNC 50914- 1	12:11:80	2790	2810	50 16	13 30		0.164
OT 51002- 1	1: 5:81	490	490	52 20	13 19		
OT 51003- 1	1: 5:81	740	760	52 01	13 02		
OT 51007- 1	2: 5:81	1020	1030	51 46	13 06		
OT 51008- 1	2: 5:81	1350	1370	51 36	13 02		
OT 51009- 1	2: 5:81	1510	1535	51 34	12 54		
OT 51010- 1	2: 5:81	1780	1800	51 19	12 29		
OT 51011- 1	3: 5:81	2165	2180	50 45	12 15		
OT 51012- 1	5: 5:81	3880	3920	49 51	13 58		
OT 51015- 1	6: 5:81	2520	2540	49 55	12 57		
OT 51021- 1	9: 5:81	1860	1875	49 39	12 41		
OT 51022- 1	9: 5:81	1575	1600	49 33	12 39		
OT 51023- 1	9: 5:81	1270	1275	49 30	12 11		
OT 51025- 1	10: 5:81	460	480	49 27	11 25		
OT 51026- 1	10: 5:81	730	750	49 25	11 34		
OT 51027- 1	10: 5:81	970	985	49 32	11 51		

						*10,000m^2	*10,000m^2
Station	Date	min D	max D	Deg. N	Deg. W	Area posn	Area Odo
BNC 51102- 1	21: 5:81	520	530	52 01	13 27	0.309	0.138
BNC 51103- 4	21: 5:81	950	960	51 48	13 10	0.272	0.145
BNC 51103- 5	21: 5:81	930	950	51 47	13 13	0.391	0.246
BNC 51104- 1	22: 5:81	1370	1390	51 24	13 04	0.391	0.141
BNC 51105- 3	22: 5:81	2020	2030	51 04	12 54	0.511	0.140
BNC 51105- 4	24: 5:81	1985	1993	51 05	12 59	0.300	
BNC 51106- 1	24: 5:81	2510	2520	50 29	13 06	0.342	0.142
BNC 51109- 1	26: 5:81	3940	3960	49 51	14 02	0.459	0.218
BNC 51109- 2	27: 5:81	3980	3990	49 48	14 09	0.649	0.221
BNC 51110- 3	28: 5:81	2785	2800	50 16	13 31	0.443	0.218
BNC 51110- 4	28: 5:81	2718	2755	50 14	13 26	0.711	0.220
BNC 51111- 1	28: 5:81	2660	2670	50 21	13 23	0.631	0.209
BNC 51111- 2	28: 5:81	2620	2620	50 23	13 20	0.212	0.205
BNC 51112- 1	29: 5:81	515	530	51 26	13 59	0.379	0.199
BNC 51112- 4	29: 5:81	550	560	51 25	13 57	0.513	0.141
BNC 51113- 2	30: 5:81	1530	1540	51 15	13 13	0.646	0.223
OT 51201- 1	16: 9:81	1970	1980	51 06	12 54	3.188	
OT 51205- 1	17: 9:81	1373	1394	51 40	12 49		
OT 51206- 1	18: 9:81	1200	1210	51 40	13 00		
BNC 51208- 1	19: 9:81	1170	1200	51 41	13 01	0.523	0.128
BNC 51208- 3	20: 9:81	1170	1185	51 41	13 01	0.241	0.080
OT 51213- 1	26: 9:81	1895	1980	50 44	11 56	1.793	
OT 51214- 1	27: 9:81	3800	3820	49 59	14 05	5.100	
BNC 51216- 1	28: 9:81	4070	4070	49 48	14 10	0.467	0.288
BNC 51216- 3	28: 9:81	4050	4050	49 50	14 07	0.461	0.278
OT 51216- 4	29: 9:81	3970	4000	49 52	14 07	6.217	
BNC 51216- 5	29: 9:81	4030	4040	49 48	14 05	0.621	0.273
BNF 51217- 1	30: 9:81	150	150	50 36	10 18	0.290	0.095
OT 51217- 2	30: 9:81	135	141	50 38	10 08	9.314	
OT 51302- 1	17: 2:82	310	350	52 41	13 31		
OT 51303- 1	18: 2:82	510	580	52 09	13 21		
OT 51304- 1	18: 2:82	760	820	51 51	13 20		
OT 51305- 1	18: 2:82	965	1005	51 50	13 05		
OT 51306- 1	19: 2:82	1205	1230	51 44	12 53	3.029	
OT 51307- 1	19: 2:82	1415	1490	51 26	13 01		
OT 51308- 1	20: 2:82	1715	1770	51 13	13 02		
OT 51309- 1	20: 2:82	4190	4255	49 35	14 01	9.883	
OT 51310- 1	21: 2:82	2455	2500	49 52	12 57		
OT 51311- 1	21: 2:82	1940	2010	49 51	12 23		
GT 51312- 1	22: 2:82	700	750	49 27	11 37		
GT 51313- 1	22: 2:82	1225	1265	49 33	12 12		
OT 51314- 1	22: 2:82	1425	1455	49 32	12 29		
GT 51315- 1	23: 2:82	980	1050	49 33	11 52		
OT 51318- 1	24: 2:82	665	705	49 23	11 34		
OT 51319- 1	24: 2:82	255	275	49 28	11 18		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m^2 Area posn	*10,000m^2 Area Odo
OT 51401- 1	24: 3:82	287	307	51 10	11 25	3.666	
BNF 51403- 1	25: 3:82	1292	1314	51 37	13 00	0.448	0.175
BNF 51403- 2	25: 3:82	1317	1325	51 37	12 59	0.236	0.092
BNF 51403- 3	25: 3:82	1319	1325	51 37	12 59	0.156	0.105
BNF 51403- 4	26: 3:82	1319	1333	51 37	13 00	0.332	0.096
BNF 51403- 5	26: 3:82	1289	1297	51 37	12 59	0.203	0.088
BNF 51403- 6	26: 3:82	1278	1295	51 37	12 59		0.094
OT 51403- 7	26: 3:82	1255	1330	51 37	12 59	4.140	
OT 51404- 1	26: 3:82	740	760	51 54	13 18	4.140	
BNC 51405- 1	27: 3:82	492	503	52 01	13 31	0.302	0.127
BNC 51406- 1	27: 3:82	1072	1091	51 23	13 22	0.251	0.150
BNC 51407- 1	27: 3:82	1489	1511	51 20	13 04	0.520	0.144
BNC 51408- 1	27: 3:82	1994	2001	51 04	12 54	0.458	0.183
OT 51409- 1	28: 3:82	1651	1717	51 18	12 58	4.460	
OT 51411- 1	29: 3:82	2470	2500	50 24	13 00	7.332	
BNC 51412- 1	29: 3:82	2760	2790	50 18	13 29	0.749	0.345
OT 51413- 1	30: 3:82	2770	2940	50 10	13 33	7.811	
OT 51414- 1	30: 3:82	4180	4310	49 41	14 13	10.278	
BNC 51414- 2	31: 3:82	4070	4090	49 47	14 09	0.574	0.299
BNC 51415- 1	31: 3:82	3470	3510	50 07	13 53	0.408	0.290
BNF 51416- 1	31: 3:82	2780	2790	50 17	13 31	0.201	0.140
BNC 51417- 1	1: 4:82	2770	2790	50 10	13 22	0.313	0.149
OT 51419- 1	1: 4:82	1488	1529	51 18	13 06	4.460	
BNF 51420- 1	2: 4:82	1326	1328	51 37	12 59	0.172	0.093
BNC 51420- 2	2: 4:82	1304	1309	51 37	12 59	0.163	0.089
BNF 51420- 3	2: 4:82	1293	1298	51 38	12 59	0.117	0.090
BNF 51420- 4	2: 4:82	1279	1287	51 38	13 00	0.163	0.091
BNC 51603- 2	18: 7:82	2730	2740	50 18	13 24	0.198	0.137
BNC 51604- 1	19: 7:82	2890	2920	50 15	13 38	0.291	0.140
OT 51608- 1	19: 7:82	4270	4370	49 38	14 27	7.992	
OT 51610- 1	20: 7:82	3310	3660	50 03	13 53	9.927	
OT 51611- 1	21: 7:82	2640	2700	50 19	13 21	10.185	
OT 51613- 1	21: 7:82	2200	2240	50 48	12 54	8.370	
BNC 51622- 1	24: 7:82	158	158	50 35	10 20	0.265	0.169
BNC 51707- 1	12: 4:83	1205	1230	51 39	13 01	0.951	
BNC 51708- 2	13: 4:83	1430	1470	51 31	12 59	0.513	0.216
BNC 51715- 2	18: 4:83	1450	1535	51 30	12 59	0.664	
BNC 51717- 2	18: 4:83	1970	1980	51 05	12 56	0.228	0.160
OT 51801- 1	24: 9:83	1700	1740	51 21	12 31		
OT 51803- 1	26: 9:83	3920	3990	49 37	13 49		
OT 51804- 1	26: 9:83	3015	3180	49 56	13 26		
OT 51805- 1	27: 9:83	2430	2545	49 55	12 58		
OT 51810- 1	29: 9:83	1011	1021	49 33	11 53		
OT 51811- 1	30: 9:83	685	707	49 34	11 33		
OT 51812- 1	30: 9:83	505	550	49 29	11 26		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m^2 Area posn	*10,000m^2 Area Odo
BNC 52009- 1	19: 8:84	1206	1236	51 41	12 59	0.311	0.156
BNC 52012- 1	20: 8:84	984	984	51 48	13 07	0.120	0.076
BNC 52013- 1	20: 8:84	515	525	52 05	13 29	0.123	0.068
BNC 52017- 1	21: 8:84	1457	1472	51 32	12 58	0.203	0.071
BNC 52019- 1	22: 8:84	1725	1736	51 25	12 46	0.212	0.199
BNC 52203- 1	16: 6:85	1521	1531	51 26	13 01	0.190	0.148
BNC 52204- 1	16: 6:85	1295	1310	51 37	13 00	0.092	0.071
BNC 52211- 1	18: 6:85	1693	1738	51 11	13 15	0.324	0.141
BNC 52213- 1	20: 6:85	2405	2420	50 33	12 59	0.320	0.136
BNC 52214- 1	21: 6:85	4050	4075	49 52	14 15	1.400	0.453
BNC 52215- 1	22: 6:85	4561	4565	49 30	14 49	0.651	0.350
BNC 52216- 8	25: 6:85	4803	4832	48 48	16 38	0.605	0.405
BNC 52218- 1	26: 6:85	1433	1447	49 25	12 50	0.431	0.232
BNC 52403-14	5:12:86	4850	4860	49 02	16 00		

B. Pelagic samples.

Station	Date	Min D	Max D	m above seabed	Deg N.	Deg W.	*10,000m^3 Vol. filt
RMT8 9756-2	10: 4:79	1000	1500	c. 2750	49 53	14 10	12.007
RMT8 9756-10	14: 4:79	3000	3500	c. 750	49 47	14 04	11.782
RMT8 9756-11	14: 4:79	4000	4012	c. 12	49 50	14 05	10.003
RMT8 50603-2	3: 7:79	3720	3940	c. 160	49 54	14 09	3.865
RMT8 50603-3	3: 7:79	3700	3900	c. 150	49 53	14 04	3.636
RMT8 50605-2	5: 7:79	2640	2750	c. 15	50 07	13 12	4.850
RMT8 52403-21	8:12:86	c.4850	c.4850	0	49 15	16 35	-

Appendix 2. Publication list.

Billett, D.S.M., 1986. The rise and rise of the sea cucumber. *New Scientist* No. 1500, 48-51.

Billett, D.S.M., 1987. Echinodermata. Section 28. In H.S.J.Roe *et al.*, Great Meteor East : A biological *characterisation.* p. 163-180. *Institute of Oceanographic Sciences Report* No. 248.

Billett, D.S.M. and B. Hansen, 1982. Abyssal aggregations of *Kolga hyalina* D and K (Echinodermata, Holothurioidea) in *the northeast* Atlantic Ocean, a preliminary report. *Deep-Sea Res.* *29*, 799-818.

Billett, D.S.M. and Q.J. Huggett, 1987. Echinodermata. Section 19. In H.S.J.Roe *et al.*, Great Meteor East : A biological *characterisation.* p. 163-180. *Institute of Oceanographic Sciences Report* No. 248.

Billett, D.S.M., B. Hansen and Q.J. Huggett, 1985. Pelagic Holothurioidea of the northeast Atlantic. In B.F. Keegan and B.D.S. O'Connor (eds.), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway*. p. 399-411. Rotterdam, Balkema.

Billett, D.S.M., C. Llewellyn and J. Watson, in press. Are deep-sea holothurians selective feeders? *Proceedings of the Sixth International Echinoderms Conference, Victoria*. Rotterdam, Balkema.

Billett, D.S.M., R.S. Lampitt, A.L. Rice and R.F.C. Mantoura, 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* *302*, 520-522.

Ellis, C.J., D.S.M. Billett and M.V. Angel, 1983. The distribution of oceanic cirripedes in the northeast Atlantic in summer 1983 and the connotations of the results to the problems of *Conchoderma* fouling. *IOS Internal Document* No. 193.

Gage, J.D. and D.S.M. Billett, 1986. The family Myriotrochidae Theel (Echinodermata : Holothurioidea) in the deep northeast Atlantic Ocean. *Zool. J. Linn. Soc.* *88*, 229-276.

Gage, J.D., D.S.M. Billett, M. Jensen and P.A.Tyler, 1985a. Echinoderms of the Rockall Trough and adjacent areas. 2. Echinoidea and Holothurioidea. *Bull. Br. Mus. nat. Hist. (Zool.)* *48*, 173-213.

Gage, J.D., M. Pearson, D.S.M. Billett, A.M. Clark, M. Jensen, G.L.J. Paterson and P.A.Tyler, 1985b. Echinoderm zonation in the Rockall Trough (NE Atlantic). In B.F. Keegan and B.D.S. O'Connor (eds.), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway*. p. 31-36. Rotterdam, Balkema.

Harvey, R., J.D. Gage, D.S.M. Billett, A.M. Clark and G.L.J. Paterson, in press. Echinoderms of the Rockall Trough and adjacent areas. 3. Additional records. *Bull. Br. Mus. nat. Hist. (Zool.)*.

Kirkegaard, J.B. and D.S.M. Billett, 1980. *Eunoe laetmogonensis*, a new species of polynoid worm, commensal with the bathyal holothurian *Laetmogone violacea*, in the North-east Atlantic. *Steenstrupia* *6*, 101-109.

Lampitt, R.S. and D.S.M. Billett, 1985. Deep-sea echinoderms: a time and motion study. In B.F. Keegan and B.D.S. O'Connor (eds), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway*. p. 160 [Absract]. Rotterdam, Balkema.

Lampitt, R.S., D.S.M. Billett and A.L. Rice 1986. Biomass of the invertebrate megabenthos from 500 to 4100m in the northeast Atlantic Ocean. *Mar. Biol*. *93*, 69-81.

Rice, A.L., R.G. Aldred, D.S.M. Billett and M.H. Thurston, 1979. The combined use of an epibenthic sledge and a deep-sea camera to give quantitative relevance to macrobenthos samples. *Ambio Spec. Rep*. *6*, 59-72.

Rice, A.L., D.S.M. Billett, J. Fry, A.W.G. John, R.S. Lampitt, R.F.C. Mantoura and R.J. Morris, 1986. Seasonal deposition of phytodetritus to the deep-sea floor. *Proc. Roy. Soc. Edinb*. *88B*, 265-279.

Thurston, M.H., D.S.M. Billett and E. Hassack, 1987. An association between *Exspina typica* Lang (Tanaidacea) and deep-sea holothurians. *J. mar. biol. Ass. U.K*. *67*,11-15.

Tyler P.A. and D.S.M. Billett, in press. The reproductive ecology of elasipodid holothurians from the N.E. Atlantic. *Biol. Oceanogr*.

Tyler, P.A., D.S.M. Billett and J.D. Gage, 1987. The ecology and reproductive biology of *Cherbonniera utriculus* and *Molpadia blakei* from the N.E. Atlantic. *J. mar. biol. Ass. U.K*. *67*, 385-397.

Tyler, P.A., J.D. Gage and D.S.M. Billett, 1985. Life-history biology of *Peniagone azorica* and *P. diaphana* (Echinodermata : Holothurioidea) from the north-east Atlantic Ocean. *Mar. Biol*. *89*, 71-81.

Tyler, P.A., A. Muirhead, D.S.M. Billett and J.D. Gage, 1985. Reproductive ecology of deep-sea holothurians *Laetmogone violacea* and *Benthogone rosea* (Elasiopoda : Holothurioidea). *Mar. Ecol. Prog. Ser.* *23*, 269-273.

Tyler, P.A., A. Muirhead, J.D. Gage and D.S.M. Billett, 1985. Gametogenic strategies in deep-sea echinoids and holothurians from the N.E. Atlantic. In B.F. Keegan and B.D.S. O'Connor (eds), *Echinodermata : Proceedings of the Fifth International Echinoderm Conference, Galway.* p. 135-140. Rotterdam, Balkema.

Tyler, P.A., S.L. Pain, J.D. Gage and D.S.M. Billett, 1984. The reproductive biology of deep-sea forcipulate sea stars (Asteroidea) from the NE Atlantic Ocean. *J. mar. biol. Ass. U.K.* *64*, 587-601.

Walker, M., P.A. Tyler and D.S.M. Billett, 1987a. Biochemical and calorific content of deep-sea aspidochirotid holothurians from the northeast Atlantic Ocean. *Comp. Biochem. Physiol.* *88A*, 549-551.

Walker, M., P.A. Tyler and D.S.M. Billett, 1987b. Organic and calorific content of the body tissues of deep-sea elasipodid holothurians in the northeast Atlantic Ocean. *Mar. Biol.* *96*, 277-282.